Université de Montréal

Caractérisation et modélisation des comportements d'une guêpe parasitoïde en fonction de la température ; conséquences populationnelles et lutte biologique

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Thèse présentée à la Faculté des arts et des sciences

en vue de l'obtention du grade de doctorat

en sciences biologiques

Juillet 2020

Page d'identification du jury

Université de Montréal
Faculté des Études Supérieures et Postdoctorales

Cette thèse intitulée :
Caractérisation et modélisation des comportements d'une guêpe parasitoïde en fonction de la température ; conséquences populationnelles et lutte biologique

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Résumé

Les réponses comportementales des insectes restent peu connues dès lors qu'on s'éloigne de leur optimum thermique. Les conditions plus extrêmes et variables de température projetées pour les prochaines décennies devraient pousser les organismes à la limite de leur capacité de fonctionnement, dans la mesure où ils ne s'adaptent pas rapidement aux changements. Les réponses comportementales à la température peuvent être kinétiques (résultant de l'accélération/ralentissement des réactions chimiques de l'organisme en fonction de la température) ou intégrées (résultant de l'intégration des informations thermo-sensorielles par le système nerveux central de l'insecte), adaptatives ou contraintes. Distinguer entre ces différents types de réponse permettra de mieux comprendre et prédire la réponse des individus aux nouvelles conditions provoquées par les changements climatiques. Les réponses individuelles pourront alors permettent d'anticiper les conséquences sur les populations.

Dans cette thèse, plusieurs comportements d'*Anaphes listronoti*, un parasitoïde des œufs du charançon de la carotte (*Listronotus oregonensis*) ont été observés, à l'intérieur de la fenêtre thermique permettant ses activités. Dans un premier temps, il a été montré que le comportement de marche des femelles *A. listronoti* ne découlait pas simplement d'une réponse kinétique à la température, mais correspondait à une réponse intégrée telle que l'évitement des conditions thermiques froides et la conservation de l'énergie aux températures élevées. Dans un second temps, l'exploitation d'agrégats d'hôtes a été comparée à différentes températures. La stratégie d'exploitation ne variait pas avec la température, mais des contraintes liées à la manipulation de l'hôte et à la détection des messages chimiques à haute température ont été révélées. Ensuite, le comportement de cour et d'accouplement a été observé en fonction de la température. Les températures suboptimales diminuaient le succès d'accouplement, mais pas le transfert de spermatozoïdes lors d'un accouplement. Des contraintes de reconnaissance entre les partenaires sexuels ont également été observées à températures infra- et supra-optimales. Enfin, un modèle de simulation dynamique intégrant le développement des différents stades de l'insecte et les comportements précédemment étudiés a été conceptualisé. Ce modèle permet de combiner les effets de la température sur les comportements d'un individu et les conséquences sur la population de parasitoïdes, ainsi que sur la population de l'hôte. L'ajout des comportements dans les modèles populationnels n'apporte pas forcément de valeur ajoutée, mais il reste essentiel de les considérer, en particulier dans le cadre des changements climatiques. En effet, si les réponses physiologiques telles que celles associées au développement augmentent jusqu'à un maximum d'environ 35°C, la plupart des comportements deviennent sub-optimaux à partir de 30°C, et cessent presque complètement à 35°C. Dans un contexte de changements climatiques, ces résultats permettent de mieux comprendre et potentiellement prédire les réponses individuelles et populationnelles des insectes aux différentes conditions thermiques.

Mots-clés : Température – Écologie comportementale – Parasitoïde - Modélisation

Abstract

The behavioural responses of insects remain poorly understood once they move away from their thermal optimum. The more extreme and variable temperature conditions projected for the coming decades should, to the extent that insects do not adapt quickly to changes, push organisms to the limit of their ability to function. Behavioural responses to temperature may be kinetic (resulting from the acceleration/slowing down of the organism's chemical reactions as a function of temperature) or integrated (resulting from the integration of thermo-sensory information by the insect's central nervous system), adaptive or constrained. Distinguishing between these different types of response will help to better understand and predict the response of individuals to new conditions caused by climate change. Individual responses can then be used to infer the consequences on populations.

In this thesis, several behaviours of *Anaphes listronoti*, a parasitoid of the carrot weevil (*Listronotus oregonensis*) eggs, were observed, depending on the thermal window allowing its activities. Firstly, it was shown that the walking behaviour of *A. listronoti* females was not simply a kinetic response to temperature, but also corresponded to an integrated response such as avoidance of cold thermal conditions and conservation of energy at high temperatures. In a second step, the exploitation of host patches was compared at different temperatures. The exploitation strategy did not vary with temperature, but constraints related to host handling and detection of chemical cues at high temperatures were revealed. Next, courtship and mating behaviour was observed as a function of temperature. Sub-optimal temperatures decreased mating success, but not sperm transfer during mating. Recognition constraints between sexual partners were also observed at infra- and supra-optimal temperatures. Finally, a model integrating the development of the different stages of the insect and the previously studied behaviours was conceptualized. This model makes it possible to combine the effects of temperature on the behaviour of an individual and the consequences on the parasitoid population, as well as the host population. Adding behaviors to population models does not necessarily add value, but it remains essential to consider them, particularly in the context of climate change. Indeed, while physiological responses such as development increase to a maximum of about 35°C, most behaviours become suboptimal from 30°C onwards, and cease almost completely at 35°C. In a context of climate change, these results allow to better understand and potentially predict the individual and population responses of insects to different thermal conditions.

Key-words: Temperature – Behavioral ecology – Parasitoid - Modeling

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CTL - Critical Thermal Limit

CT_{min} - Critical Thermal Minimum

CT_{max} - Critical Thermal Maximum

DD – Degree Day

DH – Degree Hour

et al. – et collaborateurs

GLM - Generalized Linear Regressions

HSP - Heat Shock Protein

IBM - Individual Based Model

LMC - Local Mate Competition

MAE - Mean Absolute Error

MTE - Metabolic Theory of Ecology

MVT - Marginal Value Theorem

N – Taille de l'échantillon

OFT - Optimal Foraging Theory

RCP - Representative Concentration Pathways

RH - Relative Humidity

RMSE - Root Mean Squared Error

SR - Sex Ratio

TCH - Temperature Coupling Hypothesis

TSR - Temperature Size Rule

Remerciements

Je voudrais tout d'abord remercier mes co-directeurs, Jacques Brodeur, Gaétan Bourgeois et Guy Boivin, pour leur disponibilité, leur patience, leur rigueur et leur humour. Merci à Jacques pour sa passion contagieuse du parasitisme, d'être un incroyable exemple pour les présentations, et pour les repas réunissant tous les étudiants du laboratoire. Merci à Gaétan pour son soutien et ses encouragements tout au long du projet, pour avoir été un modèle de rigueur mathématique pour la modélisation, mais également un exemple pour les questions administratives du métier de chercheur. Merci à Guy pour l'aide incroyable durant le projet, et pour constituer une source incroyable d'informations dans tous les domaines imaginables ! Je m'estime extrêmement chanceuse d'avoir pu travailler avec eux.

Je voudrais également remercier Danielle Thibodeau, Julie Frenette et Josianne Vaillancourt pour leur aide lors des expériences en laboratoire et sur le terrain, pour leur dynamisme et surtout pour leur bonne humeur. Merci à Mathieu Pominville-Racette pour son aide pour l'extraction des œufs de charançons. Merci également aux équipes de la ferme expérimentale de Sainte-Clotilde : Michel, Missy, Julie, Frank, Martin, Vicky. Merci à Dominique Plouffe, Danielle Choquette, Gaétan Racette et Nathalie Beaudry pour leur bonne humeur dans les réunions de bioclimatologie. Je souhaite également remercier Annie-Eve Gagnon, qui a pris la succession de Guy, pour son dynamisme et ses observations durant les réunions de laboratoire.

Merci à tous les professionnels de recherche et étudiants des 3 laboratoires dans lesquels j'ai eu la chance de travailler. Merci à Paul Abram, Jean-Philippe Parent et Gongyu Lin d'avoir été d'incroyables amis, d'exemples d'étudiants gradués, et maintenant de chercheurs accomplis. Merci en particulier à Paul pour les Rippers, à Jean-Philippe pour les films étranges, et à Gongy pour les expériences uniques de science et de burlesque ! Merci à Josée Doyon, Jean-François Duval, Felix-Antoine Robert, Alexandre Leblanc, Axel Gutman, Fredéric Hadi et Kévin Tougeron, pour les discussions sur tous les sujets. Le laboratoire a également eu la chance d'acceuillir plusieurs étudiants étrangers qui ne restent jamais assez longtemps : Victor Burté, Deborah Kapantaidaki, Letizia Martorana et Valeria Bertoldi. Merci également, et mes encouragements pour la suite à ceux qui n'ont pas encore terminé au moment où j'écris ces lignes : Mathilde Gaudreau, Jérôme Gélinas Bélanger, Elysée Emmanuel Dabre, Jules Dumotier, Marianne Bessette ! Merci également à Tales of Pi, Histoires au coin du D20 et à la Tronche en biais pour m'avoir aidé à conserver un semblant de santé mentale durant le visionnage des vidéos d'exploitation d'agrégat.

En plus du travail de recherche, cette thèse m'a permis d'être auxiliaire d'enseignement à l'Université de

Montréal, ce qui fut une expérience incroyablement formatrice. Merci en particulier à Jean Rivoal et Evgenia Auslender de m'avoir fait confiance pour des charges de chef-démos, qui m'ont énormément appris et donné envie d'enseigner. Merci aux auxiliaires d'enseignements avec qui j'ai eu la chance de travailler, en particulier Valentin Joly, Sébastien Dumont, Steve Dagenais-Bellefeuille, Henry Béral et Carl Bowazolo. Merci également à Josée Letellier pour son aide dans la préparation des TP, pour sa bonne humeur et sa gentillesse, aussi bien avec les étudiants qu'avec nous.

En plus de la recherche et l'enseignement, le doctorat permet de s'impliquer en parallèle dans des projets important. J'ai ainsi la chance de travailler pour le Beagle, un blog de vulgarisation géré et rédigé par les étudiants du Centre de la Science de la Biodiversité du Québec. Merci donc à l'équipe du blog le Beagle, Anne-Sophie Caron, Nathalie Jredini, Naila Barbosa da Costa, Catherine Pelletier, Philippe Auzel, Guillaume Laroque et Helen Elina pour contribuer à donner une visibilité aux étudiants en biodiversité au Québec :)

Il est difficile de penser aux années de doctorat sans évoquer les personnes n'ayant pas de lien direct avec la thèse, mais avec qui j'ai passé le plus clair de mon temps en dehors du laboratoire. Merci à Christopher pour son humour, pour les discussions philosophiques et pour être un excellent partenaire d'escape room. Merci à Marcela pour le dynamisme et la bonne humeur dans les charges d'auxiliaires d'enseignement, et d'être toujours partante pour n'importe quoi !

Merci à mes amis musiciens, les Bambies (Samuel, Felipe et maintenant Freddie) grâce à qui j'ai découvert et joué dans les bars les plus underground de Montréal, les Autres jours (Francis et Clément), et les Cathy's (Sophie, Nahame et Menahan). Merci également aux Rippers déjà cités plus haut : Paul, Gongyu et Victor !

Merci à Philippe et aux étudiants du dojo Tsunawatari, en particulier Luc, Olivier et Geneviève, pour m'avoir fait découvrir le plaisir de se faire projeter à l'autre bout du dojo ou se retrouver immobilisé à terre contre un tatami. L'aïkido est une excellente manière de se changer les idées !

Merci à mes amis en France pour leur soutien indéfectible, et pour avoir l'impression de s'être quitté la veille chaque fois qu'on se retrouve, même après toutes ces années : Paul, Blaise, Clara, Amaury, Bertille, Laurie, Manon et Clémence.

Merci à ma famille pour leur soutien depuis toujours. On est encore dans la partie en français de la thèse (et seulement à la seizième page) donc vous devriez lire au moins jusqu'ici : je vous aime !
Merci enfin à Jean-Sébastien, sans qui cette thèse aurait été terminée deux ans plus tôt ;)

Description des chapitres

Chapitre 1. Ce chapitre introduit la problématique générale et les objectifs de la thèse.

Chapitre 2. Ce chapitre décrit, par une revue de littérature, le contexte général lié aux changements climatiques et les concepts biologiques requis pour la compréhension de la suite du document.

Chapitre 3. Dans ce chapitre, j'identifie la contribution de mes co-auteurs ainsi que la mienne pour les quatre articles scientifiques inclus dans cette thèse.

Chapitre 4. Le premier article scientifique de cette thèse, intitulé : *« Effect of temperature on the walking behaviour of an egg parasitoid: disentangling kinetic response from integrated response »* décrit la relation entre la température et le comportement de marche d'une guêpe parasitoïdes des œufs, *Anaphes listronoti.*

Chapitre 5. Le second article scientifique, intitulé « *The effect of temperature on host patch exploitation by an egg parasitoid* » décrit l'impact de la température sur le comportement d'exploitation d'agrégat d'*Anaphes listronoti.*

Chapitre 6. Le troisième article scientifique, intitulé « *Low and high temperatures decrease the mating success of an egg parasitoid and the proportion of females in the population* » étudie comment le comportement d'accouplement d'*Anaphes listronoti* est affecté par la température.

Chapitre 7. Le dernier article scientifique, intitulé « *Individual behaviour and population dynamics under climate change : Simulation of an insect parasitoid life cycle* » décrit un modèle de simulation des populations du parasitoïde crée à partir des données comportementales des trois chapitres précédents.

Chapitre 8. Le dernier chapitre, la discussion générale, résume les principaux résultats obtenus, analyse leurs implications pour les réponses des insectes aux changements climatiques, et suggère des perspectives de recherche.

Chapitre 1 : Introduction générale

Tableau : Christian Augustin – Photo : Nolwen Lemercier

Les changements climatiques actuels vont provoquer des conditions thermiques plus extrêmes et variables à l’échelle de la planète (IPCC, 2013). Les organismes peuvent utiliser diverses stratégies d'adaptation incluant la modification des aires de répartition, la plasticité phénotypique et l'évolution (Williams et al., 2008). Cependant, la rapidité, la variabilité et l’intensité des changements en cours rendent difficile l'adaptation pour la plupart des organismes (Chevin et al., 2010). Les insectes étant poïkilothermes, la température affecte fortement tous les aspects de leur cycle de vie (Kingsolver, 2009). Si les effets de la température sur la physiologie des insectes sont relativement bien connus, il en va autrement des effets sur leurs comportements. En particulier, la distinction reste complexe entre les réponses kinétiques (qui résultent de l'accélération/ralentissement des réactions chimiques de l'organisme en fonction de la température) et les réponses intégrées (qui s'ensuivent de l'intégration des informations thermo-sensorielles par le système nerveux central de l'insecte) à la température (Abram et al., 2017). Les théories d'optimalité considèrent que les individus agissent de manière à augmenter leur valeur adaptative dans l'environnement où ils ont évolué (Parker et Smith, 1990). Les nouvelles conditions thermiques limiteront probablement la réalisation de leur plein potentiel. De plus, les conséquences des réponses comportementales individuelles sur la population demeurent inconnues, mais constituent une information cruciale si nous voulons être en mesure de prédire les réponses des populations et des communautés aux changements climatiques (Tenhumberg, 2004; Wong et Candolin, 2015).

Dans ce contexte, cette thèse explore l'effet de la température sur trois comportements d'une guêpe parasitoïde des œufs, *Anaphes listronoti* : la marche lorsqu’associée à la recherche de l'hôte, l'exploitation d'agrégats d’hôtes, et l'accouplement. Pour chaque comportement, j’ai tenté de déterminer si les réponses observées étaient kinétiques ou intégrées, adaptatives ou en réponse à certaines contraintes. L'inclusion de ces comportements dans un modèle de simulation dynamique a ensuite permis de simuler selon la température les conséquences des réponses comportementales des individus sur une population de parasitoïdes. Les objectifs de la thèse étaient de :

1. Dissocier les effets kinétiques des effets intégrés pour le comportement de marche, d’exploitation d’agrégats et de reproduction ;
    a. Hypothèse 1 : La température affecte les comportements de manière kinétique;
        i. Prédiction 1 : Les comportements testés suivent la courbe théorique physiologique.
    b. Hypothèse 2 : La température affecte les comportements selon une réponse intégrée;
        i. Prédiction 1 : Des réponses intégrées de type fuite, maintien du comportement ou conservation de l’énergie seront observées.
    c. Hypothèse 3 : Les réponses kinétiques et intégrées ne sont pas mutuellement exclusives;
        i. Prédiction 1 : Des réponses kinétiques et intégrées seront observées pour un même type de comportement.
    d. Hypothèse 4 : Des contraintes physiologiques supplémentaires affectent les comportements;
        i. Prédiction 1 : Des modifications comportementales ne pouvant être expliquées par

une réponse kinétique ou intégrée seront observées.

2. Comparer les stratégies d'exploitation d'agrégats d'hôtes et de reproduction en fonction de la température;
    a. Hypothèse 1 : Les températures aux limites de la gamme thermique de fonctionnement contraignent les stratégies d'exploitation d'agrégat d'hôtes;
        i. Prédiction 1 : Le temps de résidence diminuera lorsque la température augmente;
        ii. Prédiction 2 : L'allocation du temps sur l'agrégat variera en fonction de la température, en particulier la méthode d'estimation du statut de l'hôte.
    b. Hypothèse 2 : Les températures aux limites de la gamme thermique de fonctionnement contraignent les stratégies de reproduction;
        i. Prédiction 1 : Le succès d'accouplement diminuera aux températures les plus basses et les plus élevées de la gamme thermique testée;
        ii. Prédiction 2 : Le sex ratio de la descendance augmentera lorsque la mère s'est accouplée aux températures les plus basses et les plus élevées de la gamme thermique testée.
3. Quantifier l'impact de la modification des comportements induite par la température sur la génération suivante ;
    a. Hypothèse 1 : Les températures aux limites de la gamme thermique de fonctionnement contraignent les comportements de reproduction des femelles;
        i. Prédiction 1 : Les femelles exploitant un agrégat à des températures infra- et supra-optimales auront moins de descendants que celles exploitant l'agrégat à température intermédiaire;
        ii. Prédiction 2 : Les femelles exploitant un agrégat à des températures infra- et supra-optimales auront une proportion de filles inférieure aux femelles exploitant un agrégat à température intermédiaire;
        iii. Prédiction 3 : Les femelles exploitant un agrégat à des températures infra- et supra-optimales déposeront moins de descendants par hôte que celles exploitant l'agrégat à température intermédiaire.
4. Analyser l'importance d'inclure les comportements individuels dans un modèle mathématique simulant la population d'un insecte en fonction des conditions thermiques ;
    a. Hypothèse 1 : Il est fondamental d'inclure les comportements dans les modèles de population ;
        i. Prédiction 1 : Un modèle incluant les comportements génère des prédictions plus fiables qu'un modèle ne les incluant pas, pour prédire une population de parasitoïdes au champ.

   b. Hypothèse 2 : Les courbes thermiques de performance des comportements diffèrent dans leur étendue et leur température correspond à la performance optimale;
      i. Prédiction 1 : Les gammes thermiques des comportements liés à la reproduction sont plus restreintes que celles des autres comportements;
      ii. Prédiction 2 : Les gammes thermiques des comportements sont plus restreintes que celles liées aux processus physiologiques de l'insecte tels que le développement.
   c. Hypothèse 3 : Inclure les comportements dans un modèle de dynamique des populations est encore plus important pour des conditions de températures projetées dans le contexte des changements climatiques;
      i. Prédiction 1 : Les populations simulées selon le modèle incluant le comportement seront significativement différentes de celles simulées sans inclure le comportement, pour des conditions thermiques telles que celles projetées par les changements climatiques.

Les résultats obtenus dans le cadre de cette thèse mettent de l'avant la variété et la complexité des réactions comportementales des insectes en réponse à la température. Ainsi, par l'utilisation d'un modèle kinétique nul tel que suggéré par Abram et al. (2017), les mécanismes sous-jacents à l'expression d'un comportement en réponse aux conditions thermiques ont pu être étudiés. De plus, l'existence de contraintes physiologiques autres que les contraintes kinétiques sont constatées. Également, les expériences ont permis d'observer des mécanismes physiologiques ou comportementaux d'adaptation aux conditions thermiques non optimales. Finalement, le modèle montre que chez les organismes ectothermes, l'ajout des comportements dans les modèles populationnels n'apporte pas forcément de valeur ajoutée, mais qu'il reste essentiel de les considérer, en particulier dans le cadre des changements climatiques. Il révèle également les limites de nos connaissances, notamment en ce qui concerne l'allocation du temps au champ, et comment les conditions thermiques affectent cet aspect. Cette thèse illustre les capacités d'adaptation remarquable à leur environnement dont font preuve les insectes, les parasitoïdes en particulier, malgré les contraintes exercées par les conditions thermiques, et ce à l'échelle de l'individu comme de la population.

Références

Abram, P.K., Boivin, G., Moiroux, J., et Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: Unifying thermal physiology and behavioural plasticity. Biol. Rev. 92, 1859–1876.

Chevin, L.-M., Lande, R., et Mace, G.M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. PLoS Biol. 8, e1000357.

Kingsolver, J.G. (2009). The well-temperatured biologist. Am. Nat. 174, 755–768.

Parker, G.A., et Smith, J.M. (1990). Optimality theory in evolutionary biology. Nature 348, 27–33.

IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp.

Tenhumberg, B. 2004. Predicting predation efficiency of biocontrol agents: linking behavior of individuals and population dynamics. Pages 864–869 in C. Pahl, S. Schmidt, and T. Jakeman, editors. Complexity and integrated resources management: transactions of the 2nd Biennial Meeting of the International Environmental Modelling and Software Society. Manno, Lugano, Switzerland

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., et Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol. 6, e325.

Wong, B.B.M., et Candolin, U. (2015). Behavioral responses to changing environments. Behav. Ecol. 26, 665–673.

Chapitre 2 : Revue de littérature

Tableau : Christian Augustin – Photo : Nolwen Lemercier

2.1 / Changements climatiques – '*The times they are a-changin'* [1]'

2.1.1 / Changements climatiques : Etat de la situation et projections

L'effet des gaz à effet de serre sur l'augmentation des températures terrestres a été prédit par Arrhénius (1896) il y a plus d'un siècle. Depuis, « l*e réchauffement du système climatique est sans équivoque. [...] L'atmosphère et les océans se sont réchauffés, les quantités de neige et de glace ont diminué, le niveau de la mer s'est élevé, et les concentrations de gaz à effet de serre ont augmenté* » (Stocker et al., 2013). D'ici la fin du siècle, la température globale de surface augmentera d'au moins 1.5°C comparé à celle de l'ère préindustrielle. Outre les augmentations moyennes de température, des phénomènes « extrêmes » tels que des vagues de chaleur, des hivers particulièrement froids et de fortes pluies sont observées plus fréquemment depuis 1950 (Stocker et al., 2013), et il est « virtuellement certain » que leurs fréquences, intensités et durées augmenteront de concert avec les températures globales moyennes (Easterling, 2000). La nature et l'intensité des changements varient d'une région du monde à l'autre et entre les saisons (Sillmann et al., 2013).

Au Québec, en particulier, les températures journalières ont augmenté de 0.2 à 0.4°C par décennie et la saison de gel s'est raccourcie (Ouranos, 2010). On prévoit d'ici 2080, dans le sud du Québec, un réchauffement hivernal allant jusqu'à 3.8°C par rapport aux températures de 1961 à 1990. Pour l'été, le réchauffement atteindra 3.1°C (Ouranos, 2015) (Figure 2-1). Les précipitations devraient augmenter de 8.6 à 18.1%. Les changements seront encore plus importants dans le nord de la province, avec des augmentations de température pouvant atteindre 6.5°C et 29.4% d'augmentation des précipitations (Ouranos, 2010). Dans le sud du Québec, l'accumulation de neige diminuera pendant l'hiver, ce qui pourrait affecter différentes espèces animales et végétales qui survivent aux rigueurs de l'hiver grâce à la protection du couvert de neige.

Différents scénarios climatiques ont été élaborés quant à la quantité de CO_2 que nous rejetterons dans l'atmosphère à l'échelle mondiale. On calcule ces scénarios selon les stratégies potentielles de réduction des gaz à effet de serre mises en place au niveau des transports, de la construction, des industries, de l'agriculture et de la foresterie (Stocker et al., 2013). Ils vont du plus pessimiste, RCP (*Representative Concentration Pathways*) 8.5 (où les concentrations de CO_2 dans l'atmosphère en 2100 atteindraient plus de 1000 ppm, menant à une augmentation de température d'au moins 4°C d'ici 2100) au plus optimiste, RCP 2.6 (450 ppm de CO_2 dans l'atmosphère en 2100, ce qui permettrait de limiter le réchauffement à 1.5°C) (Stocker et al., 2013). Selon tous les scénarios envisagés, à l'exception du plus optimiste (RCP 2.6), les températures continueront à augmenter après 2100 (GIEC, 2013) (Figure 2-2).

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[1] Bob Dylan - *The Times They Are a-Changin'* (1964)

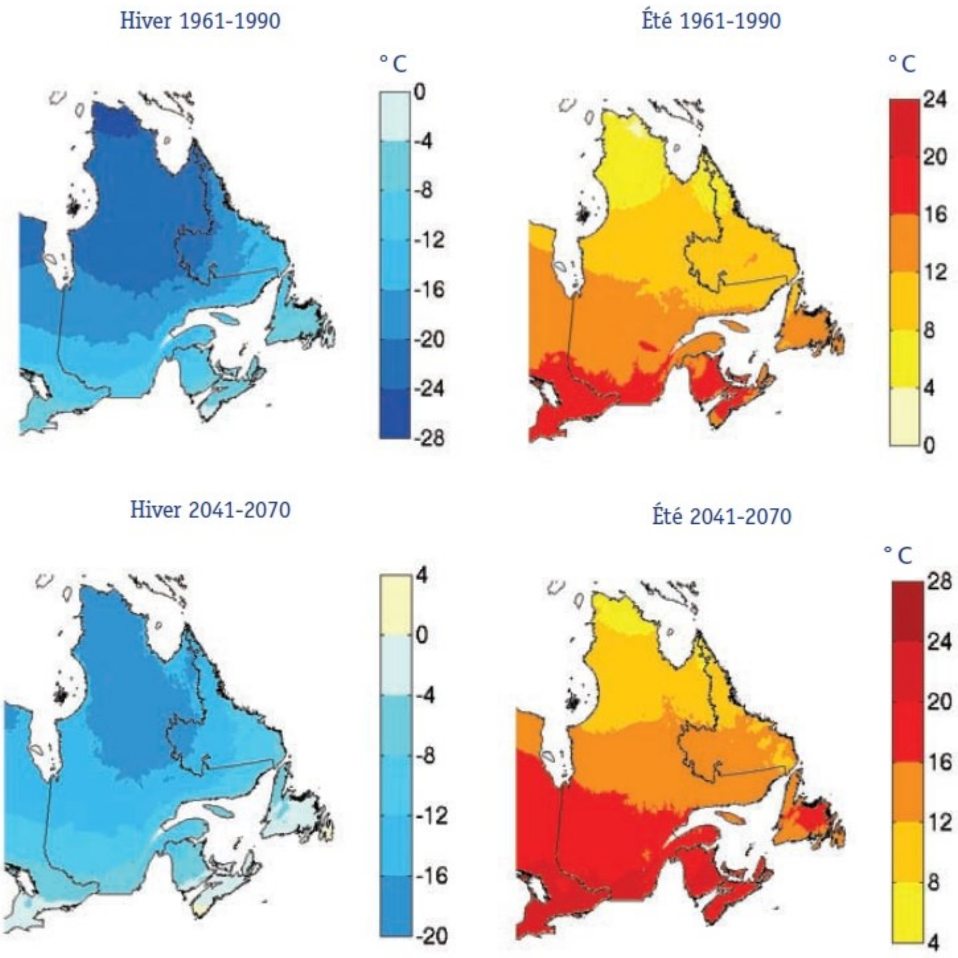

Figure 2-1: Moyennes des températures hivernales et estivales observées (1961-1990) et projetées (2041-2070) (Ouranos, 2010)

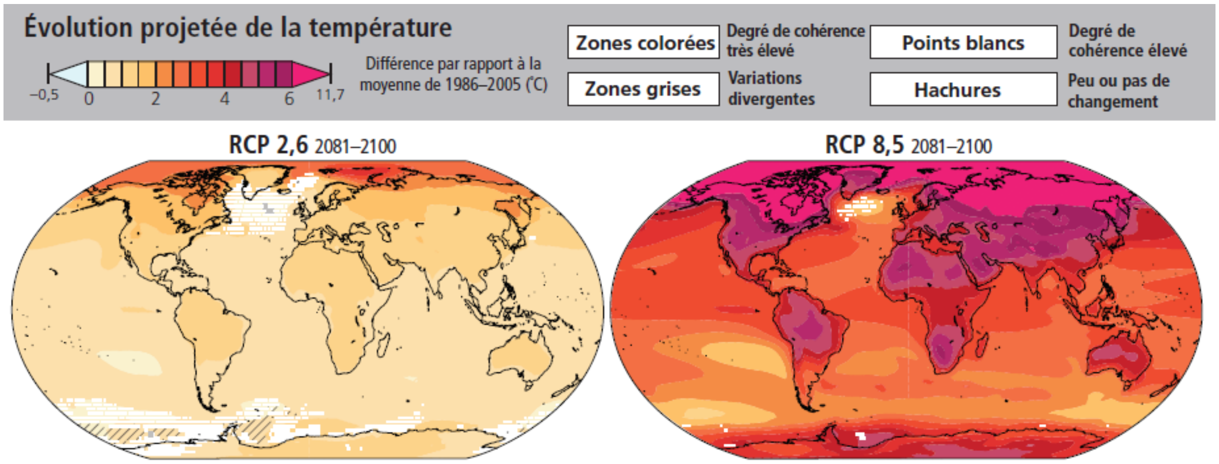

Figure 2-2: Variations observées et projetées de la moyenne annuelle de la température à la surface du globe. Figure tirée du Résumé à l'intention des décideurs du **GIEC** (2014)

2.1.2 / Conséquences générales sur les organismes

Des modifications écologiques en réponse aux changements climatiques s'observent déjà (Hughes, 2000 ; Walther et al., 2002) et s'inscrivent selon les prédictions d'un réchauffement climatique (Rosenzweig et al., 2008). Les effets des changements climatiques sur les organismes varient fortement en fonction de la région étudiée ; ils risquent ainsi d'être plus problématiques pour les organismes vivant dans des zones auparavant très stables au niveau météorologique, telles que les zones tropicales (Deutsch et al., 2008; Huey et al., 2009; Kingsolver, 2009; Bonebrake et Mastrandrea, 2010; Bonebrake et Deutsch, 2012; Diamond et al., 2012), arctiques ou en altitude (Parmesan, 2006). Ainsi en Arctique, où le réchauffement s'avère le plus important, des changements conséquents de compositions des communautés s'observent déjà (Koltz et al., 2018). Les changements climatiques pourraient également favoriser les populations d'espèces invasives (Chown et al., 2007). De plus, les événements imprévisibles (Zhu et al., 2019) et extrêmes (Bale et al., 2002; Clusella-Trullas et al., 2011; Sergio et al., 2018), ainsi que la variabilité des changements (Drake, 2005; Folguera et al., 2011; Paaijmans et al., 2013; Estay et al., 2014; Vasseur et al., 2014) auront probablement plus d'importance pour les organismes que l'augmentation moyenne de température. Williams et al. (2008) définissent trois types de réponse des populations animales à une perturbation environnementale : la dispersion, la plasticité phénotypique des traits d'histoire de vie et l'adaptation génétique.

Dispersion

La dispersion vers des régions aux conditions plus adaptées constitue une adaptation en réponse aux changements. Plusieurs espèces « suivent » ainsi déjà les conditions météorologiques/biotiques permettant leur développement (Parmesan, 2006; Chen et al., 2011) en se déplaçant vers le nord ou en altitude en réponse aux changements climatiques (Parmesan et Yohe, 2003). Les capacités de dispersion de certaines espèces semblent cependant insuffisantes pour suivre les changements environnementaux (Sirois-Delisle et Kerr, 2018). La diminution de la connectivité des habitats limite également cette possibilité (Warren et al., 2001; Senior et al., 2019). Ainsi, plusieurs espèces sont en retard dans leur distribution géographique par rapport aux changements de leur environnement (Menéndez et al., 2006). Actuellement, en considérant un réchauffement global de 3.2°C, 49 % des espèces d'insectes verraient leur distribution géographique diminuer de moitié (Warren et al., 2018). A l'inverse, d'autres espèces, plus adaptées aux nouvelles conditions (par exemple certaines espèces invasives), gagneront en distribution (Thuiller, 2007).

A plus petite échelle spatiale, la recherche de microclimats adaptés au sein de l'environnement pourrait jouer un rôle important dans l'adaptation aux changements climatiques (Bonebrake et Deutsch, 2012; Woods et al., 2015). Potter et al. (2013) et Pincebourde et Casas (2015) suggèrent ainsi de considérer le microclimat plutôt que le macroclimat pour estimer les capacités d'adaptation et de dispersion des organismes en réponse aux changements climatiques.

Réponse plastique

La plasticité phénotypique correspond aux différentes manières dont un génome peut s'exprimer en fonction de son environnement. Ainsi, la réponse plastique, incluant les réponses phénologiques, morphologiques, physiologiques (Fuller et al., 2010) et comportementales (Candolin et al., 2014), représente un tampon face aux changements environnementaux (Chevin et al., 2010; Kellermann et van Heerwaarden, 2019). Ces adaptations constituent les premières réponses à une perturbation observée au niveau des populations (Wong et Candolin, 2015). La réponse plastique permet de s'adapter à un changement environnemental sans nécessiter de changements génétiques dans la population (Reed et al., 2011). Dans le cadre des changements climatiques, la plasticité phénotypique s'avère la réponse la plus souvent observée (Bradshaw et Holzapfel, 2008; Charmantier et al., 2008; Gienapp et al., 2008). A cause de la rapidité des changements documentés, elle pourrait représenter la seule possibilité d'adaptation pour les organismes à long cycle de vie (Fuller et al., 2010). Elle présente cependant plusieurs limites : les coûts de production et de maintien (Sgrò et al., 2016), la question de son adaptativité (Ghalambor et al., 2007; Sih, 2013), son ampleur face aux perturbations environnementales prévues (van Baaren et Candolin, 2018) et finalement la diminution de la valeur adaptative des organismes par rapport aux conditions optimales (Reed et al., 2011; Huey et al., 2012) (Figure 2-3).

L'une des réponses plastiques les plus fréquemment documentées en réponse aux changements climatiques est le décalage phénologique (Parmesan et Yohe, 2003; Root et al., 2003). Ainsi, les arbres en Europe produisent leurs feuilles plus tôt dans l'année, suivant l'amplitude des changements climatiques (Menzel et al., 2006), les oiseaux migrent plus tôt (Gienapp et al., 2007) et les insectes s'activent plus rapidement au printemps (Forrest, 2016). Dans le cas particulier des ectothermes, grâce à un début de la saison plus précoce et à leur développement plus rapide à température plus élevée (Bale et al., 2002), le nombre de générations par année augmente chez les espèces multivoltines, qui ont plusieurs générations par année (Forrest, 2016). La plasticité phénotypique reste malgré tout peu intégrée dans les modèles de simulation des réponses des espèces aux changements climatiques, entre autres parce que nous manquons d'informations sur la plasticité des réponses, leur coût et les conséquences pour les populations (Sgrò et al., 2016). Stillman (2003) et Sørensen et al. (2016) ont cependant montré que la réponse plastique sous forme d'acclimatation aux températures élevées reste limitée, en particulier pour les organismes qui exploitent un environnement déjà aux limites de leur capacité thermique.

Evolution

L'évolution est une stratégie d'adaptation qui se déroule à plus long terme. Bien que certaines études décrivent des exemples d'évolution rapide en réponse aux changements climatiques (Bradshaw et Holzapfel, 2006; Parmesan, 2006), le rôle de l'évolution demeure souvent difficile à démontrer (Gienapp et al., 2008;

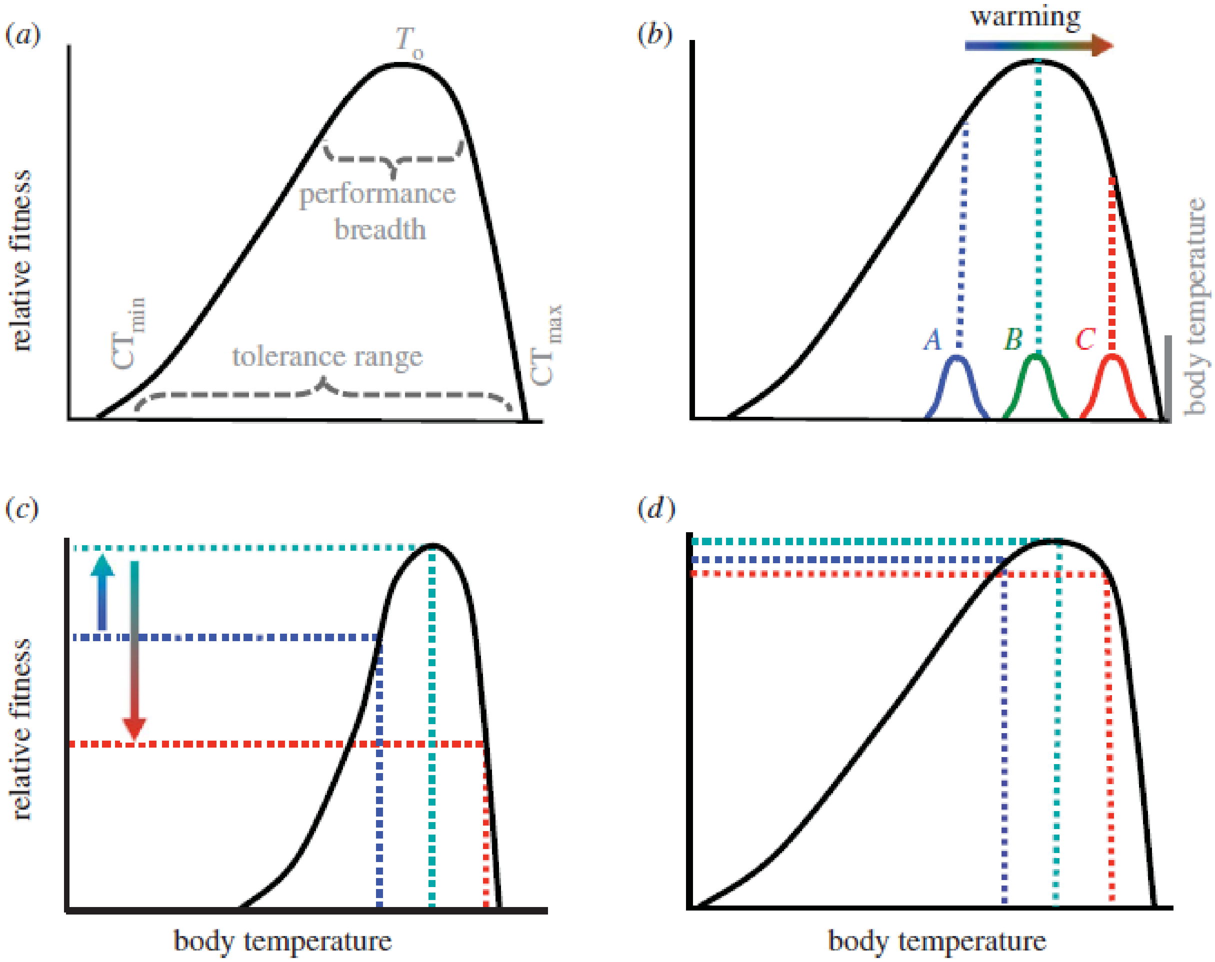

Figure 2-3 : (a) Courbe de valeur adaptative thermique (performance) pour un ectotherme hypothétique, avec les paramètres descriptifs clés CT_{min} (Critical thermal minimum), CT_{max} (Critical thermal maximum), gamme de tolérance, ampleur de performance et température optimale (T_o) identifiés. (b) Avec les changements climatiques, la distribution réalisée T_b (*body temperature*) peut se décaler plus haut. Si le réchauffement résulte en un T_b plus proche du T_o d'une espèce (par exemple T_b se décale de A vers B), alors le réchauffement devrait améliorer la valeur adaptative ; mais si le réchauffement augmente T_b au-delà de T_o (si T_b se décale de B vers C), la valeur adaptative sera diminuée. (c,d) Les augmentations dans la distribution de T_b par le réchauffement peuvent avoir des effets supérieurs sur les (c) spécialistes thermiques que sur les (d) généralistes thermiques. Traduction de la légende de (Huey et al., 2012)

Chown et al., 2010). Plusieurs facteurs limitent cependant l'adaptation par évolution : elle requiert en effet la présence de variants génétiques sur lesquels agir (Hoffmann et Sgrò, 2011; Reed et al., 2011), que les traits d'intérêt soient héritables, et enfin que les changements observés ne soient pas trop rapides (Visser, 2008). De plus, la variabilité prévue des conditions environnementales dans le cadre des changements climatiques pourrait ralentir, voire empêcher l’expression constante des pressions de sélection, et donc freiner l'évolution de la population (Wong et Candolin, 2015). Du reste, des expériences en laboratoire sur différentes espèces de drosophile ont montré que la capacité évolutive de résistance à la chaleur était généralement limitée (Krebs et Loeschcke, 1994;

Kellermann et van Heerwaarden, 2019). A cause de ces contraintes, l'adaptation par évolution semble limitée dans le contexte de très rapides changements climatiques (Etterson et Shaw, 2001). Ainsi, Quintero et Wiens (2013) ont calculé que, pour s'adapter à la vitesse des changements environnementaux prévus, le taux d'évolution des vertébrés devrait être 10 000 fois plus rapide que les taux habituellement observés pour la plupart des espèces.

Réseaux trophiques

L'écologie des organismes jouera un rôle important dans leur potentiel d'adaptation aux nouvelles conditions (Berg et al., 2010). On estime ainsi que les niveaux trophiques supérieurs ont des probabilités d'adaptation moindre comparé aux niveaux inférieurs (Voigt et al., 2003) à cause des effets « *bottom-up* » de perturbations des systèmes (Aguilar-Fenollosa et Jacas, 2014). En effet, les niveaux supérieurs doivent s'adapter non seulement aux nouvelles conditions environnementales, mais également aux changements provoqués par ces nouvelles conditions sur les niveaux inférieurs (qualité de l'hôte, indices chimiques, phénologie, distribution, etc.). L'une des problématiques de l'adaptation différentielle des espèces aux nouvelles conditions reste la perte potentielle de synchronisme entre les espèces qui interagissent entre elles (Bale et al., 2002; Visser et Both, 2005; Hance et al., 2007; Castex et al., 2018; Renner et Zohner, 2018). Cependant, les études relatives aux effets thermiques sur les organismes individuels, mais surtout sur les réseaux trophiques manquent cruellement (Petchey et al., 2010; Thomson et al., 2010; Jamieson et al., 2012; Jeffs et Lewis, 2013).

Risque d'extinction

Face à des changements trop rapides ou importants, certaines espèces n’ont pas la capacité de s'adapter (Chevin et al., 2010). Dans ce cas, les populations peuvent diminuer ou même s'éteindre. Les changements climatiques représentent aujourd'hui la 4$^{\text{ème}}$ cause d'extinction des espèces d'insectes après la destruction des habitats, la pollution (en particulier causée par les pesticides) et les causes biotiques (pathogènes et espèces introduites) (Thomas et al., 2004; Sánchez-Bayo et Wyckhuys, 2019). On observe ainsi un déclin des populations de certaines espèces de papillons depuis quelques années (Carnicer et al., 2019; Wepprich et al., 2019). Chez les insectes en général, la biomasse a diminué de 80% dans les 30 dernières années (Hallmann et al., 2017) et jusqu'à 40% des espèces d'insectes pourraient disparaître (Sánchez-Bayo et Wyckhuys, 2019) en raison de tous ces facteurs. Le problème n'est pas limité aux insectes : nous observons actuellement les prémices de la 6$^{\text{ème}}$ extinction massive de la planète (Barnosky et al., 2011; Bellard et al., 2012). Ainsi, 47% des 976 espèces étudiées (plantes et animaux vertébrés et invertébrés) ont déjà subi des extinctions locales en lien avec les changements climatiques, et ce malgré le fait que les changements environnementaux actuels demeurent moins importants que ceux prévus à la fin du siècle (Wiens, 2016). De plus, les effets négatifs du climat pourraient se voir amplifiés par d'autres facteurs déstabilisant les écosystèmes tels que la destruction des habitats, la diminution de biodiversité (Macfadyen et al., 2018), et les espèces invasives (Molina-Montenegro et al., 2009), ou encore la multiplicité des facteurs de stress, par exemple la chaleur, la sécheresse et l'exposition aux pesticides (Rohr et Palmer, 2013).

Précédents changements climatiques

D'après le scénario RCP 4.5 du Modèle de Système Climatique version 4 (*Climate System Model version 4* - CCSM4) de la phase 5 du Projet d'Intercomparaison des Modèles Couplés (*Coupled Model Intercomparison Project phase* 5 - CMIP5) (Meehl et al., 2012), le climat de 2040 sera similaire à celui du milieu du Pléiocène. À l'inverse, le scénario RCP 8.5 prévoit que le climat de 2150 ressemblera à celui de l'Eocène, selon un réchauffement 65 fois plus rapide que celui de la dernière déglaciation (Nolan et al., 2018). Cela revient à inverser des millions d'années de refroidissement sur une période de seulement quelques générations humaines (Burke et al., 2018). L'étude des fossiles de ces époques nous aide à prédire les changements possibles au sein des populations et des communautés, tels que les modifications importantes observées dans la composition des communautés d'insectes, en particulier la proportion d'herbivores (Wilf et Labandeira, 1999) lors du passage Paléocène-Éocène, ou encore les changements de répartition géographique des espèces d'insectes (Coope, 1970), de végétaux (Graham et Grimm, 1990; Davis et Shaw, 2001), de mammifères et de mollusques (Graham et Grimm, 1990) selon les périodes glaciaires et interglaciaires de l'ère Quaternaire. Les changements d'aires de répartition tendent à se faire à l'échelle de l'espèce plutôt que de l'écosystème (Graham et Grimm, 1990; Kidwell, 2015). La possibilité pour les organismes de suivre spatialement les changements climatiques est malheureusement plus limitée aujourd'hui que durant le Quaternaire, à cause de la destruction des habitats par l'activité humaine (Parmesan et al., 2000). D'autres espèces ne modifiaient pas leurs aires de répartition mais s'adaptaient aux changements (Parmesan et al., 2000).

Cependant, le rôle du climat seul dans les adaptations biologiques, ainsi que dans l'extinction des espèces, reste moins évident (Kidwell, 2015). Les extinctions du Quaternaire pourraient avoir été causées par des changements de composition des communautés (Graham et Grimm, 1990) résultant de changements climatiques plutôt que directement des changements climatiques. Seulement, en se basant sur les observations datant de la dernière glaciation, il demeure possible de prédire l'ampleur des changements que subiront les communautés en termes de composition, de structure et de fonction (Nolan et al., 2018). Les écosystèmes pourraient ainsi retrouver une stabilité au 22ème siècle (Nolan et al., 2018).

2.2 / Les insectes et la température – '*Light my fire*[2]'

Les insectes entrent dans la catégorie des organismes poïkilothermes. Ils ne régulent pas leur température corporelle de manière physiologique, laquelle se maintient près de la température ambiante. La température constitue le facteur abiotique ayant le plus d'impact sur l'écologie des insectes (Messenger, 1959; Kingsolver, 2009) puisqu'elle affecte fortement tous les aspects de leur métabolisme, développement, reproduction (Clarke et

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[2] The Doors – *The Doors* (1967)

Fraser, 2004) et comportement.

Les insectes ont la capacité de tolérer physiologiquement une certaine gamme de températures, comprise entre le point thermique critique minimum (CT_{min} : température basse à laquelle les individus perdent la coordination de leurs mouvements ou la force de se tenir debout ou de se relever (MacMillan et Sinclair, 2011), et le point thermique critique maximum (CT_{max} : température la plus élevée à laquelle l'insecte peut bouger). En deçà et au-delà de ces deux points, l'insecte tombe dans un coma puis meurt (Figure 2-4) (Vannier, 1994). Le coma froid se traduit par une absence de mouvement spontané ou de réponse à un stimulus à basse température. Cet état réversible dépend de la température et de la durée d'exposition, ainsi que de la température de récupération (MacMillan et Sinclair, 2011). Les valeurs des CTL (*Critical Thermal Limits*) dépendent de la vitesse d'augmentation ou de diminution des températures (Lutterschmidt et Hutchison, 1997; Chown et al., 2009; Terblanche et al., 2011; Allen et al., 2012; Overgaard et al., 2012). Les limites thermiques supérieures maximales varient généralement d'un niveau trophique à l'autre, ce qui peut perturber l'équilibre des réseaux (Agosta et al., 2018). De plus, leur potentiel d'augmentation chez les ectothermes terrestres semble limité, aussi bien par la plasticité, l'évolution (Hoffmann et al., 2013) que l'acclimatation (Allen et al., 2012). Dans le cadre des changements climatiques, on utilise les CT_{min} et CT_{max} pour prédire la distribution géographique de plusieurs espèces selon différents scénarios, bien que cette méthode ait ses limites (Kellermann et van Heerwaarden, 2019).

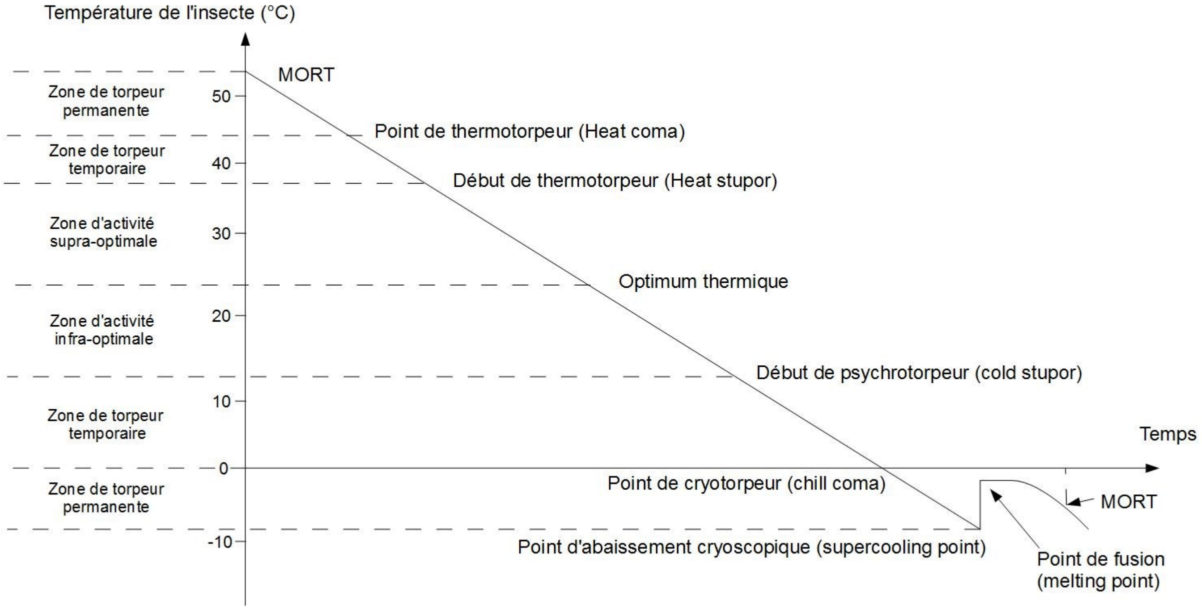

Figure 2-4 : Courbe thermique d'un insecte hypothétique. Adapté de Vannier (1994)

On définit la température comme « optimale » dès lors que le trait observé y est maximal. En dessus et en deçà de cette température (lorsque le trait reste exprimé mais de façon moindre), on considère la température comme suboptimale. On définit ainsi les températures infra- et supra-optimales comme la gamme de température allant de l’optimum thermique de l’insecte jusqu’aux températures inférieures et supérieures (Figure 2-4) à partir desquelles la performance de l'insecte diminue (Angilletta et al., 2002; Angilletta, 2006; Huey et al., 2012). Les températures causant la mortalité de l'insecte sont définies comme des températures extrêmes. Les courbes thermiques définissent la sensibilité thermique d'un ectotherme et peuvent être utilisées pour prédire la réponse des organismes aux changements climatiques, malgré le manque de connaissances des mécanismes sous-jacents de la température sur les ectothermes (Schulte et al., 2011).

2.2.1 / Effets biochimiques de la température

Enzymatique

Selon le modèle Boltzmann-Arrhenius, la vitesse des réactions chimiques se déroulant à l'intérieur du corps de l'insecte est proportionnelle à la température (Dell et al., 2011). Deux facteurs conditionnent essentiellement les réactions chimiques : la vitesse d'action des enzymes et le pourcentage de compaction des protéines (leur structure 3D). La conformation des enzymes et donc leur vitesse de liaison avec le substrat dépend de la température (Neven, 2000; Damos et Savopoulou-Soultani, 2012). Les changements dans la fluidité des membranes peuvent affecter l'activité des enzymes liées, mais aussi poser des problèmes au niveau de l'équilibre ionique des compartiments biologiques et du potentiel électrique (Neven, 2000). Un mécanisme semblable gouverne les protéines et les acides nucléiques : à température élevée, leur conformation 3D sera altérée (Neven, 2000).

Respiration et métabolisme

La respiration augmente avec la température jusqu'à atteindre un maximum, au-delà duquel elle diminue (Neven, 2000). Une limitation en oxygène pourrait amplifier les effets délétères des températures élevées (Neven, 2000; Verberk et Bilton, 2011) : l'oxygène est en effet nécessaire à la création d'ATP. Le métabolisme des lipides et des glucides, la synthèse des protéines et le maintien de l'intégrité de la membrane phospholipidiques par l'altération des acides gras nécessitent également de l'oxygène (Neven, 2000). Le système de livraison de l'oxygène pourrait ainsi fixer les limites thermiques, plutôt que les fonctions moléculaires (Pörtner, 2001; Pörtner, 2002).

La respiration est fréquemment utilisée pour mesurer le taux métabolique des organismes (Chown and Gaston, 1999). La taille et la température sont les plus grands prédicteurs du taux métabolique chez les ectothermes (Gillooly, 2001). Ce dernier augmente avec la température, jusqu'à atteindre un maximum au-delà duquel il décline (Schulte, 2015). Cet effet de déclin à hautes températures s'explique par la perte de stabilité des protéines. D'autres mécanismes pourraient préciser cette réponse métabolique à la température, dont la Théorie métabolique de l'écologie « *Metabolic Theory of Ecology* » (MTE) (Brown et al., 2004), l'hypothèse de limite thermique par la capacité de transport de l'oxygène (Portner, 2001; Verberk et Bilton, 2011; Schulte, 2015), ou encore les considérations bioénergétiques (Sokolova et al., 2012; Sokolova, 2013). Certains poïkilothermes peuvent cependant compenser les changements de température en modifiant leur métabolisme pour maintenir une certaine activité sur une large gamme thermique (Prosser et Nelson, 1981). D'après la MTE, le taux métabolique des individus dirige tous les aspects biologiques, écologiques et même écosystémiques (Brown et al., 2004). Selon certains auteurs, cette théorie représente une base conceptuelle à l'écologie. Elle permet d'expliquer plusieurs comportements qui varient en fonction de la température, par exemple la prédation (Vucic-Pestic et al., 2010; Sentis et al., 2012, 2013, 2014), le parasitisme (Wu et al., 2011; O'Connor et Bernhardt, 2018) ou la vitesse d'alimentation (Rall et al., 2012).

Système nerveux

L'effet de la température sur le système nerveux des insectes varie selon le type de nerfs, allant de « pas d'effet » jusqu'à une augmentation de l'activité (Kerkut et Taylor, 1958; Neven, 2000). Les mécanismes en jeu incluent le gain synaptique et les délais synaptiques et de conduction (Montgomery et Macdonald, 1990). La perturbation du système nerveux peut diminuer la capacité de l'insecte à percevoir la température, à intégrer les informations environnementales et à réagir de manière musculaire ou endocrine (Neven, 2000). Il existe cependant des mécanismes de compensation à la température permettant le fonctionnement comportemental à différents régimes de températures (Montgomery et Macdonald, 1990).

2.2.2 / Température et développement pré-imaginal

Une température élevée accélère les réactions chimiques, et donc la vitesse de développement des insectes. En dessous d'une certaine température aucun développement ne se produit. Le développement accélère lorsque la température augmente, puis diminue après avoir atteint un maximum (Davidson, 1944; Damos et Savopoulou-Soultani, 2012). Les effets de la température sur le développement des insectes ont été largement étudiés et modélisés (Taylor, 1981; Régnière et al., 2012) et sont fréquemment considérés dans l'évaluation des effets des changements climatiques sur les espèces et les communautés (Bale et al., 2002; Hance et al., 2007; Folguera et al., 2011).

Les températures basses (Pandey et Johnson, 2005) ou élevées (Lepage et al., 2012) expérimentées durant le développement diminuent la survie et la fécondité des différents stades et sexes (Wilkes, 1959; Colinet et al., 2006). Cependant, à température élevée, le développement se faisant plus rapidement, des effets bénéfiques peuvent se produire (Arendt, 1997). Par exemple, la mortalité liée à la prédation baisse, par réduction du temps passé à un stade plus sensible (Bale et al., 2002). L'exposition à des températures assez basses pour arrêter le développement (ex : 4°C) mène à une diminution de la valeur adaptative directe, plus tard dans le développement (Colinet et Boivin, 2011), ou à une diminution des capacités d'apprentissage (van Baaren et al., 2005, 2006) et de discrimination de l’hôte chez l'adulte (van Baaren et al., 2005; Jerbi-Elayed et al., 2015). A température élevée, un ectotherme se développe plus rapidement, mais l'individu grandira moins qu'un autre qui se serait développé à une température plus basse : ce phénomène correspond au *Temperature Size Rule*, ou TSR (Atkinson, 1994; Colinet et al., 2007). La taille étant positivement corrélée à la valeur adaptative chez les insectes, aussi bien chez les mâles que chez les femelles, mais surtout chez ces dernières (Charnov et al., 1981; Honěk, 1993), cet aspect pourrait se révéler critique dans le cadre des changements climatiques (Gardner et al., 2011; Tseng et al., 2018), mais nous manquons encore d'études à ce sujet (Teplitsky et Millien, 2014).

2.2.3 / Effet de la température sur la physiologie/métabolisme de l'adulte

Longévité

En conséquence des changements dans le taux métabolique, la longévité des individus varie en fonction de la température : à température élevée, les individus vivent moins longtemps, le métabolisme étant accéléré par les réactions chimiques se produisant plus rapidement à hautes températures (Miquel et al., 1976).

Fécondité/Fertilité

Les traits reproducteurs sont plus sensibles à la température que les autres traits du cycle de vie (Jørgensen et al., 2006; Keena, 2006; Zizzari et Ellers, 2011). Par exemple, la température expérimentée durant le développement d'un individu a des conséquences directes sur sa fertilité/fécondité (Ali et al., 1997) en diminuant la production des œufs et des spermatozoïdes (Walsh et al., 2019), et en modifiant la quantité et la composition des phéromones sexuelles émises (Roeser-Mueller et al., 2010). La température de développement peut également avoir des conséquences indirectes par le TSR (Colinet et al., 2007). Cependant, les expositions à des températures suboptimales au stade adulte affectent aussi la fécondité/fertilité des individus (Lecato et Pienkowski, 1972; Roux et al., 2010), en particulier les mâles (Sales et al., 2018). De plus, l'exposition de ces derniers à des températures suboptimales peut diminuer la préférence des femelles à leur égard (Zizzari et Ellers, 2011).

Mortalité

La mortalité peut résulter de l'exposition à de hautes ou basses températures, mais les mécanismes diffèrent. A haute température, la mort de l'individu résultera directement d'un choc thermique (Cloudsley-Thompson, 1962a), provoqué par l'accumulation de déchets que l'organisme ne métabolise pas assez rapidement (Kenneth, 1932) ou par perte d'eau (Beament, 1959; Barker, 1988; Sterling et al., 1990). La mortalité thermique varie d'un stade à l'autre, les stades immatures (Johnson et al., 2004; Greenberg et al., 2005), en particulier les œufs, étant généralement les plus sensibles à la mort thermique (Zhao et al., 2007; Lepage et al., 2012).

A basse température, le gel cause souvent la mort. On distingue à ce niveau deux types d'organismes : ceux qui le tolèrent et survivent à la formation de cristaux de glace dans leurs tissus *(freeze tolerant)*, et ceux qui ne le font pas *(freeze intolerant*) (Lee, 1989; Sinclair et al., 2003). Les seconds, pour des températures inférieures à zéro, modifient leur métabolisme pour que leurs tissus gèlent à une température plus basse : ce qui correspond au point de surfusion (*supercooling point*) (Renault et al., 2002). A cette fin, les individus diminuent la quantité d'eau dans leurs tissus, éliminent les agents formateurs de noyaux de glace et produisent des cryoprotecteurs et des antigels (Lee, 1989; Bale, 2002; Hance et al., 2007), et des noyaux de glace extra-cellulaires (Michaud et Denlinger, 2004). L'exposition à des températures supérieures au point de surfusion peut cependant causer la mort par l'épuisement des réserves énergétiques (Renault et al., 2002), les coûts physiologiques (Amice et al., 2008) ou l'accumulation des dégâts, selon la température et de la durée d'exposition (Hance et al., 2007). Les effets défavorables des températures extrêmes changent avec la durée d'exposition (Johnson et al., 2004) et la vitesse de diminution ou d'augmentation de la température (Yan et al., 2014).

2.2.4 / Adaptations

Acclimatation

L'acclimatation correspond à « *toute modification facultative d'un trait physiologique en réponse aux changements d'une variable environnementale. Les changements peuvent apparaître en réponse à l'environnement de développement ou aux modifications environnementales à long terme durant les derniers stades du cycle de vie de l'organisme. Ces réponses peuvent être bénéfiques, neutres ou négatives* » (Wilson and Franklin, 2002). Les conséquences de l'acclimatation sur le comportement et la performance de l'adulte varient selon le stade d'exposition (adulte ou immature) (Krstevska et Hoffmann, 1994; Scharf et al., 2015).

L'acclimatation permet d'atténuer les effets néfastes de l'exposition aux températures basses (Powell et Bale, 2005; Geister et Fischer, 2007; Marais et Chown, 2008; Lachenicht et al., 2010; Lessard et Boivin, 2013) et élevées (Ma et Ma, 2012; Kim et al., 2015). Par exemple, elle augmente le succès d'accouplement (Geister et Fischer, 2007) et la locomotion (Lachenicht et al., 2010; Cavieres et al., 2016) à des températures où la performance était, sans acclimatation, plus basse. L'acclimatation a cependant des coûts, sous forme d'une perte de valeur adaptative aux autres températures (Kristensen et al., 2008).

HSP : Heat shock protein

Lorsqu'exposés à des températures extrêmes, les insectes synthétisent des protéines de protection, appelées *Heat Shock Proteins* (HSP) (Feder et Hofmann, 1999; Lurie et Jang, 2007). Elles se caractérisent par leur masse moléculaire, les plus étudiées étant celles de 60 à 80 kDA, en particulier les HSP70 (Neven, 2000). Plusieurs HSP sont des molécules chaperonnes, qui aident au repliement des protéines lors de la maturation (la chaleur causant la formation de protéines mal formées) (Parsell et Lindquist, 1993; Neven, 2000; Bowler, 2005). Elles protègent ainsi l'organisme contre les effets délétères des températures extrêmes.

L'exposition de courte durée à des températures basses ou élevées, presque létales, s'appelle le choc thermique (*heat shock*). Il se caractérise par la production supplémentaire de HSP dans les cellules (Bowler, 2005). Ce mécanisme permet de compenser localement les effets des températures suboptimales (Sgrò et al., 2016). Ainsi, la survie des organismes augmente pour des températures supérieures à la température de choc thermique, mais cet effet entraîne des coûts, généralement relatifs à la longévité, l'efficacité d'exploitation des ressources (Scott et al., 1997) et la reproduction (Jørgensen et al., 2006; Cui et al., 2008; Roux et al., 2010; Zizzari et Ellers, 2011; Porcelli et al., 2017). Le choc froid (*cold shock*) peut, quant à lui, avoir des effets bénéfiques sur les capacités reproductrices (Shreve, 2004), mais induit également des coûts métaboliques (Hoffmann et Hewa-Kapuge, 2000).

L'endurcissement (*hardening*), également déclenché par l'exposition à des températures presque létales, n'induit pas forcément, à la différence du *heat shock*, la production de HSP par les cellules (Bowler, 2005). D'autres mécanismes qui augmentent la stabilité des protéines entrent en jeu, par exemple l'accumulation de solutés de faibles poids moléculaires et la modification du pH (Bowler, 2005). Le *cold hardening* résulte quant à lui de l'accumulation de cryoprotecteurs tels que le glycérol (Lee et al., 1987; Lee, 1989) ainsi que des changements dans la composition des acides gras phospholipidiques (Overgaard et al., 2005).

Thermorégulation comportementale

Les insectes utilisent plusieurs stratégies pour réguler leur température corporelle (Romanovsky, 2007), aussi bien de manière physiologique (Bicego et al., 2007) que comportementale (Stevenson, 1985a; Sunday et al., 2014). Ces stratégies pourraient compenser, dans certaines conditions, les effets des changements climatiques (Huey et Tewksbury, 2009).

Les insectes régulent leur température corporelle en se déplaçant dans l'environnement jusqu'à trouver la température correspondant au préférendum de fonctionnement (Dreisig, 1984). Ils détectent la température grâce à des sensilles thermosensibles situées sur les antennes et les pattes (Flores et Lazzari, 1996), et par la sensibilité aux infrarouges (Robertson et al., 1996). Ils évitent ainsi les températures suboptimales (Coutant, 1977; Wittenburg et Baumeister, 1999; Wang et al., 2008; Ma et Ma, 2012) ou dangereuses (Hadley, 1970), et se déplacent vers les zones thermiques préférées pour eux (Cloudsley-Thompson, 1962b; Wiktelius, 1987; Bach, 1993; Blanford et Thomas, 2000; Ahnesjö et Forsman, 2006; Dillon et al., 2009) ou leur progéniture (Roy et Thomas, 2003; Potter et al., 2009; Krämer et al., 2012). Cet évitement des conditions suboptimales résulte de comportements ortho-kinétiques (modification de la vitesse de mouvement) (Kivivuori et Lagerspetz, 1990) ou klino-kinétiques (modification du taux de rotation) (Lagerspetz, 2000; Luo et al., 2010).

Si cette méthode de thermorégulation se montre efficace pour les petits insectes (Dillon et al., 2009), les plus gros peuvent utiliser le comportement de *basking* (« lézarder » au soleil) (Stevenson, 1985b; Moriyama et Numata, 2019), ou encore changer leur posture et orientation de son corps par rapport au soleil (Harmon et Barton, 2013) pour augmenter leur température corporelle (Stevenson, 1985b). La couleur de l'insecte a une importance pour ces comportements, en affectant la quantité de chaleur transférée de l'environnement au corps (Willmer et Unwin, 1981; Umbers et al., 2013). Certaines espèces utilisent cette technique afin de contrôler les infections causées par des pathogènes et des parasites ; comportement appelé « fièvre comportementale » (Adamo, 1998; Karban, 1998; Elliot et al., 2002). A l'inverse, pour diminuer leur température corporelle, les insectes peuvent rechercher de l'ombre, (Dreisig, 1984; Moriyama et Numata, 2019), ou encore favoriser l'évaporation de l'eau à la surface de leur corps (Prange, 1996), dans un mécanisme proche de la transpiration chez les mammifères (Moriyama et Numata, 2019).

Une autre stratégie de thermorégulation possible consiste en l'activation des muscles de vol pour créer de la chaleur endogène, similaire au frissonnement chez les endothermes (Heinrich, 1974, 1995; Moriyama et Numata, 2019). Cela permet à certaines espèces d'augmenter la température de leur thorax jusqu'à 20°C par rapport à la température de l'environnement (Adams et Heath, 1964). Ce phénomène s'observe surtout chez les « gros » insectes (ex : papillons de nuit (Heath et Adams, 1967), bourdons, abeilles (Stone et Willmer, 1989), guêpes (Ghazoul et Willmer, 1994), coléoptères et cigales (Sanborn et al., 1995).

2.3 / Comportement – '*Twist and Shout*[3]'

« *Le comportement correspond aux réponses coordonnées (actions ou inactions) des organismes complets (individus ou groupes) à des stimuli internes et/ou externes, excluant les réponses plus facilement comprises comme des changements développementaux* » (Levitis et al., 2009). Changer son comportement constitue souvent la première réponse d'un animal à une perturbation (Tuomainen et Candolin, 2011; Wong et Candolin, 2015). Ces changements ne sont pas toujours adaptatifs (Tuomainen et Candolin, 2011) ou suffisants pour compenser les changements environnementaux (van Baaren et Candolin, 2018) et ils auront des conséquences positives ou négatives, selon les conditions et les espèces, sur la population, les interactions interspécifiques et les écosystèmes (Wong et Candolin, 2015). Nos connaissances sur les rétroactions entre comportements individuels et processus de population demeurent très limitées (Ives, 1995; Levin, 2000; Tenhumberg, 2004; Wong et Candolin, 2015). Si le comportement des insectes est étudié depuis des décennies (Matthews and Matthews, 2009), il fait l'objet depuis quelques années d'un intérêt recrudescent ; par exemple dans le cadre de la lutte biologique (Ramirez-Romero et al., 2012; Beltrà et al., 2014; Mills et Heimpel, 2018; Heimpel, 2019; Kruidhof et al., 2019), de la problématique des espèces invasives (Holway et Suarez, 1999) ou des changements climatiques et des atténuations potentielles (Huey et Tewksbury, 2009; Sih et al., 2011; Tuomainen et Candolin, 2011; Andrew et al., 2013b; Harmon et Barton, 2013; Sih, 2013; Sih et al., 2016).

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[3] The Beatles – *Please Please Me* (1963)

2.3.1 / Modèles d'optimalité

En écologie comportementale, la plupart des hypothèses reposent sur l'idée que les individus tendent à se comporter de manière optimale dans les conditions environnementales dans lesquelles ils ont évolué (Parker et Smith, 1990), la sélection naturelle ayant favorisé les individus les plus efficaces pour ces conditions. On s'attend donc à ce que, pour des températures optimales, l'insecte exprime des comportements qui maximisent sa valeur adaptative, soit la capacité d'un individu à propager ses gènes. Différents modèles théoriques dit d'optimalité permettent de tester des hypothèses relatives aux différents comportements exprimés par les insectes. Ainsi, la théorie de recherche optimale de ressources (*Optimal Foraging Theory* - OFT) stipule que l'effort de recherche d'un prédateur/parasitoïde devrait s'adapter à la répartition spatiale de son hôte (Stephens et Krebs, 1986). L'un des cas particuliers du OFT est le MVT, ou Théorème de la valeur marginale (*Marginal Value Theorem)* (Charnov, 1976), qui décrit le temps que devrait passer un parasitoïde ou prédateur à exploiter un agrégat de ressources, selon la qualité de l'agrégat et la durée de transit entre les agrégats. La compétition locale pour l'accouplement, *Local Mate Competition* (LMC) (Hamilton, 1967) prédit que les femelles gagnent à déposer plus de fils en présence de femelles compétitrices, car ses fils s'accoupleront avec les filles de ses compétitrices et propageront ainsi ses gènes à la génération suivante. D'après tous ces modèles théoriques, afin d'agir de manière optimale, les individus doivent prendre des décisions en relation avec leur connaissance de l'environnement et leur capacité à recueillir des informations sur cet environnement (van Alphen et al., 2003).

La notion de comportement « optimal » et les théories qui en découlent restent discutables (Pierce et Ollason, 1987), entre autres les postulats sur lesquels elles se basent (Pyke, 1984). Malgré tout, l'étude du comportement des insectes demeure souvent conditionnée par cette notion d'optimalité. Or, comme vu précédemment, les conditions environnementales telles que la température affectent la physiologie de l'insecte, créant des contraintes métaboliques avec lesquelles il doit fonctionner. Dans ces conditions suboptimales, les comportements des insectes, leur adaptabilité potentielle, ainsi que les mécanismes sous-jacents restent méconnus.

2.3.2 / Comportement et température

Gamme thermique du comportement

Les comportements sont considérés « optimaux » dans une certaine gamme thermique, et suboptimaux en deçà ou au-delà (Huey et Stevenson, 1979; Huey et al., 2012) (Figure 2-3.a; Figure 2-4). En dessous de cette gamme, pour les températures infra-optimales, la fréquence et/ou l'intensité du comportement diminue graduellement avec la température jusqu'à atteindre une fréquence nulle, avant l'entrée en psychrotorpeur (*Cold stupor*). Pour les températures supra-optimales, la fréquence ou l'intensité du comportement augmente graduellement avec les températures jusqu'à l'atteinte d'un maximum à partir duquel la fréquence ou l'intensité chute brusquement, jusqu'à atteindre une valeur nulle, avant la thermotorpeur (*Heat stupor*) (Vannier, 1994). La gamme de températures optimales et les seuils inférieurs et supérieurs à partir desquels les comportements cessent varient d'une espèce à l'autre et d'un comportement à l'autre (Heath et al., 1971; Moriyama et Numata, 2019) (Figure 2-5). Les seuils thermiques des comportements diffèrent parfois entre les sexes (Heath, 1967). Les comportements liés à la reproduction ont généralement des gammes thermiques réduites par rapport aux autres comportements, qui ont eux-mêmes des gammes réduites comparées au fonctionnement physiologique de l'individu (Moriyama et Numata, 2019) (Figure 2-5).

Comportements affectés par la température

La température ambiante affecte la plupart des comportements d'un insecte, dont la marche (Rott et Ponsonby, 2000; Abram et al., 2015; Moiroux et al., 2016) et le vol (Caprio et Grafius, 1990; Ishiguri et Shirai, 2004). Ces modifications dans le déplacement influencent directement les comportements de recherche (Biever, 1972; Arnett et Gotelli, 2001; Kroder et al., 2007) et d'exploitation de l'hôte. L'altération de la ponte (Ables et Shepard, 1976), du taux de parasitisme (Zilahi-Balogh et al., 2006) et de prédation (Sentis et al., 2012; 2013), ainsi que des capacités de défense des proies (Le Lann et al., 2014), influencent d'autant plus ce dernier. La température modifie également la réponse fonctionnelle (Englund et al., 2011; Sentis et al., 2012, 2013). Des comportements plus complexes, tels que l'accouplement, impliquant une certaine communication entre les individus, sont également altérés (Cook, 1994; Katsuki et Miyatake, 2009). Finalement, la température perturbe les interactions entre les niveaux d'un réseau trophique, en modifiant le comportement de ces composantes (Rothley et Dutton, 2006). En plus des effets directs sur le comportement, la température a des effets indirects, en affectant d'autres aspects du fonctionnement de l'insecte, par exemple la capacité de reconnaissance des indices chimiques. Ainsi, l'anesthésie par le froid diminue la capacité de discrimination de certaines espèces de fourmis (Tanner, 2009), et les insectes stockés au froid durant leur développement émergent avec des capacités réduites d'apprentissage et de reconnaissance des indices chimiques (van Baaren et al., 2005; 2006).

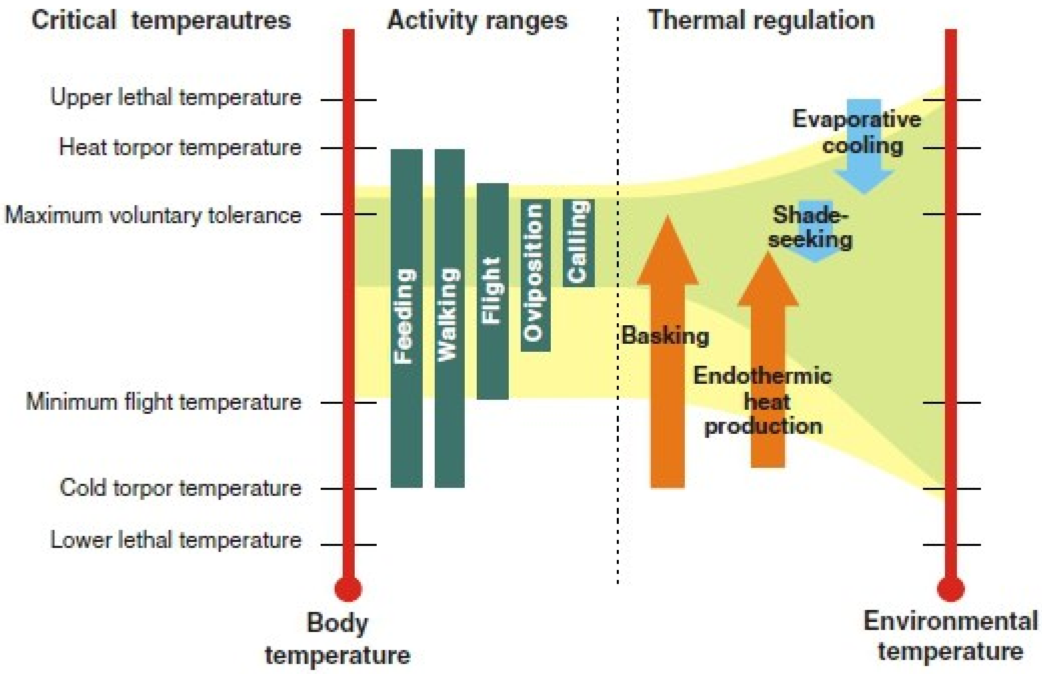

Figure 2-5: Illustration schématique de la physiologie thermique des cigales adultes. Chaque activité est effectuée dans une gamme limitée de température corporelle (barres vertes), entre les températures létales limites. (Moriyama and Numata, 2019).

2.3.3 / Comportement vs physiologie

Les insectes, les hyménoptères en particulier, se révèlent capables de tâches cognitives assez complexes, telles que l'apprentissage (Hollis et al., 2015) et la mémoire (de Bruijn et al., 2018), la stratégie de minimisation des risques (*bet-hedging*) (Hopper, 1999; Starrfelt et Kokko, 2012) et la mesure d'intervalle de temps (Parent et al., 2016, 2017). Les bases neurologiques du comportement des insectes, en particulier la prise de décision, commencent à être étudiées (Barron et al., 2015). Malgré ces avancées, la distinction entre les réactions physiologiques et comportementales reste encore difficile.

Abram et al. (2017) ont défini deux voies mutuellement non-exclusives par lesquelles la température peut affecter le comportement des ectothermes. Premièrement, les effets *bottom-up*, pour lesquels les réactions biochimiques influencent directement les comportements à travers le taux métabolique, ce que les auteurs appellent la “réponse kinétique”. Deuxièmement, les effets *top-down*, résultent de l'intégration de l'information thermique par le système nerveux central qui va définir le comportement qui s'ensuit, soit “la réponse intégrée” (Figure 2-6). La distinction entre ces deux voies demeure complexe. Pour les dissocier, les auteurs suggèrent la création d'un modèle kinétique “nul”, c’est-à-dire de déterminer comment un individu se comporterait s'il n'était soumis qu'aux effets *bottom-up*. Le comportement suivrait par exemple la réponse physiologique (Huey et Stevenson, 1979), les individus démontrant un comportement optimal seulement pour une certaine gamme de températures. On observe typiquement cet effet chez les insectes pour la vitesse de marche par exemple (Dillon et Frazier, 2006; Lachenicht et al., 2010). Dans le cas d'une réponse intégrée, ne pouvant s'expliquer par ce mécanisme biochimique, le comportement ne suivrait pas la courbe physiologique de performance, avec trois alternatives : (1) le maintien de l'efficacité du comportement malgré des conditions suboptimales (Pigliucci, 2006), (2) des comportements de thermorégulation (Bicego et al., 2007; Hückesfeld et al., 2011), et (3) la conservation de l'énergie (Sokolova et al., 2012). Abram et al., (2017) proposent également l'utilisation de mutants insensibles à la température pour distinguer les réponses kinétiques des réponses intégrées. Cette approche a par exemple permis de montrer que le mouvement de drosophiles suivait une réponse intégrée à la température plutôt que kinétique (Soto-Padilla et al., 2018).

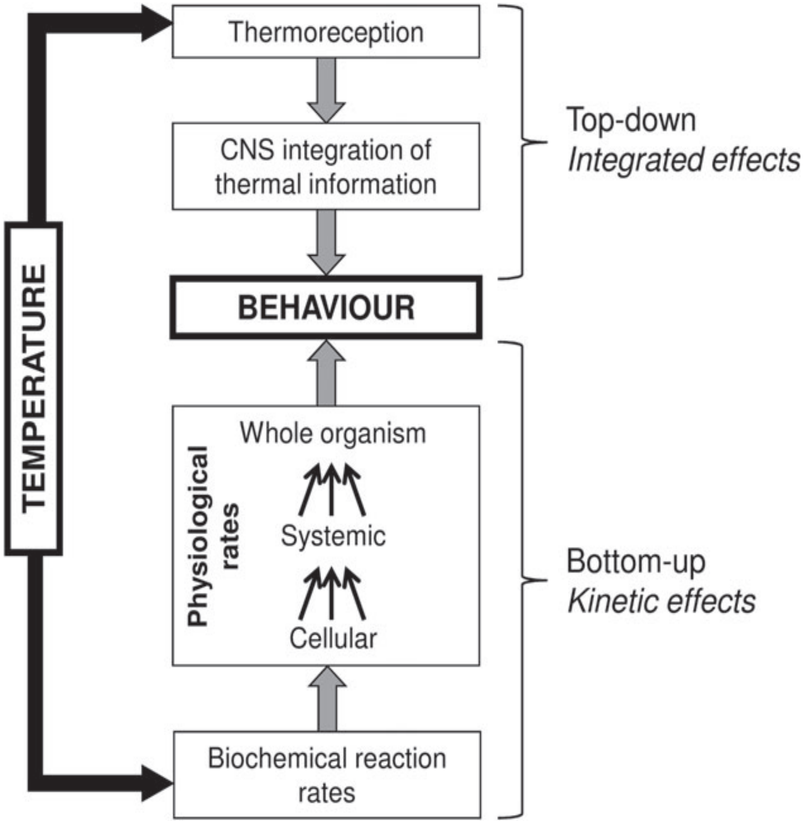

Figure 2-6: Effets kinétiques et intégrés de la température sur le comportement d'un ectotherme. Les effets kinétiques (« *bottom-up »)* résultent ultimement des changements dans les taux de réactions biochimiques, qui s'intensifient avec les multiples processus physiologiques cellulaires et systémiques pour influencer les processus à l'échelle de l'organisme (le comportement). Les effets intégrés (« *top-down* ») résultent de la thermo-réception et l'intégration de l'information thermique par le système nerveux central (SNC) qui module ensuite les produits comportementaux. Les effets kinétiques et intégrés agissent de concert pour déterminer le phénotype comportemental d'un animal. Traduction de la légende de Abram et al. (2017).

Ces définitions permettent de distinguer les réponses comportementales qui découlent uniquement de la physiologie de celles dites « intégrées ». Cependant, le fait de savoir si une réponse découle d'un mécanisme kinétique ou intégré ne renseigne pas sur son potentiel adaptatif. On distingue donc les réactions contraintes (kinétiques ou intégrées), qui empêchent l'individu de réaliser son plein potentiel, et les réactions adaptatives, qui permettent à l'individu de maintenir ou d'augmenter sa valeur adaptative selon les conditions environnementales. Expérimentalement, distinguer entre ces deux options s'avère tout aussi complexe. Certaines hypothèses appuient cependant l'idée que les organismes maintiennent certaines capacités lorsque la température change. Ainsi, d'après l'hypothèse de couplage des températures : *Temperature Coupling Hypothesis* (TCH), les signaux envoyés par les émetteurs et reconnus par les récepteurs d'un message varient en parallèle avec la température afin de maintenir le même niveau de communication entre les deux participants sur une certaine gamme thermique (Doherty, 1985). De même, chez certaines espèces, les femelles ajustent leur comportement de ponte en fonction de la température pour maximiser leur valeur adaptative ou celle de leur descendance (Mousseau et Fox, 1998). Dans le cas de l'allocation des sexes, Moiroux et al. (2014) ont montré que les températures basses et élevées provoquaient toutes deux une augmentation du sex ratio de la descendance déposée par les femelles parasitoïdes, mais que dans le premier cas, la réponse était adaptative, alors que dans le second elle résultait d'une contrainte.

2.4 / Modélisation – 'Welcome to the machine[4]'

2.4.1 / Principe général

La modélisation constitue une représentation mathématique simplifiée de la réalité. Elle permet de tester des hypothèses, de réaliser des simulations, et peut servir d'outils d'aide à la décision. De nombreux modèles ont été développés dans le but de prédire les dates d'apparition des insectes et l'importance des populations. Ils se basent généralement sur la phénologie et les calculs d'unités thermiques (ex : degrés-jours) (Pruess, 1983; Logan, 1988; Satake et al., 2006), et permettent de prédire la phénologie des espèces dans le temps et l'espace, et ainsi la mise en place des stratégies adaptées de lutte contre les ravageurs (Damos et Savopoulou-Soultani, 2012). Dans le cadre d'études sur les changements climatiques, on utilise les modèles pour prédire la distribution géographique de certaines espèces (Araújo et Luoto, 2007), ainsi que les facteurs météorologiques influençant le plus cette distribution (ex : Gevrey et Worner, 2006). L'un des facteurs les plus important reste la température, qui affecte directement le cycle de vie, la phénologie et la distribution des arthropodes (Bale et al., 2002). Les modèles basés

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[4] Pink Floyd – *Wish you were here* (1975)

sur la température, qui utilisent les données de développement et de physiologie telles que la reproduction et le taux de survie, ou la tolérance physiologique tels que les CT_{min} et CT_{max}, sont largement utilisés pour prédire la phénologie (Satake et al., 2006; Nietschke et al., 2007; Régnière et al., 2012) et la distribution des populations d'insectes (Addo-Bediako et al., 2000; Jeschke and Strayer, 2008; Keith et al., 2008; Kearney et al., 2009a; Kearney and Porter, 2009; Woodin et al., 2013).

La plupart des modèles considèrent pourtant peu (voire pas du tout) les réponses comportementales des insectes, immatures ou adultes, à la température. Or, ces réponses sont nombreuses et variées et pourraient conduire à des modifications importantes au niveau des effectifs des populations (Tenhumberg et al., 2004). Bien que depuis quelques années, un intérêt se manifeste pour les effets des facteurs abiotiques sur le comportement des organismes concernés, par exemple dans le cadre de la lutte biologique (Traniello et al., 1984; Villani et Wright, 1990; Wang et al., 2004; Rothley et Dutton, 2006; Mills et Kean, 2010; Sentis et al., 2015), dans le contexte des changements climatiques, peu de modèles de simulation incluent le comportement ou les interactions entre espèces (Araújo et Luoto, 2007). Ces omissions pourraient résulter en des prédictions erronées de la réponse des espèces aux changements climatiques (Araújo et Luoto, 2007). Les comportements pourraient en effet être décisifs dans l'adaptation (Huey and Tewksbury, 2009; Kearney et al., 2009b; Sih et al., 2011; Tuomainen and Candolin, 2011; Andrew et al., 2013; Sih, 2013; Sih et al., 2016) et les interactions entre espèces (Davis et al., 1998; Jiang and Morin, 2004; Van der Putten et al., 2010; Harmon and Barton, 2013). Par conséquent, il devient crucial de créer rapidement des liens entre l'écologie comportementale et la dynamique des populations (Ives, 1995; Levin, 2000; Vet, 2001; Tenhumberg, 2004; Knowlton and Graham, 2010; Wong and Candolin, 2015).

2.4.2 / Modèles de population basés sur les processus : *Process-oriented population models*

Les modèles de population basés sur les processus permettent d'inclure les mécanismes physiologiques et comportementaux dans les modèles de dynamique des populations (Stimac, 1982; Bolliger et al., 2005; Hayes et al., 2009). Ils se basent sur la représentation des différents « états » d'un objet selon une séquence temporelle définie. Des « événements » font passer ces objets d'un état au suivant. Ce type de modélisation permet de décrire le cycle de vie des insectes, les différents stades phénologiques mais aussi et surtout leurs comportements. On retrouve par exemple ce type de modèle en écologie et en agriculture afin de modéliser les cycles de vie (Shaffer et Gold, 1985; Graf et al., 2002; Satake et al., 2006). Les « états » de l'objet dans ce cas correspondent aux stades phénologiques de l'espèce, et les « événements » aux processus physiologiques ou comportements qui régissent le passage d'un stade au suivant. L'une des problématiques liées à l'utilisation de ce type de modèle reste le manque de variabilité entre les individus : tous les individus du même âge se comportent de manière identique. Si l'on désire tenir compte de la variabilité inter-individuelle, il est possible de conceptualiser le modèle à l'échelle des individus plutôt qu'à l'échelle de la population complète ou de cohortes du même âge. On parle dans ce cas de modèle basés sur l'individu (*Individual-Based Model* ou *Agent-Based Model*) (Huston et al., 1988; DeAngelis and Mooij, 2005; Grimm et al., 2006).

2.4.3 / Modèles basés sur l'individu : *Individual-Based Models*

Les modèles basés sur l'individu : *Individual Based Models* (IBM) se développent depuis plusieurs années (Huston et al., 1988; DeAngelis et Mooij, 2005; Grimm et al., 2006). Ils simulent les populations composées d'individus ou de groupes d'individus similaires, dont les jeux de traits varient entre les individus (DeAngelis et Mooij, 2005). Les IBM se basent sur l'idée que les individus suivent plusieurs règles de base, desquelles peuvent émerger des effets à plus grande échelle dans le système (Huston et al., 1988). Ce type de modèle se montre utile en présence de complexité comportementale et de petites populations (Judson, 1994; DeAngelis et Mooij, 2005). Les IBM sont largement utilisés en écologie et dans d'autres disciplines (Grimm et al., 2006). Ils permettent l'inclusion de variabilité entre les individus et dans leurs interactions avec l'environnement (Huston et al., 1988; Judson, 1994; Grimm et al., 2006).

2.4.4 / Modèles dynamiques

Lorsque les modèles incluent une composante temporelle, ils sont appelés modèles dynamiques. Ils calculent les variables du système au temps t en se basant sur l'état du système au temps t-1 (Hannon and Ruth, 2009). Des exemples d'utilisation de modèles dynamiques basés sur l'individu incluent la prédiction du niveau de contrôle en serre par les parasitoïdes (van Roermund et al., 1997), ou encore les flux de nutriments et les rendements en biomasse pour une ferme de moules (Brigolin et al., 2009). Un modèle dynamique orienté vers les processus et basé sur l'individu permettrait ainsi de simuler une population d'insectes au cours du temps (dynamique) en tenant compte de la variabilité entre les individus (basé sur l'individu) et des processus physiologiques et comportementaux régissant leur passage d'un stade au suivant (orienté vers les processus). Un tel modèle admet ainsi l'inclusion des effets de la température sur les différents processus, et permet d'en mesurer les impacts sur la population finale.

2.5 / Modèles biologiques – '*Who are the mystery girls?*[5]'

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[5] The New York Dolls – *Too much too soon* (1974)

2.5.1 / *Listronotus oregonensis*

Le charançon de la carotte *Listronotus oregonensis* (LeConte) (Coleoptera : Curculionidae) est un coléoptère ravageur natif d'Amérique du Nord. On le détecte pour la première fois en 1967 au Québec où il peut causer jusqu'à 35% de dommages dans les champs de carotte (Perron, 1971). Plus récemment, en Ontario, les dommages sont d'environ 5% dans les parcelles commerciales et atteignent 23.4% dans les parcelles non traitées (Telfer et al., 2019), le seuil économique étant de 2% (Stevenson et Barscsz, 1997). Les adultes émergent au printemps, se nourrissent sur les pétioles et les feuilles de la carotte, et pondent leurs œufs dans le pétiole et le calice à partir du stade 4 feuilles (Boivin, 1988). Les larves de premier et second stades se retrouvent dans le feuillage, puis, en vieillissant, descendent dans la racine de la carotte (Collins et Grafius, 1986a). Les larves de dernier stade sortent de la racine de la carotte pour former leur pupe dans le sol à une profondeur d'environ 7 cm (Justus et Long, 2019). Les adultes émergent ensuite et, si la saison le permet, débutent la ponte de la génération suivante (Figure 2-7). Une seconde génération s'observe depuis quelques années au Québec (Boivin, 1999) et commence à poser des problèmes économiques (Mason et Gillespie, 2013).

Le développement chez le charançon de la carotte est possible au moins de 18,3°C (47,8 jours) à 32,3°C (27,2 jours) (Simonet et Davenport, 1981; Stevenson, 1986). À température plus basse, les œufs éclosent, mais les larves ne complètent pas toujours leur développement. La température la plus basse à laquelle les individus deviennent actifs après la sortie de diapause hivernale est 3,43°C (Rhéaume, 2009). Les conditions thermiques affectent la ponte des femelles de façon similaire au développement : ces dernières ne déposent des œufs qu'entre 18,3°C et 32,3°C, avec un maximum à 29,4°C (Simonet et Davenport, 1981). Une interaction entre la température et la photopériode régule également l'activité de ponte : afin de déclencher un même taux de ponte, la température doit être d'autant plus élevée que la photopériode est courte (Stevenson et Boivin, 1990). Les dommages économiques sont causés principalement par les larves qui creusent des galeries dans la racine des carottes, ce qui provoque la mort de la plante ou des dégâts suffisant pour la rendre invendable (Justus et Long, 2019). Différents moyens de lutte existent pour contrôler le charançon de la carotte (Boivin, 1999; Justus et Long, 2019). Le principal reste l'utilisation de pesticides (Martel et al., 1975; Pree et al., 1996; Bonham et al., 2009) malgré une efficacité limitée (Telfer et al., 2018). Des méthodes culturales peuvent également être employées (Rekika et al., 2008) ou encore la lutte biologique incluant *Bacillus thuringiensis* (Saadé et al., 1996), les nématodes (Boivin et Bélair, 1989; Bélair et Boivin, 1995; Miklasiewicz et al., 2002; Gagnon et al., 2019), les carabes prédateurs (Baines et al., 1990; Zhao et al., 1990; Lemay et al., 2018) et les guêpes parasitoïdes telles que *Microctonus hyperodae* (Cournoyer et Boivin, 2004, 2005a). Les hyménoptères parasitoïdes du genre *Anaphes* (Hymenoptera : Mymaridae) demeurent cependant l'ennemi naturel le plus efficace contre le charançon de la carotte (Boivin, 1999).

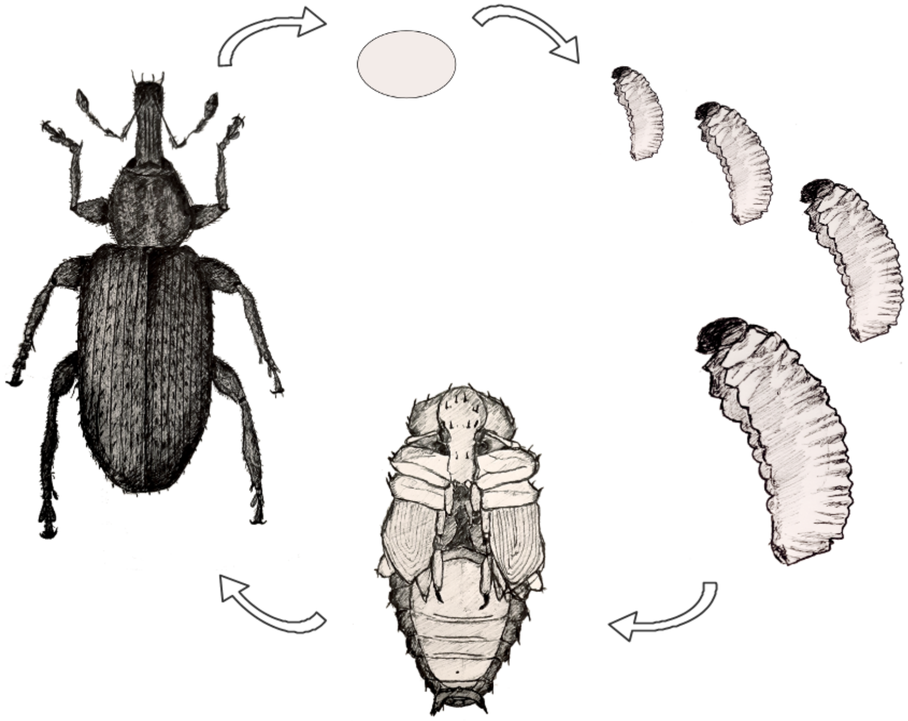


Figure 2-7 : Cycle du charançon de la carotte. Dessins de larves à partir de la photo de Justus et Long (2018), pupe et adulte à partir des dessins de Boyce (1927).

2.5.2 / *Anaphes listronoti*

Anaphes listronoti Huber (Hymenoptera : Mymaridae) est une guêpe parasitoïde des œufs du charançon de la carotte, décrite par Huber (Huber, 1992; Huber et al., 1997), présente en Amérique du Nord (Boivin, 1986). Son seul autre hôte connu appartient également au genre *Listronotus* : *Listronotus sparsus* (Say) (Huber et al., 1997). *Anaphes listronoti* et l'espèce morphologiquement (Huber et al., 1997) et génétiquement proche (Landry et al., 1993) *A. victus* représentent le principal facteur de mortalité biotique du charançon de la carotte (Zhao et al., 1991; Boivin, 1993). Dans les champs traités en Ontario, ces deux espèces parasitent 33% des œufs du charançon de la carotte, contre 68 à 94% de parasitisme dans les champs non traités (Cormier et al., 1996). Au Québec, environ 23% des œufs de charançon de la carotte échantillonnés se trouvent parasités (Collins et Grafius, 1986a).

Anaphes listronoti est une espèce grégaire facultative : les femelles déposent 1 à 6 œufs dans un même hôte (Collins et Grafius, 1986b), mais vivent ensuite de manière solitaire. Ce mode de vie affecte le potentiel reproducteur des mâles et des femelles à travers la diminution de leur taille, lorsque plusieurs frères et sœurs partagent le même hôte. Ceci a pour conséquence la diminution du nombre de gamètes disponibles chez les deux sexes (Boivin et Martel, 2012) et une longévité réduite (Collins et Grafius, 1986b). Comme pour de nombreux hyménoptères parasitoïdes, les mâles émergent plus tôt et attendent l'émergence des femelles sur l'agrégat d'hôtes (Landry et al., 1993). Dès leur émergence, les femelles émettent des phéromones à longue distance pour attirer les mâles (Cormier et al., 1998).

Dans un contexte de changements climatiques, plusieurs facteurs pourraient affecter négativement le cycle de vie et les populations d'*A. listronoti,* en termes de recherche et d'exploitation de l'hôte, ou encore d'accouplement. Ainsi, chez l'espèce sœur *A. victus,* les femelles ont la capacité de reconnaître des kairomones déposées par leur hôte. Elles sont attirées par les odeurs de la matière utilisée pour fermer les trous de ponte contenant les œufs (*egg plug*) et des fèces de leurs hôtes (Cournoyer et Boivin, 2005b). Les femelles *A. victus* apprennent à associer des indices chimiques externes sur l'hôte avec la présence d'un œuf déposé par une femelle conspécifique à l'intérieur de cet hôte (van Baaren et Boivin, 1998). Plus rare au sein des parasitoïdes, les femelles *A. victus* ont la capacité de discriminer entre des hôtes parasités par des individus de leur propre espèce (discrimination intraspécifique) et ceux parasités par des individus de *A. listronoti* (discrimination interspécifique) (van Baaren et al., 1994). Ces capacités de détection et de reconnaissance des indices chimiques de la présence de l'hôte pourraient se trouver affectées à des températures suboptimales, la quantité et qualité des indices chimiques émis et détectés variant avec la température chez les insectes (Sentis et al., 2015). De même, l'exposition à différentes températures affecte les capacités d'apprentissage et d'exploitation de l'agrégat des femelles (van Baaren et al., 2005; 2006). Le contrôle exercé par *A. listronoti* sur le charançon de la carotte pourrait ainsi diminuer. La durée de développement et la longévité des parasitoïdes diminuent lorsque la température augmente ; chez *A. victus*, le développement est possible entre 11,5 (36,8 jours) et 34°C (11,4 jours), avec une durée minimale de 7,9 jours à 32°C (Traoré et al., 2006). La longévité d'*A. listronoti* varie selon la température : les individus vivent environ 10 jours à 17°C, contre seulement 3 à 4 jours à 29°C (Collins et Grafius, 1986b).

2.6 / Références

Ables, J.R., et Shepard, M. (1976). Influence of temperature on oviposition by the parasites *Spalangia endius* and *Muscidifurax raptor*. Environ. Entomol. 5, 511-513.

Abram, P.K., Cusumano, A., Peri, E., Brodeur, J., Boivin, G., et Colazza, S. (2015). Thermal stress affects patch time allocation by preventing forgetting in a parasitoid wasp. Behav. Ecol. 26, 1326-1334.

Abram, P.K., Boivin, G., Moiroux, J., et Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biol. Rev. 92, 1859-1876.

Adamo, S.A. (1998). The specificity of behavioral fever in the cricket *Acheta domesticus*. J. Parasitol. 84, 529-533.

Adams, P.A., et Heath, J.E. (1964). Temperature regulation in the sphinx moth, *Celerio lineata*. Nature 201, 20-22.

Addo-Bediako, A., Chown, S.L., et Gaston, K.J. (2000). Thermal tolerance, climatic variability and latitude. Proc. R. Soc. Lond. B Biol. Sci. *267*, 739–745.

Agosta, S.J., Joshi, K.A., et Kester, K.M. (2018). Upper thermal limits differ among and within component species in a tritrophic host-parasitoid-hyperparasitoid system. PLoS one 13.

Aguilar-Fenollosa, E., et Jacas, J.A. (2014). Can we forecast the effects of climate change on entomophagous biological control agents? Pest Manag. Sci. 70, 853-859.

Ahnesjö, J., et Forsman, A. (2006). Differential habitat selection by pygmy grasshopper color morphs: Interactive effects of temperature and predator avoidance. Evol. Ecol. 20, 235-257.

Ali, M.F., Abdel-Reheem, E.F.M., et Abdel-Rahman, H.A. (1997). Effect of temperature extremes on the survival and biology of the carpet beetle, *Attagenus fasciatus* (Thunberg) (Coleoptera: Dermestidae). J. Stored Prod. Res. 33, 147-156.

Allen, J.L., Clusella-Trullas, S., et Chown, S.L. (2012). The effects of acclimation and rates of temperature change on critical thermal limits in *Tenebrio molitor* (Tenebrionidae) and *Cyrtobagous salviniae* (Curculionidae). J. Insect Physiol. 58, 669-678.

van Alphen, J.J.M., Bernstein, C., et Driessen, G. (2003). Information acquisition and time allocation in insect parasitoids. Trends Ecol. Evol. 18, 81-87.

Amice, G., Vernon, P., Outreman, Y., Van Alphen, J., et Van Baaren, J. (2008). Variability in responses to thermal stress in parasitoids. Ecol. Entomol. 33, 701-708.

Andrew, N.R., Hart, R.A., Jung, M.-P., Hemmings, Z., et Terblanche, J.S. (2013). Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. J. Insect Physiol. *59*, 870–880.

Andrew, N.R., Hill, S.J., Binns, M., Bahar, M.H., Ridley, E.V., Jung, M.-P., Fyfe, C., Yates, M., et Khusro, M. (2013b). Assessing insect responses to climate change: What are we testing for? Where should we be heading? PeerJ 1, e11.

Angilletta, M.J. (2006). Estimating and comparing thermal performance curves. J. Therm. Biol. 31, 541-545.

Angilletta, M.J., Niewiarowski, P.H., et Navas, C.A. (2002). The evolution of thermal physiology in ectotherms. J. Therm. Biol. 27, 249-268.

Araújo, M.B., et Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. Glob. Ecol. Biogeogr. 16, 743-753.

Arendt, J.D. (1997). Adaptive intrinsic growth rates: an integration across taxa. Q. Rev. Biol. 72, 149-177.

Arnett, A.E., et Gotelli, N.J. (2001). Pit-building decisions of larval ant lions: effects of larval age, temperature, food, and population source. J. Insect Behav. 14, 89-97.

Arrhenius, S. (1896). XXXI. On the influence of carbonic acid in the air upon the temperature of the ground. Lond. Edinb. Dubl. Phil. Mag., 41, 237-276.

Atkinson, D. (1994). Temperature and organism size—A biological law for ectotherms? In Advances in Ecological Research, (Elsevier), pp. 1-58.

van Baaren, J., et Boivin, G. (1998). Learning affects host discrimination behavior in a parasitoid wasp. Behav. Ecol. Sociobiol. 42, 9-16.

van Baaren, J., et Candolin, U. (2018). Plasticity in a changing world: behavioural responses to human perturbations. Curr. Opin. Insect Sci. 27, 21-25.

van Baaren, J., Boivin, G., et Nénon, J.-P. (1994). Intra-and interspecific host discrimination in two closely related egg parasitoids. Oecologia 100, 325-330.

van Baaren, J., Outreman, Y., et Boivin, G. (2005). Effect of low temperature exposure on oviposition behaviour and patch exploitation strategy in parasitic wasps. Anim. Behav. 70, 153-163.

van Baaren, J., Boivin, G., et Outreman, Y. (2006). Deleterious effects of low temperature exposure on learning expression in a parasitoid. Int. J. Comp. Psychol. 19.

Bach, C.E. (1993). Effects of microclimate and plant characteristics on the distribution of a willow flea beetle, *Altica subplicata*. Am. Midl. Nat. 130, 193-208.

Baines, D., Stewart, R., et Boivin, G. (1990). Consumption of carrot weevil (Coleoptera: Curculionidae) by five species of carabids (Coleoptera: Carabidae) abundant in carrot fields in southwestern Quebec. Environ. Entomol. 19, 1146-1149.

Bale, J.S. (2002). Insects and low temperatures: from molecular biology to distributions and abundance. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 357, 849-862.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., et al. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Change Biol. 8, 1-16.

Barker, G.M. (1988). Effect of temperature on development and survival of Argentine stem weevil (*Listronotus bonariensis*) immature stages. N. Z. J. Zool. 15, 387-390.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., et al. (2011). Has the Earth's sixth mass extinction already arrived? Nature 471, 51-57.

Barron, A.B., Gurney, K.N., Meah, L.F.S., Vasilaki, E., et Marshall, J.A.R. (2015). Decision-making and action selection in insects: inspiration from vertebrate-based theories. Front. Behav. Neurosci. 9.

Beament, J.W.L. (1959). The waterproofing mechanism of arthropods: I. The effect of temperature on cuticle permeability in terrestrial insects and ticks. J. Exp. Biol. 36, 391-422.

Bélair, G., et Boivin, G. (1995). Evaluation of *Steinernema carpocapsae* Weiser for control of carrot weevil adults, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae), in organically grown carrots. Biocontrol Sci. Technol. 5, 225-232.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., et Courchamp, F. (2012). Impacts of climate change on the future of biodiversity: Biodiversity and climate change. Ecol. Lett. 15, 365-377.

Beltrà, A., Pekas, A., Soto, A., et Tena, A. (2014). Employing evolutionary theory to improve biological pest control: Causes of non-adaptive sex allocation behavior in parasitoid wasps and implications. Basic Appl. Ecol. 15, 625-632.

Berg, M.P., Kiers, E.T., Driessen, G., van der Heijden, M., Kooi, B.W., Kuenen, F., Liefting, M., Verhoef, H.A., et Ellers, J. (2010). Adapt or disperse: understanding species persistence in a changing world. Glob. Change Biol. 16, 587-598.

Bicego, K.C., Barros, R.C.H., et Branco, L.G.S. (2007). Physiology of temperature regulation: Comparative aspects. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 147, 616-639.

Biever, K.D. (1972). Effect of temperatures on the rate of search by Trichogramma and its potential application in field releases. Environ. Entomol. 1, 194-197.

Blanford, S., et Thomas, M.B. (2000). Thermal behavior of two acridid species: effects of habitat and season on body temperature and the potential impact on biocontrol with pathogens. Environ. Entomol. 29, 1060-1069.

Boivin, G. (1986). *Anaphes sordidatus* (Girault) (Hymenoptera: Mymaridae), an egg parasite of the carrot weevil, *Listronotus oregonensis* (Le Conte). Can. Entomol. 118, 393-394.

Boivin, G. (1988). Effect of carrot developmental stages on feeding and oviposition of carrot weevil, *Listronotus oregonensis* (Le Conte) (Coleoptera: Curculionidae). Environ. Entomol. 17, 330-336

Boivin, G. (1993). Density dependence of *Anaphes sordidatus* (Hymenoptera: Mymaridae) parasitism on eggs of *Listronotus oregonensis* (Coleoptera: Curculionidae). Oecologia 93, 73-79.

Boivin, G. (1999). Integrated management for carrot weevil. Integr. Pest Manag. Rev. 4, 21-37.

Boivin, G., et Belair, G. (1989). Infectivity of two strains of *Steinernema feltiae* (Rhabditida: Steinernematidae) in relation to temperature, age, and sex of carrot weevil (Coleoptera: Curculionidae) adults. J. Econ. Entomol. 82, 762-765.

Boivin, G., et Martel, V. (2012). Size-induced reproductive constraints in an egg parasitoid. J. Insect Physiol. 58, 1694-1700.

Bolliger, J., Lischke, H., et Green, D. G. (2005). Simulating the spatial and temporal dynamics of landscapes using generic and complex models. Ecol. Complex. *2*, 107-116

Bonebrake, T.C., et Deutsch, C.A. (2012). Climate heterogeneity modulates impact of warming on tropical insects. Ecology 93, 449-455.

Bonebrake, T.C., et Mastrandrea, M.D. (2010). Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. Proc. Natl. Acad. Sci. 107, 12581-12586.

Bonham, M., Ghidiu, G.M., Hitchner, E., et Rossell, E.L. (2009). Effect of seed treatment, in-furrow, and foliar application of insecticides on the carrot weevil in processing carrot. HortTechnology 19, 617-619.

Bowler, K. (2005). Acclimation, heat shock and hardening. J. Therm. Biol. 30, 125-130.

Boyce, A. M. (1927). A study of the biology of the parsley stalk-weevil *Listronotus Latiusculus* Boheman Coleoptera: Curculionidae. J. Econ. Entomol. 20, 814-821.

Bradshaw, W.E., et Holzapfel, C.M. (2006). Evolutionary response to rapid climate change. Science 312, 1477-1478.

Bradshaw, W.E., et Holzapfel, C.M. (2008). Genetic response to rapid climate change: it's seasonal timing that matters. Mol. Ecol. 17, 157-166.

Brigolin, D., Dal Maschio, G., Rampazzo, F., Giani, M., et Pastres, R. (2009). An individual-based population dynamic model for estimating biomass yield and nutrient fluxes through an off-shore mussel (Mytilus galloprovincialis) farm. *Estuarine, Coastal and Shelf Science*, *82*(3), 365-376.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., et West, G.B. (2004). Toward a metabolic theory of ecology. Ecology 85, 1771-1789.

de Bruijn, J.A.C., Vet, L.E.M., Jongsma, M.A., et Smid, H.M. (2018). Automated high-throughput individual tracking system for insect behavior: Applications on memory retention in parasitic wasps. J. Neurosci. Methods 309, 208-217.

Burke, K. D., Williams, J. W., Chandler, M. A., Haywood, A. M., Lunt, D. J., et Otto-Bliesner, B. L. (2018). Pliocene and Eocene provide best analogs for near-future climates. Proc. Natl. Acad. Sci. USA. 115, 13288–13293.

Candolin, U., Nieminen, A., et Nyman, J. (2014). Indirect effects of human-induced environmental change on offspring production mediated by behavioural responses. Oecologia 174, 87-97.

Caprio, M.A., et Grafius, E.J. (1990). Effects of light, temperature, and feeding status on flight initiation in postdiapause Colorado potato beetles (Coleoptera: Chrysomelidae). Environ. Entomol. 19, 281-285.

Carnicer, J., Stefanescu, C., Vives-Ingla, M., López, C., Cortizas, S., Wheat, C., Vila, R., Llusià, J., et Peñuelas, J. (2019). Phenotypic biomarkers of climatic impacts on declining insect populations: A key role for decadal drought, thermal buffering and amplification effects and host plant dynamics. J. Anim. Ecol. 88, 376-391.

Castex, V., Beniston, M., Calanca, P., Fleury, D., et Moreau, J. (2018). Pest management under climate change: The importance of understanding tritrophic relations. Sci. Total Environ. 616-617, 397-407.

Cavieres, G., Bogdanovich, J.M., et Bozinovic, F. (2016). Ontogenetic thermal tolerance and performance of ectotherms at variable temperatures. J. Evol. Biol. 29, 1462-1468.

Charmantier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B., et Sheldon, B.C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320, 800-803.

Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9, 129-136.

Charnov, E.L., Los-den Hartogh, R.L., Jones, W.T., et van den Assem, J. (1981). Sex ratio evolution in a variable environment. Nature 289, 27-33.

Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B., et Thomas, C.D. (2011). Rapid range shifts of species associated with high levels of climate warming. Science 333, 1024-1026.

Chevin, L.-M., Lande, R., et Mace, G.M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. PLoS Biol. 8.

Chown, S. L., et Gaston, K. J. (1999). Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. Biol. Rev. 74, 87-120.

Chown, S., Hoffmann, A., Kristensen, T., Angilletta, M., Stenseth, N., et Pertoldi, C. (2010). Adapting to climate change: a perspective from evolutionary physiology. Clim. Res. 43, 3-15.

Chown, S.L., Slabber, S., McGeoch, M.A., Janion, C., et Leinaas, H.P. (2007). Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. Proc. R. Soc. B Biol. Sci. 274, 2531-2537.

Chown, S.L., Jumbam, K.R., Sørensen, J.G., et Terblanche, J.S. (2009). Phenotypic variance, plasticity and heritability estimates of critical thermal limits depend on methodological context. Funct. Ecol. 23, 133-140.

Clarke, A., et Fraser, K.P.P. (2004). Why does metabolism scale with temperature? Funct. Ecol. 18, 243-251.

Cloudsley-Thompson, J.L. (1962a). Lethal temperatures of some desert arthropods and the mechanism of heat death. Entomol. Exp. Appl. 5, 270-280.

Cloudsley-Thompson, J.L. (1962b). Microclimates and the distribution of terrestrial arthropods. Annu. Rev. Entomol. 7, 199-222.

Clusella-Trullas, S., Blackburn, T.M., et Chown, S.L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. Am. Nat. 177, 738-751.

Colinet, H., et Boivin, G. (2011). Insect parasitoids cold storage: A comprehensive review of factors of variability and consequences. Biol. Control 58, 83-95.

Colinet, H., Renault, D., Hance, T., et Vernon, P. (2006). The impact of fluctuating thermal regimes on the survival of a cold-exposed parasitic wasp, *Aphidius colemani*. Physiol. Entomol. 31, 234-240.

Colinet, H., Boivin, G., et Hance, T. (2007). Manipulation of parasitoid size using the temperature-size rule: fitness consequences. Oecologia 152, 425-433.

Collins, R.D., et Grafius, E. (1986a). Impact of the egg parasitoid, *Anaphes sordidatus* (Hymenoptera: Mymaridae), on the carrot weevil (Coleoptera: Curculionidae). Environ. Entomol. 15, 469-475.

Collins, R.D., et Grafius, E. (1986b). Biology and life cycle of *Anaphes sordidatus* (Hymenoptera: Mymaridae), an egg parasitoid of the carrot weevil (Coleoptera: Curculionidae). Environ. Entomol. 15, 100-105.

Cook, D.F. (1994). Influence of temperature on copula duration and mating propensity in *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae). Austral Entomol. 33, 5-8.

Coope, G.R. (1970). Interpretations of Quaternary insect fossils. Annu. Rev. Entomol. 15, 97–121

Cormier, D., Stevenson, A.B., et Boivin, G. (1996). Seasonal ecology and geographical distribution of *Anaphes listronoti* and *A. victus* (Hymenoptera: Mymaridae), egg parasitoids of the carrot weevil (Coleoptera: Curculionidae) in central Ontario. Environ. Entomol. 25, 1376-1382.

Cormier, D., Royer, L., Vigneault, C., Panneton, B., et Boivin, G. (1998). Effect of female age on daily cycle of sexual pheromone emission in gregarious egg parasitoid *Anaphes listronoti*. J. Chem. Ecol. 24, 1595-1610.

Cournoyer, M., et Boivin, G. (2004). Infochemical-mediated preference behavior of the parasitoid *Microctonus hyperodae* when searching for its adult weevil hosts. Entomol. Exp. Appl. 112, 117-124.

Cournoyer, M., et Boivin, G. (2005a). Short distance cues used by the adult parasitoid *Microctonus hyperodae* Loan (Hymenoptera: Braconidae, Euphorinae) for host selection of a novel host *Listronotus oregonensis* (Coleoptera: Curculionidae). J. Insect Behav. 18, 577-591.

Cournoyer, M., et Boivin, G. (2005b). Evidence for kairomones used by the egg parasitoid *Anaphes victus* (Hymenoptera: Mymaridae) when searching for its host. Can. Entomol. 137, 230-232.

Coutant, C.C. (1977). Compilation of temperature preference data. J. Fish. Board Can. 34, 739-745.

Cui, X., Wan, F., Xie, M., et Liu, T. (2008). Effects of heat shock on survival and reproduction of two whitefly species, *Trialeurodes vaporariorum* and *Bemisia tabaci* biotype B. J. Insect Sci. 8, 1-10.

Damos, P., et Savopoulou-Soultani, M. (2012). Temperature-driven models for insect development and vital thermal requirements. Psyche J. Entomol. 2012, 1-13.

Davidson, J. (1944). On the relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. 13, 26-38.

Davis, A.J., Lawton, J.H., Shorrocks, B., et Jenkinson, L.S. (1998). Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. J. Anim. Ecol. *67*, 600–612.

Davis, M.B., et Shaw, R.G. (2001). Range shifts and adaptive responses to quaternary climate change. Science 292, 673–679.

DeAngelis, D.L., et Mooij, W.M. (2005). Individual-based modeling of ecological and evolutionary processes. Annu. Rev. Ecol. Evol. Syst. 3, 147-168.

Dell, A.I., Pawar, S., et Savage, V.M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. Proc. Natl. Acad. Sci. 108, 10591-10596.

Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., et Martin, P.R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl. Acad. Sci. 105, 6668-6672.

Diamond, S.E., Sorger, D.M., Hulcr, J., Pelini, S.L., Toro, I.D., Hirsch, C., Oberg, E., et Dunn, R.R. (2012). Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. Glob. Change Biol. 18, 448-456.

Dillon, M.E., et Frazier, M.R. (2006). *Drosophila melanogaster* locomotion in cold thin air. J. Exp. Biol. 209, 364-371.

Dillon, M.E., Wang, G., Garrity, P.A., et Huey, R.B. (2009). Thermal preference in Drosophila. J. Therm. Biol. 34, 109-119.

Doherty, J.A. (1985). Temperature coupling and “trade-off” phenomena in the acoustic communication system of the cricket, *Gryllus bimaculatus* de Geer (Gryllidae). J. Exp. Biol. 114, 17-35.

Drake, J.M. (2005). Population effects of increased climate variation. Proc. R. Soc. B Biol. Sci. 272, 1823-1827.

Dreisig, H. (1984). Control of body temperature in shuttling ectotherms. J. Therm. Biol. 9, 229-233.

Easterling, D.R. (2000). Climate extremes: observations, modeling, and impacts. Science 289, 2068-2074.

Elliot, S.L., Blanford, S., et Thomas, M.B. (2002). Host-pathogen interactions in a varying environment: temperature, behavioural fever and fitness. Proc. R. Soc. Lond. B Biol. Sci. 269, 1599-1607.

Englund, G., Öhlund, G., Hein, C.L., et Diehl, S. (2011). Temperature dependence of the functional response: Temperature dependence of consumption. Ecol. Lett. 14, 914-921.

Estay, S.A., Lima, M., et Bozinovic, F. (2014). The role of temperature variability on insect performance and population dynamics in a warming world. Oikos 123, 131-140.

Etterson, J.R., et Shaw, R.G. (2001). Constraint to adaptive evolution in response to global warming. Science 294, 151-154.

Feder, M.E., et Hofmann, G.E. (1999). Heat-shock proteins, molecular chaperones, and the stress response: Evolutionary and ecological physiology. Annu. Rev. Physiol. 61, 243-282.

Flores, G.B., et Lazzari, C.R. (1996). The role of the antennae in *Triatoma infestans*: orientation towards thermal sources. J. Insect Physiol. 42, 433-440.

Folguera, G., Bastías, D.A., Caers, J., Rojas, J.M., Piulachs, M.-D., Bellés, X., et Bozinovic, F. (2011). An experimental test of the role of environmental temperature variability on ectotherm molecular, physiological and life-history traits: Implications for global warming. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 159, 242-246.

Forrest, J.R. (2016). Complex responses of insect phenology to climate change. Curr. Opin. Insect Sci. 17, 49-54.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R.S., Mitchell, D., et Maloney, S.K. (2010). Physiological mechanisms in coping with climate change. Physiol. Biochem. Zool. 83, 713-720.

Gagnon, A.-È., Boivin, G., Bélair, G., et Mimee, B. (2019). Prevalence of a nematode castrator of the carrot weevil and impact on fecundity and survival. Parasitology 146, 702-707.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., et Heinsohn, R. (2011). Declining body size: a third universal response to warming? Trends Ecol. Evol. 26, 285-291.

Geister, T.L., et Fischer, K. (2007). Testing the beneficial acclimation hypothesis: temperature effects on mating success in a butterfly. Behav. Ecol. 18, 658-664.

Gevrey, M., et Worner, S.P. (2006). Prediction of global distribution of insect pest species in relation to climate by using an ecological informatics method. J. Econ. Entomol. 99, 8.

Ghalambor, C.K., McKay, J.K., Carroll, S.P., et Reznick, D.N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct. Ecol. 21, 394-407.

Ghazoul, J., et Willmer, P.G. (1994). Endothermic warm-up in two species of sphecid wasp and its relation to behaviour. Physiol. Entomol. 19, 103-108.

GIEC (2013) : Résumé à l'intention des décideurs, Changements climatiques 2013 : Les éléments scientifiques. Contribution du Groupe de travail I au cinquième Rapport d'évaluation du Groupe d'experts intergouvernemental sur l'évolution du climat [sous la direction de Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex et P.M. Midgley]. Cambridge University Press, Cambridge, Royaume-Uni et New York (État de New York), États-Unis d'Amérique.

GIEC (2014) : Changements climatiques 2014 : Incidences, adaptation et vulnérabilité - Résumé à l'intention des décideurs. Contribution du Groupe de travail II au cinquième Rapport d'évaluation du Groupe d'experts intergouvernemental sur l'évolution du climat [sous la direction de Field, C.B., V.R. Barros, D.J. Dokken,K.J. Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma,E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea et L.L. White]. Organisation météorologique mondiale, Genève (Suisse), 34 pages (publié en anglais, en arabe, en chinois, en espagnol, en français et en russe).

Gienapp, P., Leimu, R., et Merilä, J. (2007). Responses to climate change in avian migration time - microevolution versus phenotypic plasticity. Clim. Res. 35, 25-35.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A., et Merilä, J. (2008). Climate change and evolution: disentangling environmental and genetic responses. Mol. Ecol. 17, 167-178.

Gillooly, J.F. (2001). Effects of size and temperature on metabolic rate. Science 293, 2248-2251.

Graf, B., Höpli, H.U., Höhn, H., et Blaise, Ph. (2002). SOPRA: A forecasting tool for insect pests in apple orchards. Acta Hortic. 584, 207-214.

Graham, R. W., et Grimm, E. C. (1990). Effects of global climate change on the patterns of terrestrial biological communities. Trends Ecol. Evol. 5, 289–292.

Greenberg, S.M., Setamou, M., Sappington, T.W., Liu, T.-X., Coleman, R.J., et Armstrong, J.S. (2005). Temperature-dependent development and reproduction of the boll weevil (Coleoptera: Curculionidae).

Insect Sci. 12, 449-459.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., et al. (2006). A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198, 115-126.

Hadley, N.F. (1970). Micrometeorology and energy exchange in two desert arthropods. Ecology 51, 434-444.

Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., et al. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PLoS one 12, e0185809.

Hamilton, W.D. (1967). Extraordinary sex ratios. Science 156, 477-488.

Hance, T., van Baaren, J., Vernon, P., et Boivin, G. (2007). Impact of extreme temperatures on parasitoids in a climate change perspective. Annu. Rev. Entomol. 52, 107-126.

Hannon, B.M., et Ruth, M. (2009). Dynamic modeling of diseases and pests (New York: Springer).

Harmon, J.P., et Barton, B.T. (2013). On their best behavior: how animal behavior can help determine the combined effects of species interactions and climate change. Ann. N. Y. Acad. Sci. 1297, 139-147.

Hayes, D., Jones, M., Lester, N., Chu, C., Doka, S., Netto, J., Stockwell, J., Thompson, B., Minns, C.K., Shuter, B. et Collins, N. (2009). Linking fish population dynamics to habitat conditions: insights from the application of a process-oriented approach to several Great Lakes species. Rev. Fish Biol. Fish., *19*, 295-312.

Heath, J.E. (1967). Temperature responses of the periodical "17-year" cicada, *Magicicada cassini* (Homoptera, Cicadidae). Am. Midl. Nat. 77, 64.

Heath, J.E., et Adams, P.A. (1967). Regulation of heat production by large moths. J. Exp. Biol. 47, 21-33.

Heath, J.E., Hanegan, J.L., Wilkin, P.J., et Heath, M.S. (1971). Adaptation of the thermal responses of insects. Am. Zool. 11, 145-156.

Heimpel, G.E. (2019). Linking parasitoid nectar feeding and dispersal in conservation biological control. Biol. Control 132, 36-41.

Heinrich, B. (1974). Thermoregulation in endothermic insects. Science 185, 747-756.

Heinrich, B. (1995). Insect thermoregulation. Endevaour 19, 28-33.

Hoffmann, A.A., et Hewa-Kapuge, S. (2000). Acclimation for heat resistance in *Trichogramma nr. brassicae*: can it occur without costs? Funct. Ecol. 14, 55-60.

Hoffmann, A.A., et Sgrò, C.M. (2011). Climate change and evolutionary adaptation. Nature 470, 479-485.

Hoffmann, A.A., Chown, S.L., et Clusella-Trullas, S. (2013). Upper thermal limits in terrestrial ectotherms: how constrained are they? Funct. Ecol. 27, 934-949.

Hollis, K.L., Harrsch, F.A., et Nowbahari, E. (2015). Ants vs. antlions: An insect model for studying the role of learned and hard-wired behavior in coevolution. Learn. Motiv. 50, 68-82.

Holway, D.A., et Suarez, A.V. (1999). Animal behavior: an essential component of invasion biology. Trends Ecol.

Evol. 14, 328-330.

Honěk, A. (1993). Intraspecific variation in body size and fecundity in insects: A general relationship. Oikos 66, 483-492.

Hopper, K.R. (1999). Risk-spreading and bet-hedging in insect population biology. Annu. Rev. Entomol. 44, 535-560.

Huber, J.T. (1992). The subgenera, species groups, and synonyms of Anaphes (Hymenoptera: Mymaridae) with a review of the described Nearctic species of the fuscipennis group of Anaphes ss and the described species of Anaphes (Yungaburra). Proc. Entomol. Soc. Ont. 123, 23-110.

Huber, J.T., Côté, S., et Boivin, G. (1997). Description of three new Anaphes species (Hymenoptera: Mymaridae), egg parasitoids of the carrot weevil, *Listronotus oregonensis* (Leconte) (Coleoptera: Curculionidae), and redescription of *Anaphes sordidatus* Girault. Can. Entomol. 129, 959-977.

Hückesfeld, S., Niederegger, S., Schlegel, P., Heinzel, H.-G., et Spieß, R. (2011). Feel the heat: The effect of temperature on development, behavior and central pattern generation in 3rd instar *Calliphora vicina* larvae. J. Insect Physiol. 57, 136-146.

Huey, R.B., et Stevenson, R.D. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. 19, 357-366.

Huey, R.B., et Tewksbury, J.J. (2009). Can behavior douse the fire of climate warming? Proc. Natl. Acad. Sci. 106, 3647-3648.

Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Álvarez Pérez, H.J., et Garland, T. (2009). Why tropical forest lizards are vulnerable to climate warming. Proc. R. Soc. B Biol. Sci. 276, 1939-1948.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M., et Williams, S.E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos. Trans. R. Soc. B Biol. Sci. 367, 1665-1679.

Hughes, L. (2000). Biological consequences of global warming: is the signal already apparent? Trends Ecol. Evol. 15, 56-61.

Huston, M., DeAngelis, D., et Post, W. (1988). New computer models unify ecological theory. BioScience 38, 682-691.

Ishiguri, Y., et Shirai, Y. (2004). Flight activity of the peach fruit moth, *Carposina sasakii* (Lepidoptera: Carposinidae), measured by a flight mill. Appl. Entomol. Zool. 39, 127-131.

Ives, A.R. (1995). Spatial heterogeneity and host-parasitoid population dynamics: Do we need to study behavior? Oikos 74, 366-376.

Jamieson, M.A., Trowbridge, A.M., Raffa, K.F., et Lindroth, R.L. (2012). Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. Plant Physiol. 160, 1719-1727.

Jeffs, C.T., et Lewis, O.T. (2013). Effects of climate warming on host-parasitoid interactions: Effects of climate warming. Ecol. Entomol. 38, 209-218.

Jeschke, J.M., et Strayer, D.L. (2008). Usefulness of bioclimatic models for studying climate change and invasive species. Ann. N. Y. Acad. Sci. *1134*, 1–24.

Jerbi-Elayed, M., Lebdi-Grissa, K., Foray, V., Muratori, F., et Hance, T. (2015). Using multiple traits to estimate the effects of heat shock on the fitness of *Aphidius colemani*. Entomol. Exp. Appl. 155, 18-27.

Jiang, L., et Morin, P.J. (2004). Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. J. Anim. Ecol. *73*, 569–576.

Johnson, J.A., Valero, K.A., Wang, S., et Tang, J. (2004). Thermal death kinetics of red flour beetle (Coleoptera: Tenebrionidae). J. Econ. Entomol. 97, 1868-1873.

Jørgensen, K.T., Sørensen, J.G., et Bundgaard, J. (2006). Heat tolerance and the effect of mild heat stress on reproductive characters in *Drosophila buzzatii* males. J. Therm. Biol. 31, 280-286.

Judson, O.P. (1994). The rise of the individual-based model in ecology. Trends Ecol. Evol. 9, 9-14.

Justus, E.J., et Long, E.Y. (2019). Biology and management of the carrot weevil (Coleoptera: Curcuclionidae) in North America. J. Integr. Pest Manag. 10.

Karban, R. (1998). Caterpillar basking behavior and nonlethal parasitism by tachinid flies. J. Insect Behav. 11, 713-723.

Katsuki, M., et Miyatake, T. (2009). Effects of temperature on mating duration, sperm transfer and remating frequency in *Callosobruchus chinensis*. J. Insect Physiol. 55, 113-116.

Kearney, M., et Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol. Lett. *12*, 334–350.

Kearney, M., Porter, W.P., Williams, C., Ritchie, S., et Hoffmann, A.A. (2009a). Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. Funct. Ecol. *23*, 528–538.

Kearney, M., Shine, R., et Porter, W.P. (2009b). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proc. Natl. Acad. Sci. *106*, 3835–3840.

Keena, M.A. (2006). Effects of temperature on *Anoplophora glabripennis* (Coleoptera: Cerambycidae) adult survival, reproduction, and egg hatch. Environ. Entomol. 35, 912-921.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B., et Rebelo, T.G. (2008). Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biol. Lett. *4*, 560–563.

Kellermann, V., et van Heerwaarden, B. (2019). Terrestrial insects and climate change: adaptive responses in key traits. Physiol. Entomol. 44, 99-115.

Kenneth, M. (1932). The influence of atmospheric humidity on the thermal death point of a number of insects. J. Exp. Biol. 9, 222-231.

Kerkut, G.A., et Taylor, B.J.R. (1958). The effect of temperature changes on the activity of poikilotherms. Behaviour 13, 259-279.

Kidwell, S.M. (2015). Biology in the Anthropocene: Challenges and insights from young fossil records. Proc. Nat. Acad. Sci, 112, 4922–4929.

Kim, H.G., Margolies, D., et Park, Y. (2015). The roles of thermal transient receptor potential channels in thermotactic behavior and in thermal acclimation in the red flour beetle, *Tribolium castaneum*. J. Insect Physiol. 76, 47-55.

Kingsolver, J.G. (2009). The well-temperatured biologist. Am. Nat. 174, 755-768.

Kivivuori, L., et Lagerspetz, K.Y. (1990). Temperature selection behaviour of the isopod *Saduria entomon* (L.). J. Therm. Biol. 15, 83-86.

Knowlton, J.L., et Graham, C.H. (2010). Using behavioral landscape ecology to predict species' responses to land-use and climate change. Biol. Conserv. *143*, 1342–1354.

Koltz, A.M., Schmidt, N.M., et Høye, T.T. (2018). Differential arthropod responses to warming are altering the structure of Arctic communities. R. Soc. Open Sci. 5, 171503.

Krämer, B., Kämpf, I., Enderle, J., Poniatowski, D., et Fartmann, T. (2012). Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. J. Insect Conserv. 16, 857-865.

Krebs, R.A., et Loeschcke, V. (1994). Effects of exposure to short-term heat stress on fitness components in *Drosophila melanogaster*. J. Evol. Biol. 7, 39-49.

Kristensen, T.N., Hoffmann, A.A., Overgaard, J., Sorensen, J.G., Hallas, R., et Loeschcke, V. (2008). Costs and benefits of cold acclimation in field-released Drosophila. Proc. Natl. Acad. Sci. 105, 216-221.

Kroder, S., Samietz, J., Schneider, D., et Dorn, S. (2007). Adjustment of vibratory signals to ambient temperature in a host-searching parasitoid. Physiol. Entomol. 32, 105-112.

Krstevska, B., et Hoffmann, A.A. (1994). The effects of acclimation and rearing conditions on the response of tropical and temperate populations of *Drosophila melanogaster* and *D. simulans* to a temperature gradient (Diptera: Drosophilidae). J. Insect Behav. 7, 279-288.

Kruidhof, H.M., Kostenko, O., Smid, H.M., et Vet, L.E.M. (2019). Integrating parasitoid olfactory conditioning in augmentative biological control: Potential impact, possibilities, and challenges. Front. Ecol. Evol. 7.

Lachenicht, M.W., Clusella-Trullas, S., Boardman, L., Le Roux, C., et Terblanche, J.S. (2010). Effects of acclimation temperature on thermal tolerance, locomotion performance and respiratory metabolism in *Acheta domesticus* L. (Orthoptera: Gryllidae). J. Insect Physiol. 56, 822-830.

Lagerspetz, K.Y. (2000). Thermal avoidance and preference in *Daphnia magna*. J. Therm. Biol. 25, 405-410.

Landry, B.S., Dextraze, L., et Boivin, G. (1993). Random amplified polymorphic DNA markers for DNA fingerprinting and genetic variability assessment of minute parasitic wasp species (Hymenoptera: Mymaridae and Trichogrammatidae) used in biological control programs of phytophagous insects. Genome 36, 580-587.

Le Lann, C., Lodi, M., et Ellers, J. (2014). Thermal change alters the outcome of behavioural interactions between antagonistic partners: Thermal change alters species interactions. Ecol. Entomol. 39, 578-588.

Lecato, L.G., et Pienkowski, R.L. (1972). High-or low-Temperature treatments affecting alfalfa weevil fecundity egg fertility, and longevity. J. Econ. Entomol. 65, 146-148.

Lee, R.E. (1989). Insect cold-hardiness: To freeze or not to freeze. BioScience 39, 308-313.

Lee, R.E., Chen, C.P., et Denlinger, D.L. (1987). A rapid cold-hardening process in insects. Science 238, 1415-1417.

Lemay, J., Telfer, Z., Scott-Dupree, C., et McDonald, M.R. (2018). The impact of the carrot rust fly and carrot weevil integrated pest management program on the ground-dwelling beetle complex in commercial carrot fields at the Holland Marsh, Ontario, Canada. Environ. Entomol. 47, 788-794.

Lepage, M.P., Bourgeois, G., Brodeur, J., et Boivin, G. (2012). Effect of soil temperature and moisture on survival of eggs and first-instar larvae of *Delia radicum*. Environ. Entomol. 41, 159-165.

Lessard, E., et Boivin, G. (2013). Effect of low temperature on emergence, fecundity, longevity and host-feeding by *Trichogramma brassicae*. BioControl 58, 319-329.

Levin, P.S. (2000). Integrating individual behavior and population ecology: The potential for habitat-dependent population regulation in a reef fish. Behav. Ecol. 11, 565-571.

Levitis, D.A., Lidicker, W.Z., et Freund, G. (2009). Behavioural biologists do not agree on what constitutes behaviour. Anim. Behav. 78, 103-110.

Logan, J.A. (1988). Toward an expert system for development of pest simulation models. Environ. Entomol. 17, 359-376.

Luo, L., Gershow, M., Rosenzweig, M., Kang, K., Fang-Yen, C., Garrity, P.A., et Samuel, A.D.T. (2010). Navigational decision making in Drosophila thermotaxis. J. Neurosci. 30, 4261-4272.

Lurie, S., et Jang, E. (2007). The influence of heat shock proteins on insect pests and fruits in thermal treatments. In Heat treatments for postharvest pest control: Theory and practice, (Wellingford: CABI), p 269-290.

Lutterschmidt, W.I., et Hutchison, V.H. (1997). The critical thermal maximum: history and critique. Can. J. Zool. 75, 1561-1574.

Ma, G., et Ma, C.-S. (2012). Effect of acclimation on heat-escape temperatures of two aphid species: Implications for estimating behavioral response of insects to climate warming. J. Insect Physiol. 58, 303-309.

Macfadyen, S., McDonald, G., et Hill, M.P. (2018). From species distributions to climate change adaptation: Knowledge gaps in managing invertebrate pests in broad-acre grain crops. Agric. Ecosyst. Environ. 253, 208-219.

MacMillan, H.A., et Sinclair, B.J. (2011). Mechanisms underlying insect chill-coma. J. Insect Physiol. 57, 12-20.

Marais, E., et Chown, S.L. (2008). Beneficial acclimation and the Bogert effect. Ecol. Lett. 11, 1027-1036.

Martel, P., Harris, C.R., et Svec, H.J. (1975). Toxicological studies on the carrot weevil, *Listronotus oregonensis* (Coleoptera: Curculionidae). Can. Entomol. 107, 471-475.

Mason, P.G., et Gillespie, D.R. (2013). Biological control programmes in Canada, 2001-2012 (Wallingford, Oxfordshire, UK; Boston, MA: CABI).

Matthews, R. W., & Matthews, J. R. (2009). The history and scope of insect behavior. In *Insect Behavior* (pp. 1-44). Springer, Dordrecht.

Meehl, G. A., Washington, W. M., Arblaster, J. M., Hu, A., Teng, H., Tebaldi, C., ... et White III, J. B. (2012). Climate system response to external forcings and climate change projections in CCSM4. J. Clim. 25, 3661-3683.

Menéndez, R., Megías, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B., et Thomas, C.D. (2006). Species richness changes lag behind climate change. Proc. R. Soc. B Biol. Sci. 273, 1465-1470.

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., et al. (2006). European phenological response to climate change matches the warming pattern. Glob. Change Biol. 12, 1969-1976.

Messenger, P.S. (1959). Bioclimatic studies with insects. Annu. Rev. Entomol. 4, 183-206.

Michaud, M.R., et Denlinger, D.L. (2004). Molecular modalities of insect cold survival: current understanding and future trends. Int. Congr. Ser. 1275, 32-46.

Miklasiewicz, T.J., Grewal, P.S., Hoy, C.W., et Malik, V.S. (2002). Evaluation of entomopathogenic nematodes for suppression of carrot weevil. BioControl 47, 545-561.

Mills, N.J., et Heimpel, G.E. (2018). Could increased understanding of foraging behavior help to predict the success of biological control? Curr. Opin. Insect Sci. 27, 26-31.

Mills, N.J., et Kean, J.M. (2010). Behavioral studies, molecular approaches, and modeling: Methodological contributions to biological control success. Biol. Control 52, 255-262.

Miquel, J., Lundgren, P.R., Bensch, K.G., et Atlan, H. (1976). Effects of temperature on the life span, vitality and fine structure of *Drosophila melanogaster*. Mech. Ageing Dev. 5, 347-370.

Moiroux, J., Brodeur, J., et Boivin, G. (2014). Sex ratio variations with temperature in an egg parasitoid: behavioural adjustment and physiological constraint. Anim. Behav. 91, 61-66.

Moiroux, J., Abram, P.K., Louâpre, P., Barrette, M., Brodeur, J., et Boivin, G. (2016). Influence of temperature on patch residence time in parasitoids: physiological and behavioural mechanisms. Sci. Nat. 103.

Molina-Montenegro, M.A., Briones, R., et Cavieres, L.A. (2009). Does global warming induce segregation among alien and native beetle species in a mountain-top? Ecol. Res. 24, 31-36.

Montgomery, J.C., et Macdonald, J.A. (1990). Effects of temperature on nervous system: implications for behavioral performance. Am. J. Physiol.-Regul. Integr. Comp. Physiol. 259, R191-R196.

Moriyama, M., et Numata, H. (2019). Ecophysiological responses to climate change in cicadas. Physiol. Entomol. 44, 65-76.

Mousseau, T.A., et Fox, C.W. (1998). The adaptive significance of maternal effects. Trends Ecol. Evol. 13, 403-407.

Neven, L.G. (2000). Physiological responses of insects to heat. Postharvest Biol. Technol. 21, 103-111.

Nietschke, B.S., Magarey, R.D., Borchert, D.M., Calvin, D.D., et Jones, E. (2007). A developmental database to support insect phenology models. Crop Prot. 26, 1444-1448.

Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Huntley, B., Ivory, S. J., Kershaw, A. P., … Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. Science 361, 920–923.

O'Connor, M.I., et Bernhardt, J.R. (2018). The metabolic theory of ecology and the cost of parasitism. PLoS Biol. 16, e2005628.

Ouranos (2010). Savoir s'adapter aux changements climatiques (Montréal: Ouranos).

Ouranos (2015). Vers l'adaptation. Synthèse des connaissances sur les changements climatiques au Québec. Partie 1 : Évolution climatique au Québec. Édition 2015. Montréal, Québec : Ouranos, 114 p.

Overgaard, J., Sørensen, J.G., Petersen, S.O., Loeschcke, V., et Holmstrup, M. (2005). Changes in membrane lipid composition following rapid cold hardening in *Drosophila melanogaster*. J. Insect Physiol. 51, 1173-1182.

Overgaard, J., Kristensen, T.N., et Sørensen, J.G. (2012). Validity of thermal ramping assays used to assess thermal tolerance in Arthropods. PLoS one 7, e32758.

Paaijmans, K.P., Heinig, R.L., Seliga, R.A., Blanford, J.I., Blanford, S., Murdock, C.C., et Thomas, M.B. (2013). Temperature variation makes ectotherms more sensitive to climate change. Glob. Change Biol. 19, 2373-2380.

Pandey, R.R., et Johnson, M.W. (2005). Effects of cool storage on *Anagyrus ananatis* Gahan (Hymenoptera: Encyrtidae). Biol. Control 35, 9-16.

Parent, J.-P., Brodeur, J., et Boivin, G. (2016). Use of time in a decision-making process by a parasitoid. Ecol. Entomol. 41, 727-732.

Parent, J.-P., Takasu, K., Brodeur, J., et Boivin, G. (2017). Time perception-based decision making in a parasitoid wasp. Behav. Ecol. 28, 640-644.

Parker, G.A., et Smith, J.M. (1990). Optimality theory in evolutionary biology. Nature 348, 27-33.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 3, 637-669.

Parmesan, C., Root, T. L., et Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota *. Bull. Am. Meteorol. Soc. 81, 443–450.

Parmesan, C., et Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37-42.

Parsell, D.A., et Lindquist, S. (1993). The function of heat-shock proteins in stress tolerance: Degradation and reactivation of damaged proteins. Annu. Rev. Genet. 27, 437-496.

Perron, J.P. (1971). Insect pests of carrots in organic soils of southwestern Quebec with special reference to the carrot weevil, *Listronotus oregonensis* (Coleoptera: Curculionidae). Can. Entomol. 103, 1441-1448.

Petchey, O.L., Brose, U., et Rall, B.C. (2010). Predicting the effects of temperature on food web connectance. Philos. Trans. R. Soc. B Biol. Sci. 365, 2081-2091.

Pierce, G.J., et Ollason, J.G. (1987). Eight reasons why optimal foraging theory is a complete waste of time. Oikos 49, 111-118.

Pigliucci, M. (2006). Phenotypic plasticity and evolution by genetic assimilation. J. Exp. Biol. 209, 2362-2367.

Pincebourde, S., et Casas, J. (2015). Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits. Ecology 96, 986-997.

Porcelli, D., Gaston, K.J., Butlin, R.K., et Snook, R.R. (2017). Local adaptation of reproductive performance during thermal stress. J. Evol. Biol. 30, 422-429.

Portner, H. (2001). Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. Naturwissenschaften 88, 137-146.

Pörtner, H.O. (2002). Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. 132, 739-761.

Potter, K., Davidowitz, G., et Woods, H.A. (2009). Insect eggs protected from high temperatures by limited homeothermy of plant leaves. J. Exp. Biol. 212, 3448-3454.

Potter, K.A., Arthur Woods, H., et Pincebourde, S. (2013). Microclimatic challenges in global change biology. Glob. Change Biol. 19, 2932-2939.

Powell, S.J., et Bale, J.S. (2005). Low temperature acclimated populations of the grain aphid *Sitobion avenae* retain ability to rapidly cold harden with enhanced fitness. J. Exp. Biol. 208, 2615-2620.

Prange, H.D. (1996). Evaporative cooling in insects. J. Insect Physiol. 42, 493-499.

Pree, D.J., Stevenson, A.B., et Barszcz, E.S. (1996). Toxicity of pyrethroid insecticides to carrot weevils: Enhancement by synergists and oils. J. Econ. Entomol. 89, 1254-1261.

Prosser, C.L., et Nelson, D.O. (1981). The role of nervous systems in temperature adaptation of poikilotherms. Annu. Rev. Physiol. 43, 281-300.

Pruess, K.P. (1983). Day-degree methods for pest management. Environ. Entomol. 12, 613-619.

Pyke, G.H. (1984). Optimal foraging theory: A critical review. Annu. Rev. Ecol. Syst. 1, 523-575.

Quintero, I., et Wiens, J.J. (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. Ecol. Lett. 16, 1095-1103.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O., et Petchey, O.L. (2012). Universal temperature and body-mass scaling of feeding rates. Philos. Trans. R. Soc. B Biol. Sci. 367, 2923-2934.

Ramirez-Romero, R., Sivinski, J., Copeland, C.S., et Aluja, M. (2012). Are individuals from thelytokous and arrhenotokous populations equally adept as biocontrol agents? Orientation and host searching behavior of a fruit fly parasitoid. BioControl 57, 427-440.

Reed, T.E., Schindler, D.E., et Waples, R.S. (2011). Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate: Evolution, plasticity, and climate change. Conserv. Biol. 25, 56-63.

Régnière, J., Powell, J., Bentz, B., et Nealis, V. (2012). Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling. J. Insect Physiol. 58, 634-647.

Rekika, D., Stewart, K.A., Boivin, G., et Jenni, S. (2008). Floating rowcovers improve germination and reduce carrot weevil infestations in carrot. HortScience 43, 1619-1622.

Renault, D., Salin, C., Vannier, G., et Vernon, P. (2002). Survival at low temperatures in insects: what is the ecological significance of the supercooling point? CryoLetters 23, 217-228.

Renner, S.S., et Zohner, C.M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. Annu. Rev. Ecol. Evol. Syst. 49, 165-182.

Rhéaume, A.-J. (2009). Modélisation d'un écosystème agricole tritrophique: la carotte cultivée, le charançon de la carotte (*Listronotus oregonensis*) et *Anaphes victus*, un parasitoïde des œufs. Mémoire. Faculté des sciences de l'agriculture et de l'alimentation. Université Laval. Québec

Robertson, R.M., Kuhnert, C.T., et Dawson, J.W. (1996). Thermal avoidance during flight in the locust *Locusta migratoria*. J. Exp. Biol. 199, 1383-1393.

Roeser-Mueller, K., Strohm, E., et Kaltenpoth, M. (2010). Larval rearing temperature influences amount and composition of the marking pheromone of the male beewolf, *Philanthus triangulum*. J. Insect Sci. 10, 1-16.

Rohr, J.R., et Palmer, B.D. (2013). Climate change, multiple stressors, and the decline of ectotherms. Conserv. Biol. 27, 741-751.

Romanovsky, A.A. (2007). Thermoregulation: some concepts have changed. Functional architecture of the thermoregulatory system. Am. J. Physiol.-Regul. Integr. Comp. Physiol. 292, R37-R46.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., et Pounds, J.A. (2003). Fingerprints of global warming on wild animals and plants. Nature 421, 57-60.

Rosenzweig, C., Karoly, D., Vicarelli, M., Neofotis, P., Wu, Q., Casassa, G., Menzel, A., Root, T.L., Estrella, N., Seguin, B., et al. (2008). Attributing physical and biological impacts to anthropogenic climate change. Nature 453, 353-357.

Rothley, K.D., et Dutton, G. (2006). Behavioral responses to environmental change alter direct and indirect trait-mediated interactions. Can. J. Zool. 84, 1053-1058.

Rott, A.S., et Ponsonby, D.J. (2000). The effects of temperature, relative humidity and hostplant on the behaviour of Stethorus punctillum as a predator of the two-spotted spider mite, *Tetranychus urticae*. BioControl 45, 155-164.

Roux, O., Le Lann, C., van Alphen, J.J.M., et van Baaren, J. (2010). How does heat shock affect the life history traits of adults and progeny of the aphid parasitoid *Aphidius avenae* (Hymenoptera: Aphidiidae)? Bull.

Entomol. Res. 100, 543-549.

Roy, D.B., et Thomas, J.A. (2003). Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. Oecologia 134, 439-444.

Saadé, F.E., Dunphy, G.B., et Bernier, R.L. (1996). Response of the carrot weevil, *Listronotus oregonensis* (Coleoptera: Curculionidae), to strains of *Bacillus thuringiensis*. Biol. Control 7, 293-298.

Sales, K., Vasudeva, R., Dickinson, M.E., Godwin, J.L., Lumley, A.J., Michalczyk, Ł., Hebberecht, L., Thomas, P., Franco, A., et Gage, M.J.G. (2018). Experimental heatwaves compromise sperm function and cause transgenerational damage in a model insect. Nat. Commun. 9, 1-11.

Sanborn, A.F., Heath, J.E., Heath, M.S., et Noriega, F.G. (1995). Thermoregulation by endogenous heat production in two South American grass dwelling cicadas (Homoptera: Cicadidae: Proarna). Fla. Entomol. 78, 319-328.

Sánchez-Bayo, F., et Wyckhuys, K.A.G. (2019). Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv. 232, 8-27.

Satake, A., Ohgushi, T., Urano, S., et Uchimura, K. (2006). Modeling population dynamics of a tea pest with temperature-dependent development: predicting emergence timing and potential damage. Ecol. Res. 21, 107-116.

Scharf, I., Galkin, N., et Halle, S. (2015). Disentangling the consequences of growth temperature and adult acclimation temperature on starvation and thermal tolerance in the red flour beetle. Evol. Biol. 42, 54-62.

Schulte, P.M. (2015). The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. J. Exp. Biol. 218, 1856-1866.

Schulte, P.M., Healy, T.M., et Fangue, N.A. (2011). Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integr. Comp. Biol. 51, 691-702.

Scott, M., Berrigan, D., et Hoffmann, A.A. (1997). Costs and benefits of acclimation to elevated temperature in *Trichogramma carverae*. Entomol. Exp. Appl. 85, 211-219.

Senior, R.A., Hill, J.K., et Edwards, D.P. (2019). Global loss of climate connectivity in tropical forests. Nat. Clim. Change 9, 623-626.

Sentis, A., Hemptinne, J.-L., et Brodeur, J. (2012). Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency. Oecologia 169, 1117-1125.

Sentis, A., Hemptinne, J.-L., et Brodeur, J. (2013). Parsing handling time into its components: implications for responses to a temperature gradient. Ecology 94, 1675-1680.

Sentis, A., Hemptinne, J.-L., et Brodeur, J. (2014). Towards a mechanistic understanding of temperature and enrichment effects on species interaction strength, omnivory and food-web structure. Ecol. Lett. 17, 785-793.

Sentis, A., Ramon-Portugal, F., Brodeur, J., et Hemptinne, J.-L. (2015). The smell of change: warming affects species interactions mediated by chemical information. Glob. Change Biol. 21, 3586-3594.

Sergio, F., Blas, J., et Hiraldo, F. (2018). Animal responses to natural disturbance and climate extremes: a review. Glob. Planet. Change 161, 28-40.

Sgrò, C.M., Terblanche, J.S., et Hoffmann, A.A. (2016). What can plasticity contribute to insect responses to climate change? Annu. Rev. Entomol. 61, 433-451.

Shaffer, P.L., et Gold, H.J. (1985). A simulation model of population dynamics of the codling moth, *Cydia pomonella*. Ecol. Model. 30, 247-274.

Shreve, S.M. (2004). Preservation of reproductive behaviors during modest cooling: rapid cold hardening fine-tunes organismal response. J. Exp. Biol. 207, 1797-1802.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Anim. Behav. 85, 1077-1088.

Sih, A., Ferrari, M.C.O., et Harris, D.J. (2011). Evolution and behavioural responses to human-induced rapid environmental change: Behaviour and evolution. Evol. Appl. 4, 367-387.

Sih, A., Trimmer, P.C., et Ehlman, S.M. (2016). A conceptual framework for understanding behavioral responses to HIREC. Curr. Opin. Behav. Sci. 12, 109-114.

Sillmann, J., Kharin, V.V., Zwiers, F.W., Zhang, X., et Bronaugh, D. (2013). Climate extremes indices in the CMIP5 multimodel ensemble: Part 2. Future climate projections: CMIP5 Projections of extremes indices. J. Geophys. Res.: Atmospheres 118, 2473-2493.

Simonet, D. E., et Davenport, B. L. (1981). Temperature requirements for development and oviposition of the carrot weevil. Ann. Entomol. Soc. Am. 74, 312-315.

Sinclair, B.J., Vernon, P., Jaco Klok, C., et Chown, S.L. (2003). Insects at low temperatures: an ecological perspective. Trends Ecol. Evol. 18, 257-262.

Sirois-Delisle, C., et Kerr, J.T. (2018). Climate change-driven range losses among bumblebee species are poised to accelerate. Sci. Rep. 8, 1-10.

Sokolova, I.M. (2013). Energy-limited tolerance to stress as a conceptual framework to integrate the effects of multiple stressors. Integr. Comp. Biol. 53, 597-608.

Sokolova, I.M., Frederich, M., Bagwe, R., Lannig, G., et Sukhotin, A.A. (2012). Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Mar. Environ. Res. 79, 1-15.

Sørensen, J.G., Kristensen, T.N., et Overgaard, J. (2016). Evolutionary and ecological patterns of thermal acclimation capacity in Drosophila: is it important for keeping up with climate change? Curr. Opin. Insect Sci. 17, 98-104.

Starrfelt, J., et Kokko, H. (2012). Bet-hedging-a triple trade-off between means, variances and correlations. Biol. Rev. 87, 742-755.

Stephens, D.W., et Krebs, J.R. (1986). Foraging theory (Princeton, New Jersey).

Sterling, W., Dean, A., Hartstack, A., et Witz, J. (1990). Partitioning boll weevil (Coleoptera: Curculionidae) mortality associated with high temperature: Desiccation or thermal death? Environ. Entomol. 19, 1457-1462.

Stevenson, R.D. (1985a). The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. Am. Nat. 126, 362-386.

Stevenson, R.D. (1985b). Body size and limits to the daily range of body temperature in terrestrial ectotherms. Am. Nat. 125, 102-117.

Stevenson, A. B. (1986). Relationship between temperature and development of the carrot weevil, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae), in the laboratory. Can. Entomol. 118, 1287-1290.

Stevenson, A.B. et Barszcz, E.S. (1997). A comparison of three methods of monitoring the carrot weevil, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae). Can. Entomol. 129: 187-194.

Stevenson, A. B., et Boivin, G. (1990). Interaction of temperature and photoperiod in control of reproductive diapause in the carrot weevil (Coleoptera: Curculionidae). Environ. Entomol. 19, 836-841.

Stillman, J.H. (2003). Acclimation capacity underlies susceptibility to climate change. Science 301, 65-65.

Stimac, J.L. (1982). History and relevance of behavioral ecology in models of insect population dynamics. Fla. Entomol. *65*, 9.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M.M.B., Allen, S.K., Boschung, J., Naeuls, A., Xia, Y., Bex, V., et Midgley, P.M. (2013). Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change (Cambridge, United Kingdom and New York, NY, USA).

Stone, G.N., et Willmer, P.G. (1989). Warm-up rates and body temperatures in bees: the importance of body size, thermal regime and phylogeny. J. Exp. Biol. 147, 303-328.

Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., et Huey, R.B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proc. Natl. Acad. Sci. 111, 5610-5615.

Tanner, C.J. (2009). Chill out: cooling promotes aggressive behavior in the ant *Formica xerophila*. Insectes Sociaux 56, 64-69.

Taylor, F. (1981). Ecology and evolution of physiological time in insects. Am. Nat. 117, 1-23.

Telfer, Z., Lemay, J., McDonald, M.R., et Scott-Dupree, C. (2018). Assessing new chemical control options for the carrot weevil (*Listronotus oregonensis*) and carrot rust fly (*Psila rosae*) in Ontario. Crop Prot. 109, 86-94.

Telfer, Z., Lemay, J., McDonald, M. R., & Scott-Dupree, C. (2019). Evaluating the current integrated pest management recommendations in Canada for carrot weevil (Coleoptera: Curculionidae) and carrot rust fly (Diptera: Psilidae). The Canadian Entomologist, 151, 391-405.

Tenhumberg, B. (2004). Predicting predation efficiency of biocontrol agents: linking behavior of individuals and population dynamics.

Teplitsky, C., et Millien, V. (2014). Climate warming and Bergmann's rule through time: is there any evidence? Evol. Appl. 7, 156-168.

Terblanche, J.S., Hoffmann, A.A., Mitchell, K.A., Rako, L., le Roux, P.C., et Chown, S.L. (2011). Ecologically relevant measures of tolerance to potentially lethal temperatures. J. Exp. Biol. 214, 3713-3725.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., et al. (2004). Extinction risk from climate change. Nature 427, 145-148.

Thomson, L.J., Macfadyen, S., et Hoffmann, A.A. (2010). Predicting the effects of climate change on natural enemies of agricultural pests. Biol. Control 52, 296-306.

Thuiller, W. (2007). Climate change and the ecologist. Nature, 448, 550-552.

Traoré, L., Pilon, J.G., Fournier, F., et Boivin, G. (2006) Adaptation of the developmental process of *Anaphes victus* (Hymenoptera: Mymaridae) to local climatic conditions across North America. Ann. Entomol. Soc. Am. 99, 1121-1126

Traniello, J.F.A., Fujita, M.S., et Bowen, R.V. (1984). Ant foraging behavior: Ambient temperature influences prey selection. Behav. Ecol. Sociobiol. 15, 65-68.

Tseng, M., Kaur, K.M., Soleimani Pari, S., Sarai, K., Chan, D., Yao, C.H., Porto, P., Toor, A., Toor, H.S., et Fograscher, K. (2018). Decreases in beetle body size linked to climate change and warming temperatures. J. Anim. Ecol. 87, 647-659.

Tuomainen, U., et Candolin, U. (2011). Behavioural responses to human-induced environmental change. Biol. Rev. 86, 640-657.

Umbers, K.D.L., Herberstein, M.E., et Madin, J.S. (2013). Colour in insect thermoregulation: Empirical and theoretical tests in the colour-changing grasshopper, *Kosciuscola tristis*. J. Insect Physiol. 59, 81-90.

Van der Putten, W.H., Macel, M., et Visser, M.E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos. Trans. R. Soc. B Biol. Sci. *365*, 2025–2034.

Van Roermund, H. J. W., Van Lenteren, J. C., et Rabbinge, R. (1997). Biological control of greenhouse whitefly with the Parasitoid *Encarsia Formosa* on tomato: an individual-based simulation approach. *Biological Control*, *9*(1), 25-47.

Vannier, G. (1994). The thermobiological limits of some freezing intolerant insects: the supercooling and thermostupor points. Acta Oecologica 15, 31-42.

Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D.G., McCann, K.S., Savage, V., Tunney, T.D., et O'Connor, M.I. (2014). Increased temperature variation poses a greater risk to species than climate warming. Proc. R. Soc. B Biol. Sci. 281, 20132612.

Verberk, W.C.E.P., et Bilton, D.T. (2011). Can oxygen set thermal limits in an insect and drive gigantism? PLoS one 6, e22610.

Vet, L. E. (2001). Parasitoid searching efficiency links behaviour to population processes. Appl. Entomol. Zool., *36*, 399-408.

Villani, M.G., et Wright, R.J. (1990). Environmental influences on soil macroarthropod behavior in agricultural systems. Annu. Rev. Entomol. 35, 249-269.

Visser, M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. Proc. R. Soc. B Biol. Sci. 275, 649-659.

Visser, M.E., et Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. Proc. R. Soc. B Biol. Sci. 272, 2561-2569.

Voigt, W., Perner, J., Davis, A.J., Eggers, T., Schumacher, J., Bährmann, R., Fabian, B., Heinrich, W., Köhler, G., Lichter, D., et al. (2003). Trophic levels are differentially sensitive to climate. Ecology 84, 2444-2453.

Vucic-Pestic, O., Rall, B.C., Kalinkat, G., et Brose, U. (2010). Allometric functional response model: body masses constrain interaction strengths. J. Anim. Ecol. 79, 249-256.

Walsh, B.S., Parratt, S.R., Hoffmann, A.A., Atkinson, D., Snook, R.R., Bretman, A., et Price, T.A.R. (2019). The impact of climate change on fertility. Trends Ecol. Evol. 34, 249-259.

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoegh-Guldberg, O., et Bairlein, F. (2002). Ecological responses to recent climate change. Nature 416, 389-395.

Wang, B., Ferro, D.N., Wu, J., et Wang, S. (2004). Temperature-dependent development and oviposition behavior of *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae), a potential biological control agent for the European corn borer (Lepidoptera: Crambidae). Environ. Entomol. 33, 787-793.

Wang, G., Gordon, T.N., et Rainwater, S. (2008). Maximum voluntary temperature of insect larvae reveals differences in their thermal biology. J. Therm. Biol. 33, 380-384.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Willis, S.G., et Greatorex-Davies, J.N. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414, 65-69.

Warren, R., Price, J., Graham, E., Forstenhaeusler, N., et VanDerWal, J. (2018). The projected effect on insects, vertebrates, and plants of limiting global warming to 1.5°C rather than 2°C. Science 360, 791-795.

Wepprich, T., Adrion, J.R., Ries, L., Wiedmann, J., et Haddad, N.M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. PloS one, 14.

Wiens, J.J. (2016). Climate-related local extinctions are already widespread among plant and animal species. PLoS Biol. 14, e2001104.

Wilf, P., et Labandeira, C.C. (1999). Response of plant-insect associations to Paleocene-Eocene warming. Science 284, 2153–2156.

Wiktelius, S. (1987). Distribution of *Rhopalosiphum padi* (Hornoptera: Aphididae) on spring barley plants. Ann. Appl. Biol. 110, 1-7.

Wilkes, A. (1959). Effects of high temperatures during postembryonic development on the sex ratio of an arrhenotokous insect, *Dahlbominus fuliginosus* (Nees) (Hymenoptera: Eulophidae). Can. J. Genet. Cytol. 1, 102-109.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., et Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol. 6, e325.

Willmer, P.G., et Unwin, D.M. (1981). Field analyses of insect heat budgets: Reflectance, size and heating rates. Oecologia 50, 250-255.

Wilson, R. S., et Franklin, C. E. (2002). Testing the beneficial acclimation hypothesis. Trends Ecol. Evol. 17, 66-70.

Wittenburg, N., et Baumeister, R. (1999). Thermal avoidance in *Caenorhabditis elegans*: an approach to the study of nociception. Proc. Natl. Acad. Sci. 96, 10477-10482.

Wong, B.B.M., et Candolin, U. (2015). Behavioral responses to changing environments. Behav. Ecol. 26, 665-673.

Woodin, S.A., Hilbish, T.J., Helmuth, B., Jones, S.J., et Wethey, D.S. (2013). Climate change, species distribution models, and physiological performance metrics: predicting when biogeographic models are likely to fail. Ecol. Evol.

Woods, H.A., Dillon, M.E., et Pincebourde, S. (2015). The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. J. Therm. Biol. 54, 86-97.

Wu, G.-M., Barrette, M., Boivin, G., Brodeur, J., Giraldeau, L.-A., et Hance, T. (2011). Temperature influences the handling efficiency of an aphid parasitoid through body size-mediated effects. Environ. Entomol. 40, 737-742.

Yan, R., Huang, Z., Zhu, H., Johnson, J.A., et Wang, S. (2014). Thermal death kinetics of adult *Sitophilus oryzae* and effects of heating rate on thermotolerance. J. Stored Prod. Res. 59, 231-236.

Zhao, D.X., Boivin, G., et Stewart, R.K. (1990). Consumption of carrot weevil, *Listronotus oregonensis*, [Coleoptera: Curculionidae] by four species of carabids on host plants in the laboratory. Entomophaga 35, 57-60.

Zhao, D.X., Boivin, G., et Stewart, R.K. (1991). Simulation model for the population dynamics of the carrot weevil, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae). Can. Entomol. 123, 63-76.

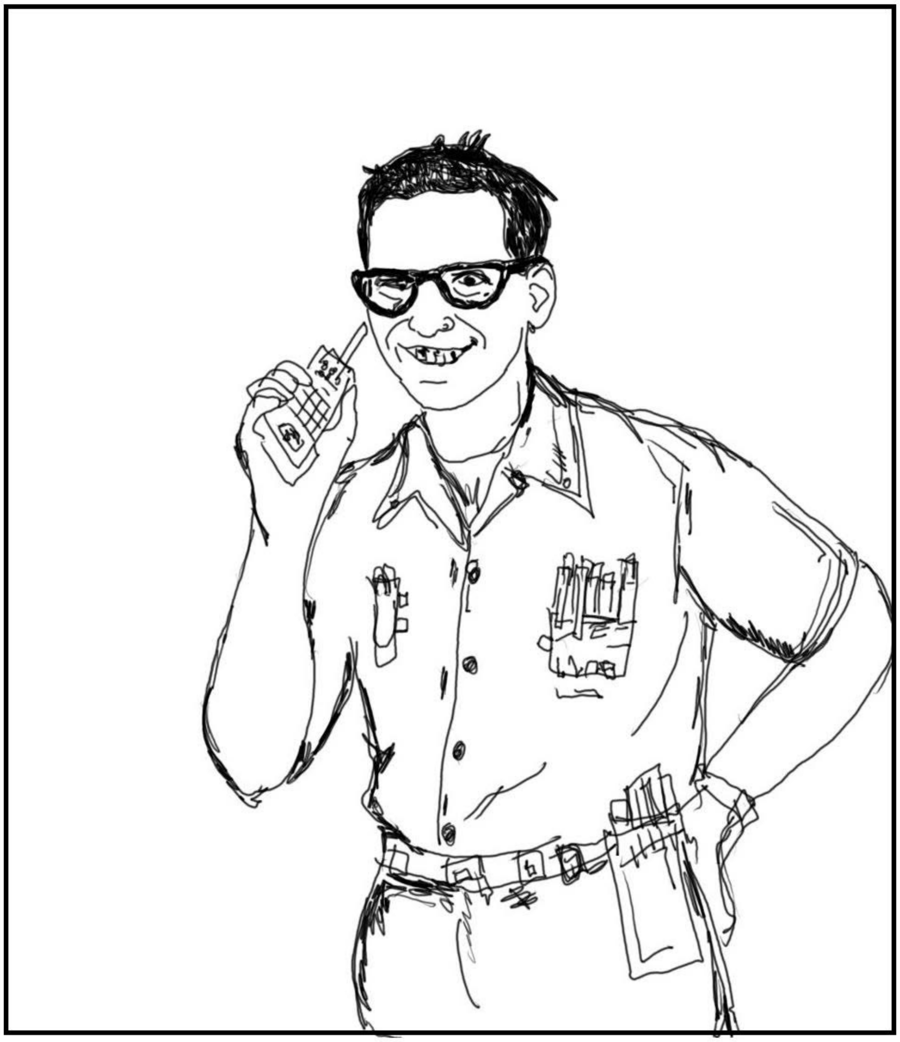
Zhao, S., Qiu, C., Xiong, S., et Cheng, X. (2007). A thermal lethal model of rice weevils subjected to microwave irradiation. J. Stored Prod. Res. 43, 430-434.

Zhu, L., Wang, L., et Ma, C.-S. (2019). Sporadic short temperature events cannot be neglected in predicting impacts of climate change on small insects. J. Insect Physiol. 112, 48-56.

Zilahi-Balogh, G.M.G., Shipp, J.L., Cloutier, C., et Brodeur, J. (2006). Influence of light intensity, photoperiod, and temperature on the efficacy of two aphelinid parasitoids of the greenhouse whitefly. Environ. Entomol. 35, 581-589.

Zizzari, Z.V., et Ellers, J. (2011). Effects of exposure to short-term heat stress on male reproductive fitness in a soil arthropod. J. Insect Physiol. 57, 421-426.

Chapitre 3: contribution de l'auteur et des co-auteurs



Jean-Sébastien Matte

L'idée d'étudier l'effet de la température sur le comportement d'*Anaphes listronoti* vient à l'origine de la continuation d'un projet sur l'impact des températures infra- et supra-optimales sur les organismes, débuté par Guy Boivin et Gaétan Bourgeois. Le projet qui a mené à cette thèse s'est défini et développé au fil des lectures et des discussions avec mes co-directeurs, Jacques Brodeur, Guy Boivin et Gaétan Bourgeois, et grâce à de nombreux échanges avec les membres des laboratoires Boivin et Brodeur.

Pour l'ensemble des chapitres, j'ai planifié et conçu les expériences, recueilli les données, réalisé les analyses statistiques, et rédigé les manuscrits, sous la supervision de mes directeurs Guy Boivin, Gaétan Bourgeois et Jacques Brodeur. Les expériences ont été réalisées dans le laboratoire de Guy Boivin, au centre de recherche et développement d'Agriculture et Agro-alimentaire Canada, à Saint-Jean-sur-Richelieu, QC. Pour chacun des articles présentés dans cette thèse, mes co-directeurs ont joué un rôle crucial, en particulier pour aider au dispositif expérimental et aux analyses statistiques, la révision des manuscrits, mais également au niveau du financement et l'accès aux infrastructures.

Je décris à présent la contribution de mes co-auteurs pour chacun des chapitres.

Chapitre 4 : Augustin J., Boivin G., Brodeur J., Bourgeois G. Effect of temperature on the walking behaviour of an egg parasitoid: disentangling kinetic response from integrated response.

J'ai conçu et réalisé l'expérience, traité les données, fait les analyses statistiques, et rédigé le manuscrit. Guy Boivin a participé à l'élaboration du dispositif expérimental, et Guy Boivin, Jacques Brodeur et Gaétan Bourgeois ont contribué à l'analyse des données et la rédaction du manuscrit.

Chapitre 5 : Augustin J., Boivin G., Bourgeois G. and Brodeur J. The effect of temperature on host patch exploitation by an egg parasitoid.

J'ai conçu et réalisé l'expérience, traité les données, fait les analyses statistiques, et rédigé le manuscrit. Guy Boivin a participé à l'élaboration du dispositif expérimental, et Jacques Brodeur, Guy Boivin et Gaétan Bourgeois ont contribué à l'analyse des données et la rédaction du manuscrit.

Chapitre 6 : Augustin J., Bourgeois G., Brodeur J., Boivin G. Low and high temperatures decrease the mating success of an egg parasitoid and the proportion of females in the population.

J'ai conçu et réalisé l'expérience, traité les données, fait les analyses statistiques, et rédigé le manuscrit. Guy Boivin a participé à l'élaboration du dispositif expérimental, et Guy Boivin, Jacques Brodeur et Gaétan Bourgeois ont contribué à l'analyse des données et la rédaction du manuscrit.

Chapitre 7 : Augustin J., Bourgeois G., Brodeur J., Boivin G. Individual behaviour and population dynamics under climate change: Simulation of an insect parasitoid life cycle

J'ai conceptualisé et codé le modèle et compilé les simulations, fait les analyses statistiques et rédigé le manuscrit. Les données d'évaluation du modèle au champ ont été récoltées par Danielle Thidodeau, Julie Frenette et moi-même. J'ai fait le traitement de ces données. Gaétan Bourgeois a participé à la conceptualisation du modèle, et Jacques Brodeur, Guy Boivin et Gaétan Bourgeois ont contribué à la rédaction du manuscrit.

Chapitre 4 : Effect of temperature on the walking behaviour of an egg parasitoid: disentangling kinetic response from integrated response

Julie Augustin, Guy Boivin, Jacques Brodeur, Gaétan Bourgeois

Publié dans Ecological Entomology (2020) *45*, 741-750

Tableau: Christian Augustin – Photo : Nolwen Lemercier

4.1 / Abstract

1. We investigated the effect of temperatures ranging from 10.8 to 34.2°C on seven walking parameters of an egg parasitoid, *Anaphes listronoti*. We compared those responses to a theoretical kinetic model in order to disentangle the kinetic response of the insect from its integrated response.
2. Walking speed increased continuously with temperature, but walking distance and duration were maximized between 25 and 30°C, and decreased at higher and lower temperatures. At the lowest temperature, females unexpectedly walked a greater distance and for a longer duration in comparison with intermediate temperatures.
3. The number of walking bouts followed the same polynomial trend as walking distance and duration, with a maximum between 30 and 35°C. The duration of walking bouts was maximised at 20°C and decreased at lower and higher temperatures, whereas the duration of resting bouts linearly decreased with increasing temperature. There was no effect of temperature on the turning rate of females.
4. For *A. listronoti*, walking speed and duration of resting bouts followed the kinetic response, but the other behavioural components did not, especially at the lowest and highest temperatures. Walking distance and duration were higher than expected under the kinetic response at 10.8 °C and lower than expected at 34.2 °C. This pattern suggests an integrated response combining behavioural escape from adverse temperature and energy saving.
5. Our detailed analysis of the walking behaviour of *A. listronoti* illustrates the complexity of insect behavioural responses to temperature and the difficulty involved in assessing underlying mechanisms.

Keywords : Walking behaviour – Thermal response – *Anaphes listronoti* – Kinetic vs. integrated response – Escape behaviour – Climate change

4.2 / Introduction

Temperature directly affects the metabolic rate of poikilothermic organisms through effects on enzyme conformation and enzyme binding to substrate (Neven, 2000). The effects of temperature on insect development have been widely studied and are frequently considered in assessments of the impact of climate warming on insect species and communities (Bale et al., 2002; Hance et al., 2007; Folguera et al., 2011). In contrast, the influence of temperature on insect behaviour has received much less attention (Abram et al., 2017), especially in the context of climate change impacts and possible mitigation (Andrew et al., 2013b).

Walking is required for most behaviours performed by insects (Bell, 1990). For instance, walking is crucial for female parasitoids that spend most of their adult life searching for hosts. Temperature can influence the time that parasitoids spend walking both within (Moiroux et al., 2016) and between (Abram et al., 2015) host patches, thereby modifying the parasitoids' overall reproductive success. In a recent review, Abram et al. (2017) defined two non-mutually exclusive pathways through which temperature may affect the behaviour of ectotherms. First, there are bottom-up effects, where biochemical reactions directly impact behaviours through metabolic rate: the "kinetic response." Second, there are top-down effects, where organisms respond to temperature through their central nervous system: the "integrated response." In order to distinguish between kinetic and integrated responses associated with walking behaviour, one has to first identify responses associated with each pathway. Under the kinetic response, behaviours are affected by the biochemical reaction rates in a bottom-up manner. As physiological processes also depend on biochemical rates we expect that, under the kinetic response, walking behaviour patterns will closely follow those of the physiological response (Huey and Stevenson, 1979), with individuals exhibiting optimal behaviour (e.g., maximum walking speed) only under a narrow range of thermal conditions. This has typically been observed in insects for walking speed (Dillon and Frazier, 2006; Lachenicht et al., 2010) as well as walking distance and duration (Suverkropp et al., 2001; Kjærsgaard et al., 2015). Under the integrated response, walking behaviour should not follow the physiological performance curve, and three main scenarios can occur. First, individuals maintain maximum walking behaviour despite suboptimal conditions (Pigliucci et al., 2006). In this scenario, walking behaviour remains constant over an extended range of temperatures. Second, individuals avoid suboptimal thermal conditions, as reported in fish (Coutant, 1977), nematodes (Wittenburg and Baumeister, 1999), branchiopods (Lagerspetz, 2000), and several groups of insects: locusts (Robertson et al., 1996), aphids (Ma and Ma, 2012), fruit flies (Rosenzweig et al., 2008), house flies (Hafez, 1950), and cicadas (Heath et al., 1971). Third, in stressful thermal conditions, individuals move less to retain energy (Sokolova et al., 2012). This results in lower activity (i.e., less time spent in movement and shorter walking distance) than expected in the kinetic response scenario. For the relationship between temperature and walking behaviour in insects, we expected the kinetic response to predominate over the integrated response because walking speed is usually proportional to metabolic rate (Berrigan and Lighton, 1994). Metabolic rate usually increases with temperature until it reaches a maximal point, after which it decreases (Schulte, 2015). Accordingly, an insect should walk faster for a longer time and over a greater distance as the temperature increases until it reaches a critical thermal point, above which hindered movements disrupt walking, as for a typical physiological response curve. However, this prediction is only based on biochemical aspects, and not energetic components; it only holds true if the organism has the energetical resources to support increasing metabolic needs.

Anaphes listronoti (Huber) (Hymenoptera: Mymaridae) (Huber et al., 1977) is an egg parasitoid of the carrot weevil, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae) (Leconte, 1862; Collins and Grafius, 1986a). In Quebec, Canada, this parasitoid wasp can cause up to 85% mortality in carrot weevil eggs in fields not treated with insecticides (Cormier et al., 1996). Since *A. listronoti* females live for only about 4 days at 25 °C and 2 days at 30 °C (Collins and Grafius, 1986b), temperature is likely to drastically influences their host searching behaviour and reproductive fitness.

We investigated seven parameters of the walking behaviour of *A. listronoti* (speed, duration, distance, number and duration of walking bouts, duration of resting bouts, and turning rate) along a gradient of six temperatures covering the developmental range of the species. Our two main objectives were to characterize the thermal response curve of each walking parameter and to distinguish between kinetic and integrated responses to temperature.

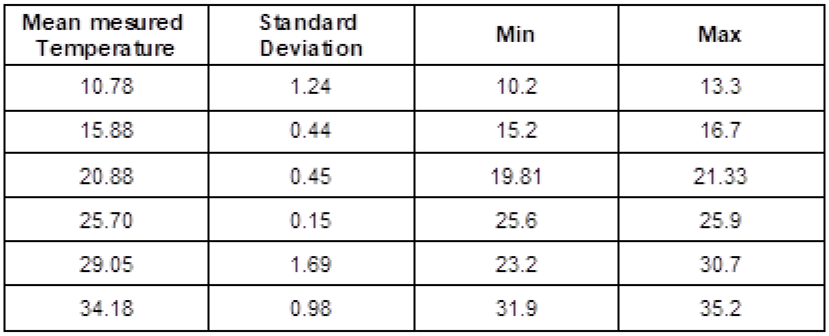
4.3 / Materials and methods

Host and parasitoid

Anaphes listronoti was reared on carrot weevil eggs in the laboratory at 24 ± 2 °C and 50% relative humidity under a photoperiod of 16 h of light and 8 h of darkness, in accordance with Boivin (1988). The colony was established in 1991 from individuals collected in an untreated carrot field in Sainte-Clotilde, Quebec, Canada (45°09′N, 73°41′W). Carrot weevil eggs were obtained as described in Martel et al. (1975).

Walking behaviour

The walking behaviour of *A. listronoti* was examined within six constant temperatures from 10.8 to 34.2 °C (Table 4-1), reflecting the range at which development occurs (Huber et al., 1997; Traoré et al., 2006). A pre-test had shown that all wasps died after 1 h of acclimation at 40 °C. Temperatures were monitored using a HOBO thermocouple temperature logger (model H08-001-02) placed inside the test Petri dish in the climatic chamber. *Anaphes listronoti* is facultative gregarious, and one to six individuals can emerge from a single host egg (Collins and Grafius, 1986b), with individuals that emerge singly from an egg being larger than those reared gregariously. Because walking parameters are closely related to body size (Hurlbert et al., 2008; Parent, 2016), we used only solitary-developed females of similar size (mean hind tibia length = 285 ± 19.07 µm; Boivin and Martel, 2012). The tested parasitoid females, aged 0 to 24 h, were all mated but had no oviposition experience and no access to food. Females maintained individually in 300-µL Beem polyethylene capsules were randomly assigned to a growth chamber (Sanyo, model MLR351H) 1 h before the test so that the insects could acclimate to the experimental conditions (tested temperature, 50% relative humidity, 16,000 lux).



Mean mesured Temperature	Standard Deviation	Min	Max
10.78	1.24	10.2	13.3
15.88	0.44	15.2	16.7
20.88	0.45	19.81	21.33
25.70	0.15	25.6	25.9
29.05	1.69	23.2	30.7
34.18	0.98	31.9	35.2

Table 4-1 : Test temperatures (°C) (X, standard deviation, minimum, and maximum) for the study of walking behaviour in *Anaphes listronoti*

Humidity higher than 50%, has been shown to have limited effects on parasitoid walking behaviour (Boldt, 1974) and searching efficiency (Henderson et al., 2017). The females were then placed singly on moistened filter paper in a 3.9-cm diameter Petri dish. Individual females were videotaped (USB digital Dino-Lite, model AM5212NZT) for 10 min, beginning when they started walking. Between the tests, the Petri dishes were washed with distilled water, and the filter paper was changed. Twelve individuals were tested per temperature, and each female was used only once. Experiments were run between 10:30 and 16:30.

Video analysis

The videos were analyzed using Biotrack software (http://www.bio-tracking.org/). Total walking distance (in mm) and walking duration (in s) were calculated using X-Y coordinates of the wasp on each video frame. Videos contained 15 images per seconds, allowing tracking both straight and curved paths through the succession of numerous X-Y positions. Curved paths then consisted of a succession of very short straight bouts. Mean walking speed (in mm s^{-1}) was calculated by dividing the total distance travelled by the time spent walking. The number of walking bouts and their duration were also calculated, as was the duration of resting bouts (periods when wasps were either grooming or standing still). Turning rate (in degrees s^{-1}) was calculated based on differences in the female orientation between each successive video frame. Their absolute values were added for the entire test duration, and this sum (total rotation of the wasp, in degrees) was divided by the duration of the trial (in s).

Data analyses

Linear and polynomial regressions were used to determine the effect of temperature on walking parameters. The degree of polynomial regression chosen was the lowest polynomial degree with statistically significant polynomial coefficients ($p < 0.05$) and the highest R^2 value. Two *A. listronoti* females walked for less than 30 s during the 10 min trial (5% of the total time) and were removed from the analysis. Data were analyzed with R software (R Core Team, 2016) using the *stats* package for the linear regression and the polynomial function.

4.4 / Results

Anaphes listronoti females walked greater distances at medium temperatures (20.9 to 29.4 °C) than at low (10.8 and 15.9 °C) and high (34.2 °C) temperatures (third-degree polynomial: $p = 0.015$, $R^2 = 0.10$; $y = -0.11x^3 + 7.12x^2 - 133.89x + 909.49$; Figure 4-1A). Interestingly, females at 10.8 °C walked a greater distance (155.8 ± 95.7 mm) than females at 15.9 °C did (108.3 ± 65.8 mm). Walking duration followed the same pattern (third-degree polynomial: $p = 0.003$, $R^2 = 0.15$; $y = -0.15x^3 + 9.50x^2 - 185.50x + 1290.57$; Figure 4-1B), with a bell-shaped curve from 15 to 34 °C and with time spent walking being higher at 10.8 °C than at 15.9 °C. Females spent the most time walking (289.7 ± 137.6 s) at 29.4 °C, but in general, walking duration was less than half the total time (206.54 ± 141.08 s). Females walked faster as the temperature increased (linear regression: $p = 0.03$, $R^2 = 0.05$; $y = 0.01x + 0.66$; Figure 4-1C). Walking speed was at its maximum at 34.2 °C (1.07 ± 0.52 mm s^{-1}) and at its minimum at 10.8 °C (0.73 ± 0.14 mm s^{-1}).

Walking bouts were more frequent at high temperatures than at low temperatures (third-degree polynomial: $p = 0.001$, $R^2 = 0.18$; $y = -0.003x^3 + 0.25x^2 - 5.26x + 41.03$; Figure 4-2A). First and second degree polynomials were also significant for number of walking bouts, but R^2 with experimental data were lower than with third-degree polynomial (first-degree polynomial : $p = 0.003$, $R^2 = 0.11$; second degree-polynomial : $p = 0.006$, $R^2 = 0.12$). The duration of walking bouts followed a bell curve, with an optimum at 20.9 °C (second-degree polynomial: $p = 0.002$, $R^2 = 0.15$; $y = -0.14x^2 + 5.69x$; Figure 4-2B). Third degree polynomial was also significant for duration of walking bouts, but the R^2 was lower than for second-degree polynomial ($p = 0.004$, $R^2 = 0.14$). Resting bouts were longer at low temperatures than at high temperatures (linear regression: $p = 0.04$, $R^2 = 0.05$; $y = -1.67x + 105.41$; Figure 4-2C).

Turning rates were similar at all tested temperatures (linear regression: $p = 0.42$, $R^2 = 0.001$; Figure 4-3) with a mean of 2.13 ± 2.84° s^{-1}. Encounters with the Petri dish border often led to a slight turn, with the insect following the border along the curve. This behaviour could have affected the mean turning rate of *A. listronoti* females, although the number of times that females encountered the Petri dish border was similar across all temperatures (6.3 ± 3.7 encounters, $p = 0.90$), as well as the time spent along the edge (250.9 ± 187.6 s, $p = 0.79$).

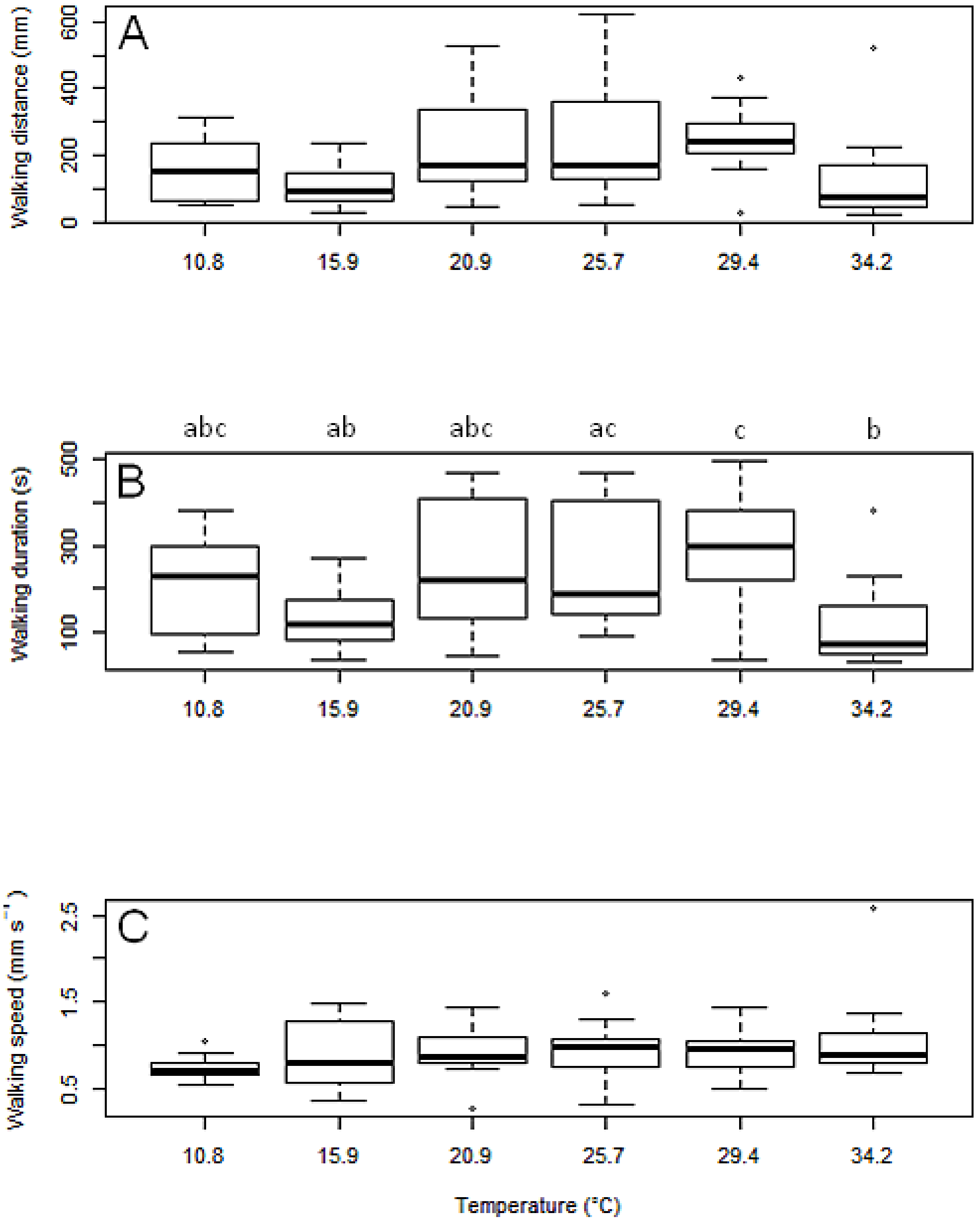


Figure 4-1 : Box plots of walking distance (A), duration (B), and speed (C) of *Anaphes listronoti* females at different temperatures during 10 min of experiment duration. Data were analyzed using linear and polynomial regressions. Boxes represent the 25th and 75th percentiles, the heavy line the median, whiskers 1.5 times the interquartile range of the data, and data points represent outliers. Differences between individual thermic treatments were not significant for walking distance (A) and speed (C) (GLM and Tukey post-hoc test), but they were significant for walking duration (B). Significant differences between thermic treatments are represented with different letters.

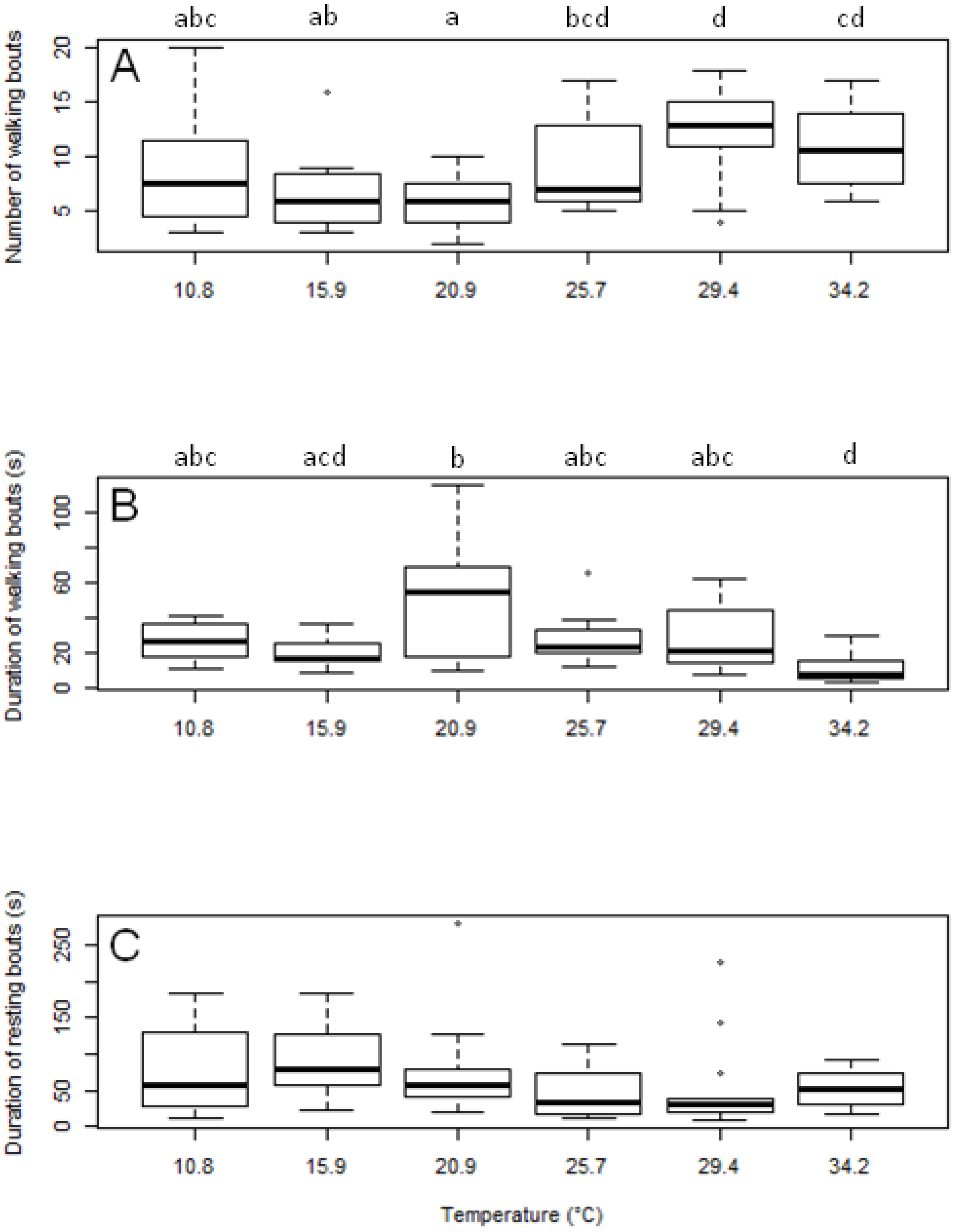


Figure 4-2: Box plots of number of walking bouts (A), duration of single walking bouts (B), and duration of single resting bouts (C) of *Anaphes listronoti* females during 10 min of experiment duration at different temperatures. Data were analyzed using linear and polynomial regressions. Boxes represent the 25th and 75th percentiles, the heavy line the median, whiskers 1.5 times the interquartile range of the data, and data points represent outliers. Differences between individual thermic treatments were significant for number of walking bouts (A) and their duration (B) (GLM and Tukey post-hoc test), but they were not for duration of resting bouts (C). Significant differences between thermic treatments are represented with different letters.

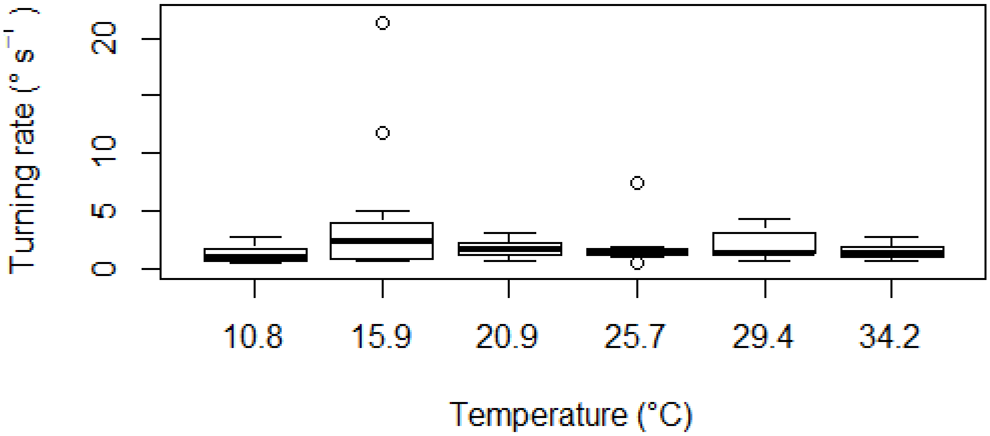


Figure 4-3: Effect of temperature on turning rate of *Anaphes listronoti* females. Boxes represent the 25th and 75th percentiles, the heavy line the median, whiskers 1.5 times the interquartile range of the data, and data points represent outliers.

4.5 / Discussion

Walking behaviour can be influenced by temperature for both invertebrate and vertebrate ectotherms (Bennett, 1990). The purpose of the study was to investigate the effect of temperature on the walking behaviour of the egg parasitoid *A. listronoti,* and to distinguish between kinetic (direct effect of biochemical reactions to temperature) vs. integrated responses (integration of and response to thermal information by the neural system) to temperature for tested parameters. The kinetic response would fit a physiological response curve (bell-shaped curve), whereas an integrated response will be noticeable through a broader thermal range, increased walking values in the case of an escape behaviour and decreased walking values in the case of energy retention.

The walking behaviour of *A. listronoti* females was greatly influenced by temperature. It is interesting to note that most walking parameters did not follow a bell-shaped curve, even though this is typically observed for arthropod development (Huey and Stevenson, 1979). At low temperatures, walking distance, walking duration, and the duration of walking bouts were higher than expected from a bell-shaped curve (Figs. 4-1A, 4-1B, 4-2B). Walking speed in ectotherms usually increases with temperature until a maximum is reached, after which walking speed decreases (Dillon and Frazier, 2006; Lachenicht et al., 2010). In contrast, the walking speed of *A. listronoti* kept increasing with temperature, up to the highest temperature tested (34.2 °C) (Figure 4-1C). A preliminary experiment had shown that all *A. listronoti* females exposed to 40°C died within the one-hour acclimation period. The expected decrease in walking speed would likely be observed between 34.2°C and 40°C. Turning rate was the only tested parameter that did not vary with temperature (Figure 4-3). These results suggest that walking behaviour is not based solely on the kinetic responses of *A. listronoti* females to temperature (the direct consequences of biochemical reaction rate), but rather corresponds to an integrated response (involving the neural network). Parasitoid females perceived and processed thermal cues from the environment and responded in a coordinated way, especially at the lower end of the species' active thermal range. When they experienced cold temperatures, females increased their walking distance and duration even though their walking speed was the lowest (Figure 4-1).

Ecologically, the distance travelled is the most important walking trait for parasitoid females, because it is closely related to the probability of finding hosts (Wajnberg and Colazza, 1998). At 34.2 °C, *A. listronoti* females walked the fastest but for the shortest duration (Figure 4-1). As a result, they travelled smaller distances than did females at 29.4 °C and 25.7 °C, which walked more slowly but for a longer time. The optimal range of temperatures for walking behaviour in *A. listronoti* females was therefore between 20 and 27 °C because walking distance was at its maximum under those conditions.

Walking duration was generally less than half of the recording time. This may be due to the fact that females were not exposed to food or host and thereby less motivated to forage in the experimental arena. Walking duration was the highest between 20.9 and 29.4 °C (Figure 4-1B) but with different profiles (Figure 4-2). The maximum duration of walking bouts was observed at 20.9 °C, whereas at higher temperatures, more walking bouts of shorter duration were observed. At 10.8 °C, walking duration was higher than it was at 15.9 °C because of both the number and the duration of walking bouts (Figure 4-2). Short walking distance and short walking duration could be due to reduced endurance at suboptimal temperatures, as found in cockroaches (Full and Tullis, 1990). Similarly, when temperature and walking speed increase, individuals tire faster and need to rest more frequently, as their metabolic rates increase with an increase of both temperature (Berrigan and Partridge, 1997) and speed (Shillington and Peterson, 2002). This results in a greater number of walking bouts of shorter duration at high temperatures (Figure 4-2). The duration of resting bouts also decreased with increasing temperature, with female walking patterns becoming more halting (Figure 4-2). Feeding the females could decrease this tiring effect, although access to food had no effect on the parasitoid *Cephalonomia stephanoderis* walking activity and searching capacity (Gomez et al., 2012).

Kinetic versus integrated response

To compare the behavioural and developmental responses of parasitoids to temperature, and to explore the relative importance of kinetic versus integrated response, we analyzed two walking parameters (distance walked and walking speed) compared to a theoretical performance response curve calculated using the formula (1) from Vasseur et al. (2014), representing the theoretical kinetic response. $\omega(T)$ designates the performance at temperature T, T_{opt} the temperature at which performance is the highest, T_{max} the last temperature before which performance becomes negative, and σ_p determines the steepness of the rising portion of the curve. Values were 34.2 for T_{opt}, 40 for T_{max} and 9.62 for σ_p.

$$(1)\ \omega(T)\begin{cases} = Exp\left[-\left(\left(T-T_{opt}\right)/2\sigma_p\right)^2\right], & T < T_{opt} \\ = 1-\left[\left(T-T_{opt}\right)/\left(T_{opt}-T_{max}\right)\right]^2, & T \geq T_{opt} \end{cases}$$

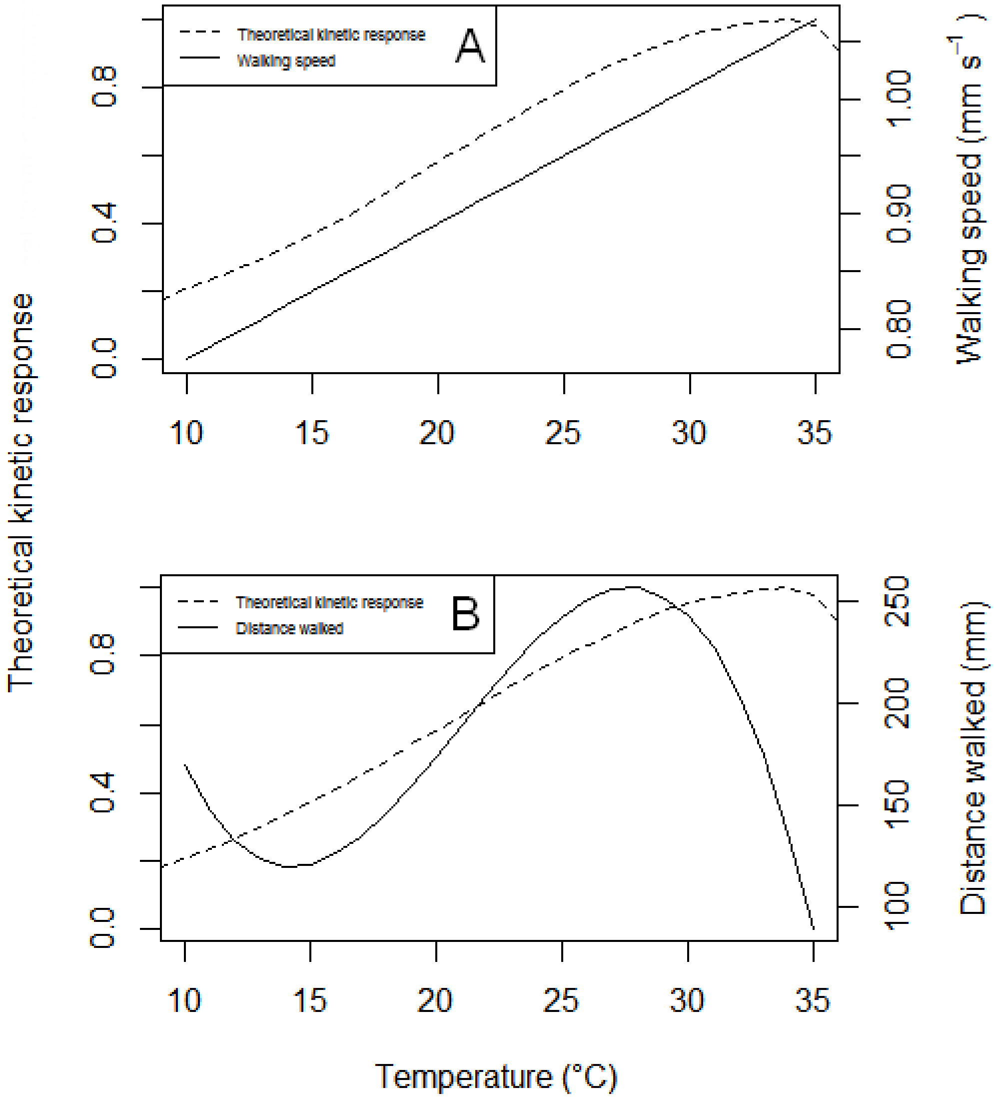


Figure 4-4: Comparison between theoretical kinetic response and walking speed (A) and distance (B) of *Anaphes listronoti* females along a temperature gradient. Theoretical kinetic response was calculated using formula (1) from Vasseur et al. (2014).

As seen in Figure 4-4A, walking speed and theoretical kinetic response follow a similar pattern over the range of temperatures, indicating that insect walking speed is closely linked to biochemical rate, thereby suggesting a kinetic response. However, it remains possible that this linear response does not correspond to a kinetic response, as we could not measure walking speed at the temperature at which the inflexion part of the curve is expected to occur. Under this uncertainty, the kinetic response represents the more conservative hypothesis, resulting only from the biochemical reactions to temperature, contrary to the integrated response that requires additional reactions: thermoreception, treatment of the information by the central nervous system, and behaviour. As a result, we favor the kinetic explanation.

The same response is observed for the duration of resting bouts, which decreased proportionally as temperature increased (Figure 4-2C). In contrast, distance walked does not follow the same pattern as kinetic response, especially at low and high temperatures (Figure 4-4B). Such a difference likely arises from an integrated response at low and high temperatures: the neurosensory system processes the thermal information and elicits a behavioural response.

We previously identified three scenarios that could be associated with an integrated response: the maintenance of the behaviour over a range of thermal conditions (Pigliucci et al., 2006), an escape response to adverse temperatures (Rosenzweig et al., 2008; Ma and Ma, 2012), and the saving of energy until the return of better conditions (Sokolova et al., 2012). We examined how each of these scenarios applies to the different walking parameters measured for *A. listronoti*. For the first scenario, *A. listronoti* females maintained constant walking distance and duration (Figure 4-1A, B) over a certain range of temperatures, from 20.9 to 29.4 °C, but not at the extreme temperatures. This first scenario does not apply to the other walking responses.

The second scenario, the escape response, would correspond to a greater walking distance and/or duration at adverse temperatures and/or to a change in turning rate. *Anaphes listronoti* females walked greater distances and for longer durations at the lowest temperature, suggesting that parasitoids spent more energy to find suitable thermal conditions (with increased walking duration leading to longer walking distance). Escape behaviour can be a component of behavioural thermoregulation, where the regulation of body temperature is achieved by selecting a thermally adequate microclimate (May, 1979; Dillon et al., 2009). In *Drosophila*, both this thermal preference (Rajpurohit and Schmidt, 2016) and walking speed of individuals (Gibert et al., 2001) can be affected by rearing temperature, suggesting that rearing temperature would likely impact the escape behaviour of parasitoids as well. Escape behaviour has been observed in insects facing high temperatures along a thermal gradient (Robertson et al., 1996; Rosenzweig et al., 2008; Ma and Ma, 2012), with klinokinesis (in which the rate of turning of a moving organism is proportional to the intensity of a stimulus) usually being the underlying mechanism (e.g., Rott and Ponsonby, 2000; Angilletta et al., 2008). However, we found no effect of temperature on the turning rate of *A. listronoti* (Figure 4-3), similar to what has been observed in other studies (see Abram et al., 2015 and references therein). The escape response of *A. listronoti* seems to be associated with increased activity rather than with intensified turning rate. Atypical elevated activity at low temperatures was also observed in crayfish by Kivivuori (1983), who suggested that the reason was “a lack of normal coordination of spontaneous walking”, with crayfish walking continuously at low temperatures, as opposed to walking and stopping when foraging at intermediate temperatures. This pattern might arise from increased excitability of the crayfish neuromuscular system in the cold, leading to changes in activity level at low temperatures. *Anaphes listronoti* females also exhibited higher activity at low temperatures by increasing walking duration but, in contrast to crayfish, walked less continuously at the lowest temperature than at the intermediate ones. The underlying biochemical mechanism could, however, be similar to the one described by Montgomery and Macdonald (1990) in crustaceans, i.e. an increase in the synaptic activity at low temperature. Changes in spontaneous movement patterns due to modifications to the central nervous system responses have also been shown in fish (Anderson and Mutchmor, 1968). Hyperexcitability of the nervous system is observed in most animals when cold and heat extremes are reached, before the loss of coordination, and is usually defined as the first step of chill coma (Hazell and Bale, 2011). This hyperexcitability could explain the increased walking distance and duration observed at 10.8 °C for *A. listronoti*. As such, this is not an integrated response to temperature, but rather a kinetic response. It would be of great interest to further test the escape response of *A. listronoti* females at low temperature. For example, by (1) placing individuals along a thermal gradient and monitoring the temperature at which they do a half-turn (Lagerspetz, 2000 ; Ma and Ma, 2012), (2) placing them at ambient temperature, presenting them a cold object and noting their response (Wittenburg and Baumeister, 1999), or (3) increasing temperature at a constant rate to observe when they escape the arena (Wang et al., 2008).

The short walking duration of *A. listronoti* females at 34.2 °C supports the third scenario, the saving of energy, despite a high metabolic rate. In ectotherms, a given behaviour is more energy-costly at high temperatures than at low temperatures (Weinstein, 1998). However, because heat damage can quickly occur when lethal temperatures are approached (Chown and Nicolson, 2004; Colinet et al., 2015), and because longevity decreases at high temperatures (Hance et al., 2007), this strategy would only be adaptive in environments where extreme conditions do not last for a long time. For example, this type of coping mechanism will be detrimental to species facing an extended heat wave. However, for prolonged extreme conditions, other adaptive behaviours could be adopted, such as entry in stupor or torpor.

The observed behavioural responses of *A. listronoti* to temperature and the described patterns indicate that the integrated response scenarios are not mutually exclusive. For instance, we observed an escape response at low temperatures (potentially driven by kinetic causes) and an energy-saving response at high temperatures for some walking parameters. In addition, it remains difficult to disentangle kinetic from integrated responses using only behavioural data: neurological insights are also required. Another option, suggested by Abram et al. (2017), is the use of temperature-insensitive mutants to discriminate the two mechanisms. Walking behaviour temperature-dependence seems more of a constraint at medium temperatures, where an increase in temperature leads to an increase in the walking behaviour performance. However, at the high and low end of the thermal range, *A. listronoti* females exhibit behaviour that could be adaptive in the thermal conditions in which they evolved: i.e. escaping cold temperatures in which they could get kinetically "trapped" and avoiding spending unnecessary energy at high temperatures. The walking behaviour of *A. listronoti* illustrates the complexity of insects' behavioural responses to temperature and the difficulty involved in assessing the underlying mechanisms. To add to the complexity, metabolic rate affects behaviour under the kinetic response, but behaviour can also affect metabolic rate, for example in the case of thermoregulation, creating a feedback loop between temperature, metabolic rate and behaviour.

From an applied perspective, walking behaviour has been used as a factor to assess the efficiency of candidate natural enemies in biological control (Wajnberg and Colazza, 1998). Our results suggest that biocontrol agents would become less efficient at finding their host when temperatures are more variable, because walking distance decreases at the low and high ends of the thermic range (Figure 4-1). The integrated behaviours, in the form of an escape response and energy-saving mechanisms, could be adaptive on the short-term, but not during long periods of sub-optimal conditions (e.g. heat waves).

Consequences of climate change

Most climate change models predict a 1.5 °C rise in global temperatures by the end of the century and an increase in the frequency of extreme events such as heat waves (Stocker et al., 2013). This scenario means that insects will more frequently encounter infra- and supra-optimal thermal thresholds. According to our results, parasitoid females in that scenario would spend less time overall foraging for hosts, leading to a lower reproduction rate. As *A. listronoti* females live for only 2 to 3 days at 29 °C in comparison with 5 to 6 days at 23 °C (Collins and Grafius, 1986b), they have less time at high temperatures than at low temperatures to find and parasitize hosts, despite being more efficient under warm conditions (Naranjo, 1993). The effects of suboptimal temperatures can, however, be locally mitigated by physiological adaptations such as heat resistance induced by heat hardening (Sgrò et al., 2016). Thermal acclimation can also play a role in mitigating exposure to both extreme low temperatures (Geister and Fischer 2007; Lachenicht et al., 2010) and extreme high temperatures (Ma and Ma, 2012; Kim et al., 2015) as well as in increasing mating performance (Geister and Fischer, 2007) and locomotion (Lachenicht et al., 2010). Finally, behavioural responses can help buffer exposure to thermal extremes when insects change the timing of their foraging activities (Candolin and Wong, 2012), thermoregulate (Kearney et al., 2009; Huey et al., 2012; Andrew et al., 2013a), select more favourable microhabitats (Wiktelius, 1987), and shift posture or orientation (Harmon and Barton, 2013). However, complex behaviours such as host searching and mating, which often involve sequential steps and chemical cues (Fasolo and Krebs, 2004; van Baaren et al., 2005; Sentis et al., 2015), could be disrupted by suboptimal temperatures more than simple behaviours such as walking are.

4.6 / Acknowledgements

This work was supported by internal funding from Agriculture and Agri-Food Canada. We thank D. Thibodeau and J. Frenette for their technical assistance; J.-P. Parent for advice on the Biotrack software; M. Varcoe for comments on the manuscript; and three anonymous reviewers for helpful suggestions to improve the manuscript. All applicable institutional and/or national guidelines for the care and use of animals were followed.

4.7 / References

Abram PK, Boivin G, Moiroux J, Brodeur J (2017) Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biological Reviews 92:1859–1876

Abram PK, Cusumano A, Peri E, Brodeur J, Boivin G, Colazza S (2015) Thermal stress affects patch time allocation by preventing forgetting in a parasitoid wasp. Behavioral Ecology 26:1326–1334

Anderson RL, Mutchmor JA (1968) Temperature acclimation and its influence on the electrical activity of the nervous system in three species of cockroaches. Journal of Insect Physiology 14:243–251

Andrew NR, Hart RA, Jung M-P, Hemmings Z, Terblanche JS (2013a) Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, *Iridomyrmex purpureus* (Formicidae), with potential climate change. Journal of Insect Physiology 59:870–880

Andrew NR, Hill SJ, Binns M, Bahar MH, Ridley EV, Jung M-P, Fyfe C, Yates M, Khusro M (2013b) Assessing insect responses to climate change: What are we testing for? Where should we be heading? PeerJ 1:e11

Angilletta MJ Jr, Roth TC II, Wilson RS, Niehaus AC, Ribeiro PL (2008) The fast and the fractalous: speed and tortuosity trade off in running ants. Functional Ecology 22:78–83

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8:1–16

Bell WJ (1990) Searching behavior patterns in insects. Annual Review of Entomology 35:447–467

Bennett AF (1990) Thermal dependence of locomotor capacity. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 259:253-258.

Berrigan D, Lighton JR (1994). Energetics of pedestrian locomotion in adult male blowflies, Protophormia terraenovae (Diptera: Calliphoridae). Physiological Zoology, 67:1140-1153.

Berrigan D, Partridge L (1997) Influence of temperature and activity on the metabolic rate of adult *Drosophila melanogaster*. Comparative Biochemistry and Physiology Part A: Physiology *118:*1301-1307.

Boivin G (1988) Laboratory rearing of *Anaphes sordidatus* [*Hym.: Mymaridae*] on carrot weevil eggs [Col.: Curculionidae]. BioControl 33:245–248

Boivin G, Martel V (2012) Size-induced reproductive constraints in an egg parasitoid. Journal of Insect Physiology 58:1694–1700

Boldt PE (1974). Temperature, humidity, and host: effect on rate of search of *Trichogramma evanescens* and *T. minutum* (not Riley, 1871). Annals of the Entomological Society of America 67:706-708.

Candolin U, Wong BBM (eds) (2012) Behavioural responses to a changing world: Mechanisms and consequences. Oxford University Press, Oxford

Chown SL, Nicolson S (2004) Insect physiological ecology: Mechanisms and patterns. Oxford University Press, Oxford

Colinet H, Sinclair BJ, Vernon P, Renault D (2015) Insects in fluctuating thermal environments. Annual Review of Entomology 60:123–140

Collins RD, Grafius E (1986a) Impact of the egg parasitoid, *Anaphes sordidatus* (Hymenoptera: Mymaridae), on the carrot weevil (Coleoptera: Curculionidae). Environmental Entomology 15:469–475

Collins RD, Grafius E (1986b) Biology and life cycle of *Anaphes sordidatus* (Hymenoptera: Mymaridae), an egg parasitoid of the carrot weevil (Coleoptera: Curculionidae). Environmental Entomology 15:100–105

Cormier D, Stevenson AB, Boivin G (1996) Seasonal ecology and geographical distribution of *Anaphes listronoti* and *A. victus* (Hymenoptera: Mymaridae), egg parasitoids of the carrot weevil (Coleoptera: Curculionidae) in central Ontario. Environmental Entomology 25:1376–1382

Coutant CC (1977) Compilation of temperature preference data. Journal of the Fisheries Research Board of Canada 34:739–745

Dillon ME, Frazier MR (2006) *Drosophila melanogaster* locomotion in cold thin air. Journal of Experimental Biology 209:364–371

Dillon ME, Wang G, Garrity PA, Huey RB (2009) Thermal preference in *Drosophila*. Journal of Thermal Biology 34:109–119

Fasolo AG, Krebs RA (2004) A comparison of behavioural change in *Drosophila* during exposure to thermal stress. Biological Journal of the Linnean Society 83:197–205

Folguera G, Bastías DA, Caers J, Rojas JM, Piulachs M-D, Bellés X, Bozinovic F (2011) An experimental test of the role of environmental temperature variability on ectotherm molecular, physiological and life-history traits: Implications for global warming. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 159:242–246

Full RJ, Tullis A (1990) Capacity for sustained terrestrial locomotion in an insect: Energetics, thermal dependence, and kinematics. The Journal of Comparative Physiology B 160:573–581

Geister TL, Fischer K (2007) Testing the beneficial acclimation hypothesis: temperature effects on mating success in a butterfly. Behavioral Ecology 18:658–664

Gibert P, Huey RB, Gilchrist GW (2001) Locomotor performance of *Drosophila melanogaster*: interactions among developmental and adult temperatures, age, and geography. Evolution 55:205-209.

Gómez J, Barrera JF, Liedo P, Valle J (2012) Influence of age and diet on the performance of *Cephalonomia stephanoderis* (Hymenoptera, Bethylidae) a parasitoid of the coffee berry borer, *Hypothenemus hampei* (Coleoptera, Curculionidae). Revista Brasileira de Entomologia 56:95-100.

Hafez M (1950) On the behaviour and sensory physiology of the house-fly larva, *Musca domestica* LI feeding stage. Parasitology 40:215–236

Hance T, van Baaren J, Vernon P, Boivin G (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. Annual Review of Entomology 52:107–126

Harmon JP, Barton BT (2013) On their best behavior: how animal behavior can help determine the combined effects of species interactions and climate change. Annals of the New York Academy of Sciences 1297:139–147

Hazell SP, Bale JS (2011) Low temperature thresholds: Are chill coma and CT_{min} synonymous? Journal of Insect Physiology 57:1085–1089

Heath JE, Hanegan JL, Wilkin PJ, Heath MS (1971). Adaptation of the thermal responses of insects. American Zoologist 11:145–156

Henderson MM., Gardner J, Raguso RA, Hoffmann MP (2017) *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) response to relative humidity with and without host cues. Biocontrol Science and Technology 27:128-138.

Huber JT, Côté S, Boivin G (1997) Description of three new *Anaphes* species (Hymenoptera: Mymaridae), egg parasitoids of the carrot weevil, *Listronotus oregonensis* (Leconte) (Coleoptera: Curculionidae), and redescription of *Anaphes sordidatus* Girault. The Canadian Entomologist 129:959–977

Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1665–1679

Huey RB, Stevenson RD (1979) Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. American Zoologist 19:357–366

Hurlbert AH, Ballantyne F IV, Powell S (2008) Shaking a leg and hot to trot: the effects of body size and temperature on running speed in ants. Ecological Entomology 33:144–154

Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proceedings of the National Academy of Sciences of the United States of America 106:3835–3840

Kim HG, Margolies D, Park Y (2015) The roles of thermal transient receptor potential channels in thermotactic behavior and in thermal acclimation in the red flour beetle, *Tribolium castaneum*. Journal of Insect Physiology 76:47–55

Kivivuori L (1983) Temperature acclimation of walking in the crayfish *Astacus astacus* L. Comparative Biochemistry and Physiology Part A: Physiology 75:375–378

Kjærsgaard A, Blanckenhorn WU, Pertoldi C, Loeschcke V, Kaufmann C, Hald B, Pagès N, Bahrndorff S (2015) Plasticity in behavioural responses and resistance to temperature stress in *Musca domestica*. Animal Behaviour 99:123–130

Lachenicht MW, Clusella-Trullas S, Boardman L, Le Roux C, Terblanche JS (2010) Effects of acclimation temperature on thermal tolerance, locomotion performance and respiratory metabolism in *Acheta domesticus* L. (Orthoptera: Gryllidae). Journal of Insect Physiology 56:822–830

Lagerspetz KYH (2000) Thermal avoidance and preference in *Daphnia magna*. Journal of Thermal Biology 25:405–410

LeConte JL (1862) Classification of the Coleoptera of North America: prepared for the Smithsonian Institution. Smithsonian institution.

Ma G, Ma C-S (2012) Effect of acclimation on heat-escape temperatures of two aphid species: Implications for estimating behavioral response of insects to climate warming. Journal of Insect Physiology 58:303–309

Martel P, Svec HJ, Harris CR (1975) Mass rearing of the carrot weevil, *Listronotus oregonensis* (Coleoptera: Curculionidae), under controlled environmental conditions. The Canadian Entomologist 107:95–98

May ML (1979) Insect thermoregulation. Annual Review of Entomology 24:313–349

Moiroux J, Abram PK, Louâpre P, Barrette M, Brodeur J, Boivin G (2016) Influence of temperature on patch residence time in parasitoids: physiological and behavioural mechanisms. The Science of Nature 103:32

Montgomery JC, Macdonald JA (1990) Effects of temperature on nervous system: implications for behavioral performance. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 259:R191–R196

Naranjo SE (1993) Life history of *Trichogrammatoidea bactrae* (Hymenoptera: Trichogrammatidae), an egg parasitoid of pink bollworm (Lepidoptera: Gelechiidae), with emphasis on performance at high temperatures. Environmental Entomology 22:1051–1059

Neven LG (2000) Physiological responses of insects to heat. Postharvest Biology and Technology 21:103–111

Parent J-P (2016) La perception du temps et sa modulation par la température chez les guêpes parasitoïdes. PhD thesis, Département de sciences biologiques, Université de Montréal, Montréal, Québec, Canada

Pigliucci M, Murren CJ, Schlichting CD (2006) Phenotypic plasticity and evolution by genetic assimilation. Journal of Experimental Biology 209:2362–2367

Rajpurohit S, Schmidt PS (2016) Measuring thermal behavior in smaller insects: A case study in *Drosophila melanogaster* demonstrates effects of sex, geographic origin, and rearing temperature on adult behavior. Fly 10:149-161.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Robertson R, Kuhnert C, Dawson J (1996) Thermal avoidance during flight in the locust *Locusta migratoria*. Journal of Experimental Biology 199:1383–1393

Rosenzweig M, Kang K, Garrity PA (2008) Distinct TRP channels are required for warm and cool avoidance in *Drosophila melanogaster*. Proceedings of the National Academy of Sciences of the United States of America 105:14668–14673

Rott AS, Ponsonby DJ (2000) The effects of temperature, relative humidity and host plant on the behaviour of *Stethorus punctillum* as a predator of the two-spotted spider mite, *Tetranychus urticae*. BioControl 45:155–164

Schulte, PM (2015). The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment Journal of Experimental Biology 218:1856-1866.

Sentis A, Ramon-Portugal F, Brodeur J, Hemptinne J-L (2015) The smell of change: warming affects species interactions mediated by chemical information. Global Change Biology 21:3586–3594

Sgrò CM, Terblanche JS, Hoffmann AA (2016) What can plasticity contribute to insect responses to climate change? Annual Review of Entomology 61:433–451

Shillington C, Peterson CC (2002) Energy metabolism of male and female tarantulas (*Aphonopelma anax*) during locomotion. Journal of Experimental Biology 205:2909-2914.

Sokolova IM, Frederich M, Bagwe R, Lannig G, Sukhotin AA (2012) Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Marine Environmental Research 79:1–15

Stocker TF, Qin D, Plattner G-K, Tignor MMB, Allen SK, Boschung J, Naeuls A, Xia Y, Bex V, Midgley PM (2013) Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge and New York

Suverkropp BP, Bigler F, van Lenteren JC (2001) Temperature influences walking speed and walking activity of *Trichogramma brassicae* (Hym., Trichogrammatidae). Journal of Applied Entomology 125:303–307

Traoré L, Pilon JG, Fournier F, Boivin G (2006) Adaptation of the developmental process of *Anaphes victus* (Hymenoptera: Mymaridae) to local climatic conditions across North America. Annals of the Entomological Society of America 99:1121-1126

van Baaren J, Outreman Y, Boivin G (2005) Effect of low temperature exposure on oviposition behaviour and patch exploitation strategy in parasitic wasps. Animal Behaviour 70:153–163

Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CD, McCann KS, ... & O'Connor MI. (2014). Increased temperature variation poses a greater risk to species than climate warming. Proceedings of the Royal Society B: Biological Sciences, 281(1779), 20132612.

Wajnberg E, Colazza S (1998) Genetic variability in the area searched by a parasitic wasp: analysis from automatic video tracking of the walking path. Journal of Insect Physiology 44:437–444

Wang G, Gordon TN, and Rainwater S (2008) Maximum voluntary temperature of insect larvae reveals differences in their thermal biology. Journal of Thermal Biology 33:380-384.

Weinstein RB (1998) Effects of temperature and water loss on terrestrial locomotor performance in land crabs: Integrating laboratory and field studies. American Zoologist 38:518–527

Wiktelius S (1987) Distribution of *Rhopalosiphum padi* (Hornoptera: Aphididae) on spring barley plants. Annals of Applied Biology 110:1–7

Wittenburg N, Baumeister R (1999) Thermal avoidance in *Caenorhabditis elegans*: An approach to the study of nociception. Proceedings of the National Academy of Sciences of the United States of America 96:10477–10482

Chapitre 5 : The effect of temperature on host patch exploitation by an egg parasitoid

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Laurie Blanchemain

5.1 / Abstract

1. The effect of temperature during host patch exploitation behaviour of parasitoids remains poorly understood, despite its importance for female reproductive success.
2. Under laboratory conditions, we explored the behaviour of *Anaphes listronoti,* an egg parasitoid of the carrot weevil (*Listronotus oregonensis*), when foraging on a high-quality host patch at five temperatures.
3. Temperature had a strong effect on the female tendency to exploit the patch. *A. listronoti* females parasitized more eggs at an intermediate temperature (20°C to 30°C) compared to those foraging at the extremes of the range (15.9°C and 32.8°C).
4. For parasitized eggs, there was no difference in offspring sex ratio and clutch size between temperatures.
5. Mechanisms of host acceptance within a patch differed between temperatures, especially at 32.8°C, where females used ovipositor insertion rather than antennal contact to assess whether a host was already parasitized or not, suggesting that host handling and chemical cues detection were probably constrained at high temperature.
6. Females spent less time on the host patch with increasing temperatures, but temperature had no effect on patch-leaving rules.
7. At low temperatures, parasitoid performance was higher than expected, possibly due to the efficiency of patch exploitation strategies.

Keywords: Patch leaving rules – Behavioral constraint – Parasitism – *Anaphes listronoti* – *Listronotus oregonensis*

5.2 / Introduction

When reproductively active, female parasitoids spend a large portion of their time searching for and exploiting host patches (Lauzière et al., 2000). In the context of the optimal foraging theory, the marginal value theorem (MVT; Charnov, 1976) explores searching and ovipositional decisions made by parasitoid females. The MVT predicts the duration a female should spend on host patches of various qualities, as modulated by travel duration between patches. Several decision rules and statistical models have been developed to assess the extent to which a female should exploit a patch (Wajnberg, 2006). Some of these rules and models stem from the idea that, unlike an assumption from MVT, females are not omniscient and need to continuously acquire information from the patch when foraging (Jorgensen and Fath, 2008). Acceptance or rejection of a given host often has an incremental or decremental effect on the propensity to stay or leave a patch, depending on the species studied (Wajnberg et al., 2003; Wajnberg, 2006). Several factors affecting patch residence time have been studied, including patch quality, female age, egg load, previous experiences and abiotic conditions (Wajnberg, 2006). However, the role of temperature, a decisive biotic factor influencing behavioural components of ectothermic organisms (Abram et al., 2017), on host patch exploitation has scarcely been investigated (Amat et al., 2006; Moiroux et al., 2016), despite the expected more extreme and variable thermic conditions under climate change scenarios (Stocker et al., 2013).

Insect performance is typically maximized along a range of temperatures. Outside this range, at sub- and supra-optimal temperatures, performances are reduced until temperature in both the low and high ends reaches a lethal point (Vannier, 1994). However, a change in performance for a trait or behaviour does not necessarily infer that an individual is operating under physiological constraints. In some cases, a behavioural change would be an adaptation to local conditions in order to gain or maintain fitness. For example, a parasitoid female can alter sex allocation in her progeny at high temperature to maximize her own reproductive fitness (Moiroux et al., 2014). High temperature during insect development usually results in individuals developing faster and being smaller at the adult stage than individuals reared at low temperature (Temperature-Size Rule (TSR); Atkinson, 1994; Colinet et al., 2007), with adult size having more fitness consequences for females than for males (Charnov et al., 1981; Honěk, 1993). However, as shown by Moiroux et al. (2014) and further reviewed by Abram et al. (2017), it can be difficult to disentangle behaviours that represent an adaptive response to abiotic conditions from those that result from a physiological constraint due to the effect of temperature on metabolic function. Abram et al. (2017) suggested the use of a kinetic null temperature model to unravel the behavioural adaptive responses from the constrained physiological responses. Such a null model describes only the kinetic effects of temperature on insect behaviour and allows comparison of this response to other potential integrated behaviours. Integrated behaviours result from the assimilation of thermic information by the central nervous system of the insect, followed by a behavioural response to this information.

The first goal of this study was to examine elements of the patch exploitation behaviour of an egg parasitoid at sub- and supra-optimal temperature: percent parasitism, offspring sex-ratio, clutch size, residence time and patch-leaving rules. We predicted that females would spend less time on the patch as temperature increases, because of two potential phenomena : (1) the increase in metabolic rate with temperature, leading to an acceleration of all behaviours (walking speed, host handling and oviposition), resulting in the patch being exploited faster (kinetic response), and (2) an increase in subjective duration perceived by the female at higher temperature (Parent, 2016), leading to a decreased residence time (integrated response). An alternative integrated response (3) would be that, at low temperature, females would increase residence time because of the decrease between pre-trial temperature and trial temperature, suggesting adverse environmental conditions such as rain or wind (Amat et al., 2006).

The second goal was to differentiate between physiologically-constrained behaviour and adaptive behaviour of females exploiting a patch at different temperatures using a kinetic null model (the metabolic rate of the insect). If the response of females to temperature is kinetic (i.e., it follows the null model), studied behaviours (number of ovipositions, antennal rejections, ovipositor rejections, residence times) will vary proportionally to females' walking speed. Walking speed is a proxy for kinetic response as it is proportional to metabolic rate (Berrigan and Lighton, 1994; Berrigan and Partridge, 1997), leading to an increase in performance as temperature increases until the reach of a tipping point, after which performance decreases (Huey and Stevenson, 1979; Angilletta, 2006). Sex allocation and clutch size should, however, remain unchanged, as well as patch-leaving rules. In the case of an integrated response, we expect the maintenance or an increase of the number of ovipositions along the tested thermal range. We also anticipate an increase in sex ratio at high temperatures, because individuals are smaller when they develop at high temperatures (TSR, Atkinson, 1994; Colinet et al., 2007), and being bigger is more important for females than for males (Charnov et al., 1981; Honěk, 1993). Accordingly, we expect females to lay a smaller clutch size as temperature increases, because siblings developing from the same host are smaller than those that developed alone in the host (Boivin and Martel, 2012). Females could compensate for smaller offspring caused by TSR by laying only one egg per host. In addition, we hypothesized that extreme temperatures would create additional constraints (indirect consequences of metabolic rate), leading to a decrease in efficiency for the following parameters: (1) handling time (Sentis et al., 2013), (2) egg fertilization (through physical impairment of the spermatheca muscular contraction or sperm motility (Moiroux et al., 2014) leading to an increase in primary sex ratio (proportion of males), and (3) detection of chemical cues (Sentis et al., 2015) used to assess patch quality (e.g. kairomones concentration) (Waage, 1979) or parasitism status (healthy vs. parasitized host) (Van Baaren et al., 2005). For females exhibiting one or several of these behaviours, we predicted a reduced performance compared to the kinetic null model. On the other hand, females could still maximize their performance under non-optimal environmental conditions by adapting their behaviour to increase their own fitness or the fitness of their offspring through integrated response to temperature, for example through maternal effect (Mousseau and Fox, 1998). In this case, we should observe a higher performance than that expected under the null model. We defined performance here as the reproductive success of females, i.e. parasitism rate.

We examined the influence of temperature on host patch exploitation by *Anaphes listronoti* Huber (Hymenoptera: Mymaridae), an egg parasitoid of the carrot weevil *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae). *Anaphes listronoti* females are moderately synovigenic, as they possess 70% of their final egg load at emergence (Boivin and Martel, 2012), and facultatively gregarious, as 1 to 6 individuals can develop in the same host (Collins and Grafius, 1986). Females of this genus can distinguish between hosts parasitized by themselves, their conspecifics and other species (Van Baaren et al., 1994). Exposure to cold temperature during the pupal stage can affect their learning capacity (Van Baaren et al., 2006), the number of eggs laid, their ability to discriminate between parasitized and unparasitized hosts, and patch-leaving rules (Van Baaren et al., 2005). However, the effects of adverse temperature during patch exploitation remain to be explored.

5.3 / Material and methods

Parasitoids

Anaphes listronoti was reared on carrot weevil eggs in the laboratory at 24°C ± 2°C, 50% RH (relative humidity) and 16L:8D following Boivin (1988). The strain originated from an Agriculture and Agri-Food Canada (AAFC) untreated carrot field in Sainte-Clotilde, Quebec, Canada (45°09′N, 73°41′W).

Patch exploitation experiment

Females' foraging behaviour on host patch was tested at five temperatures: 15.9°C, 20.2°C, 24.9°C, 28.4°C, and 32.8°C (maximum temperature variation = 1.4°C; N = 267). During pre-tests, no oviposition occurred at 10°C, and all wasps were dead after 1-hour acclimation at 40°C. Temperatures were measured in the experimental arena (Petri dish) using a thermocouple (Omega, model HH23). Host patches consisted of 16 freshly-extracted carrot weevil eggs that were less than 24 h old. Eggs were placed inside a Petri dish (5.6 mm diameter) on a humidified filter paper along a 1.5 cm square grid consisting of 4 × 4 eggs. Each egg on the grid was given a position (rows: A, B, C, D and columns: 1, 2, 3, 4) so what emerged from the host egg could be linked to the behaviour of the mother. The patch area was delimited by a 2.5-cm-diameter circle around the eggs. A 1-day-old mated naive (no previous contact with hosts) female contained in a 300-µL Beem® polyethylene capsule and the Petri dish containing the eggs were placed in a growth chamber (Sanyo, model MLR351H) during 1 hour for acclimation to tested temperatures. The female was then released in the center of the host patch and, based on pre-tests, videotaped for 3 h or until she left the patch for 2 min. At the end of the behavioural observations, eggs were placed individually in identified 300-µL Beem® polyethylene capsule and reared at 24°C ± 2°C, 50% RH, 16L:8D until host or parasitoid emergence. Each female was only tested once. Experiments ran between 10:00 and 16:30.

Video analyzing

Only videos of females that exploited a patch (oviposited in at least one host) and laid at least one female progeny were included in the analysis (N = 4, 14, 20, 23 and 20 at 15.9°C, 20.2°C, 24.9°C, 28.4°C, and 32.8°C, respectively). Females that laid only sons were considered unmated and were removed from analysis (N = 7) because the behaviour of virgin females could differ from that of mated females (Fauvergue et al., 2008). The proportion of ovipositing females over all tested females was calculated for each temperature. The frequency and duration of three types of interactions with host eggs were quantified: (1) antennal rejection – the female moves away from the host egg following antennal contact; (2) ovipositor rejection – the female climbs on the host egg, inserts her ovipositor for a short period of time (a few seconds to a few minutes) and then leaves; and (3) oviposition – the female climbs on the host egg, inserts her ovipositor for several minutes, marks the egg by walking around it and then leaves. We also calculated the time spent by the female without interacting with the host (when she was exploring, resting or grooming) and the frequency of exploration outside the host patch.

Offspring production

Capsules containing host eggs were checked for emergence every 2 to 3 days. At 25°C, development lasts 10 to 11 days (Traoré et al., 2006). After 21 days, the remaining eggs were dissected, and the content was identified as either a wasp, a weevil larva or an aborted egg. Wasps detected from dissection were included in the offspring data (N = 77, over 171 dissected eggs). In *A. listronoti*, primary sex ratio cannot be determined during oviposition as for other egg parasitoid species (Van Baaren et al., 1995). The sex ratio was therefore assessed using emerged wasps. Clutch size was also noted.

Null model

Previous data on *A. listronoti* walking speed under different temperatures (Augustin et al., 2020) was used as a proxy for metabolic rate. This proxy represents the null thermic model (*sensu* Abram et al., 2017), i.e. the metabolic effect of temperature on behaviour, without further response or constraint from the organism. Walking speed (mm s^{-1}) in relation to temperature was calculated using the following equation:

(1) $\text{Walking Speed (T)} = a*\text{T} + b$

where T is the temperature (°C), *a* represents the increase in walking speed corresponding to an increase in temperature, with a value of 0.01184, and *b* represents the theoretical walking speed of *A. listronoti* females at 0°C, with a value of 0.65471.

Data analyses

Linear and polynomial regressions were used to analyse the effect of temperature on the different variables studied (oviposition/rejection behaviours and offspring parameters). A Cox proportional hazards model (Cox,

1972) was used to determine cues used by females to leave the patch as related to temperature. The Cox model is expressed in term of hazard rate or the probability per unit of time that a female would leave the patch. It is based on the assumption that the hazard rate is the product of a baseline hazard and the effects of all the explanatory variables. The model can be expressed as:

$$h(t;z)=h_0(t)\exp\left\{\sum_{i=1}^{p}\beta_i z_i(t)\right\} \quad (2)$$

where $h(t;z)$ is the hazard rate, $h_o(t)$ the baseline hazard, t the time since the female entered the patch, and β_i the regression coefficient giving the relative contribution of the covariates $z_i(t)$. The hazard ratio, given by the expression $exp(\beta_i z_i)$, determines whether the covariable z_i influences the patch-leaving tendency of the females. If the hazard ratio is inferior to 1, the female patch-leaving tendency is reduced by this covariable. If the hazard ratio is higher than 1, the patch-leaving tendency is increased by the covariable (Wajnberg et al., 2003; Van Baaren et al., 2005). The variables tested were: number of antennal and ovipositor rejections, number of ovipositions, number of times the female exited the patch (for less than 2 min), number of rejections of non-parasitized hosts, number of rejections of parasitized hosts, rates of oviposition and rejection. The effect of each variable and the overall significance of the model were tested using likelihood ratio tests.

5.4 / Results

Patch acceptance

Fewer *A. listronoti* females exploited the patches at low and high temperatures than at intermediate temperatures (second degree polynomial, $p \leq 0.001$, $R^2 = 0.16$; Figure 5-1), with patch acceptance being maximum at 28.4°C. The total number of females accepting the patch was low at 15°C (N=4), and analyses were run with and without them. There was no difference in the significance of tested variables with and without the 15°C treatment, except for duration of ovipositor rejection and clutch size, with lost and gained significance without the 15°C treatment, respectively. Therefore, we kept the 15°C treatment in our analyses.

Patch time allocation

When *A. listronoti* females did exploit the patch, patch time allocation was significantly affected by temperature: both the frequency and duration of behaviours varied between temperatures (Figure 5-2). Temperature had a significant effect on the number of antennal rejections ($p = 0.003$), ovipositor rejections (p =

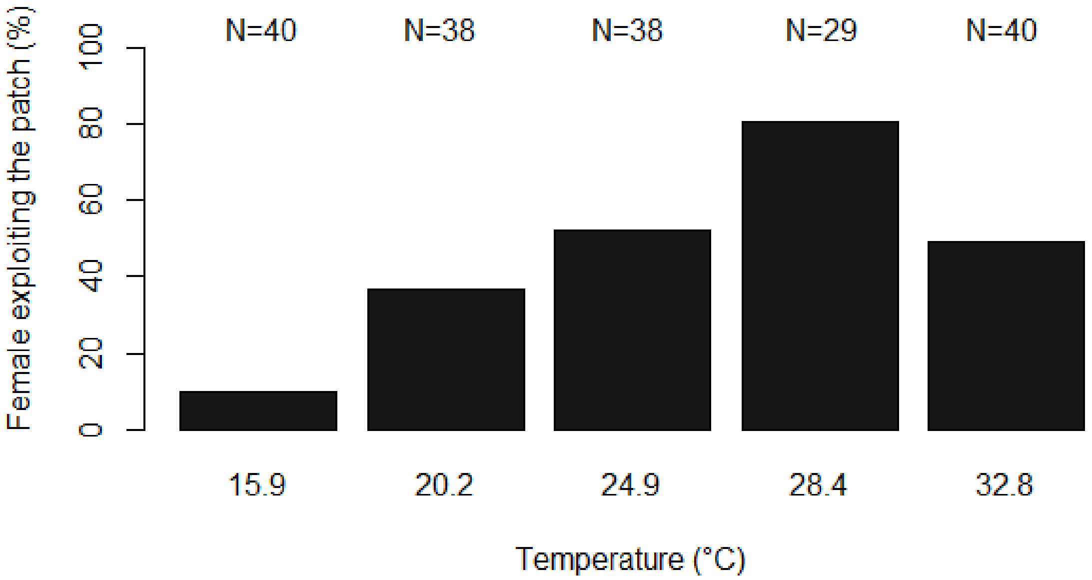

Figure 5-1: Percentage of tested *Anaphes listronoti* females that oviposited in at least one host egg (*Listronotus oregonensis*) at different temperatures.

0.006) and ovipositions ($p \leq 0.001$; Figure 5-2b). Females spent overall more time performing antennal rejection at low and intermediate temperatures compared to 32.8°C ($p \leq 0.001$, $R^2 = 0.30$; Figure 5-2a) due to a decrease in both frequency and duration at high temperature ($p \leq 0.001$; Figure 5-2b). In contrast, they spent more time performing ovipositor rejections at 32.8°C compared to other temperatures ($p \leq 0.001$, $R^2 = 0.32$; Figure 5-2a) due to a higher frequency of this behaviour. The durations of ovipositor rejections and ovipositions decreased from 15°C to 28.4°C but increased at 32.8°C ($p = 0.002$ and $p \leq 0.001$, respectively). Despite this change in oviposition duration, females spent relatively more time ovipositing at intermediate temperatures than at low and high temperatures ($p = 0.01$, $R^2 = 0.09$; Figure 5-2a) because of the increased frequency of the behaviour. There were no significant relationships between temperatures and the number and duration of other behaviours (exploring, resting and grooming, $p = 0.09$) or the frequency of temporary exploration outside the host patch ($p = 0.14$).

Patch-exploitation strategy

Females left the host patch earlier as temperature increased ($p = 0.008$; Figure 5-3), but cues used in patch-leaving decisions did not change with temperature (Table 5-1). Females' tendency to leave the patch increased together with oviposition and rejection rates at almost all temperatures. All other tested covariables had no effect. There was a significant correlation between the number of rejections and the number of oviposition (Pearson's correlation: 0.62 for antennal rejection and 0.24 for ovipositor rejection; $p = 6.7 \times 10^{-10}$ et 0.03 respectively).

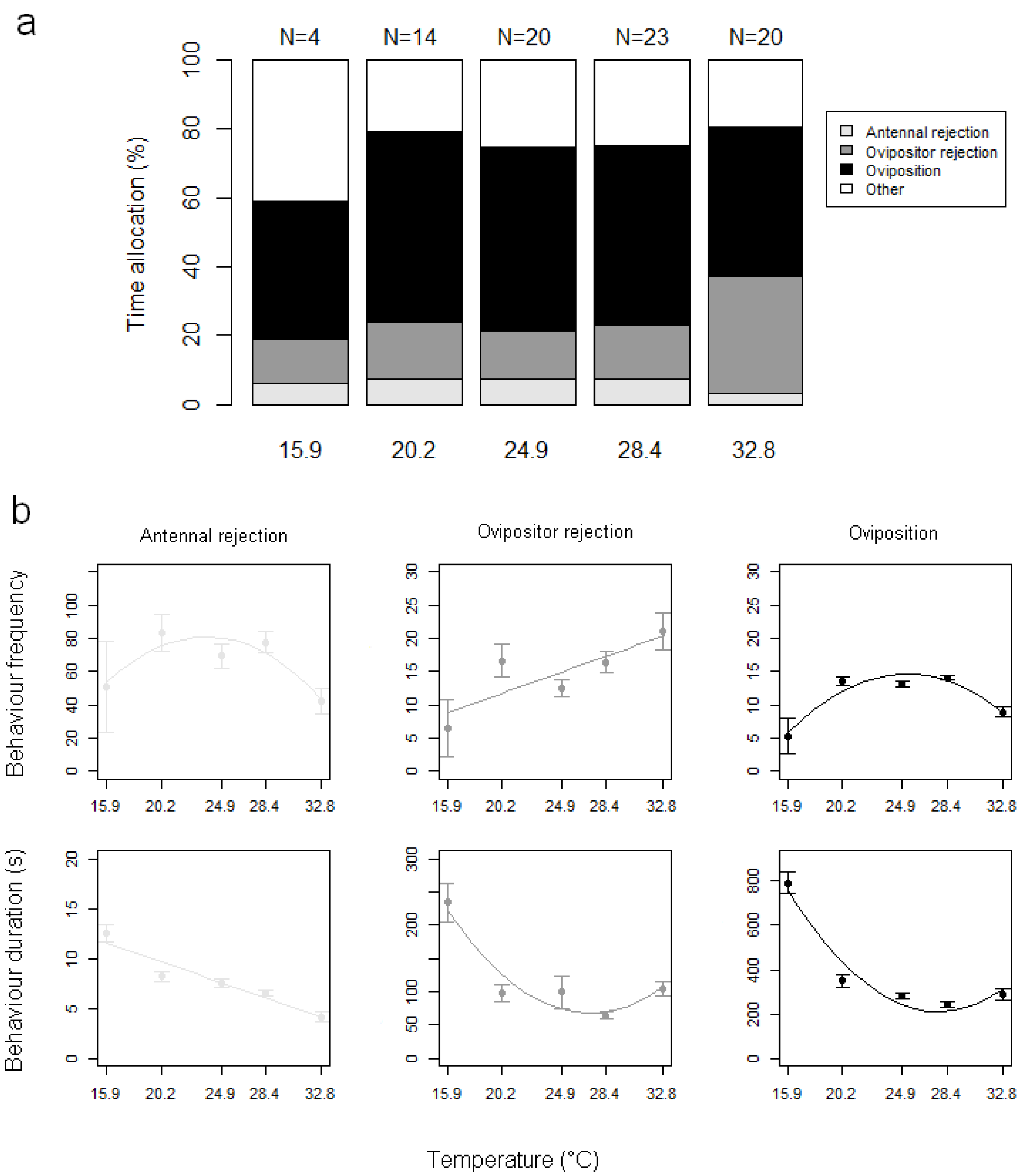

Figure 5-2: (a) Time allocation of behaviours of *Anaphes listronoti* females during host patch exploitation (*Listronotus oregonensis*) as related to temperature. Other behaviours include grooming, resting and walking. (b) Frequency and duration of *A. listronoti* females' behaviours at different temperatures.

	15.9°C			20.2°C			24.9°C			28.4°C			32.8°C		
	β ± se	exp(β)	p	β ± se	exp(β)	p	β ± se	exp(β)	p	β ± se	exp(β)	p	β ± se	exp(β)	p
Number of antennal rejection	-0.01 ± 0.02	0.99	0.4	0.02 ± 0.01	1.02	0.1	0.006 ± 0.008	1.006	0.5	-0.005 ± 0.007	0.99	0.5	-0.003 ± 0.009	0.99	0.7
Number of ovipositor rejection	-0.09 ± 0.13	0.91	0.4	-0.005 ± 0.04	0.99	0.9	0.04 ± 0.04	1.04	0.3	-0.05 ± 0.04	0.95	0.2	-0.02 ± 0.02	0.98	0.4
Number of oviposition	-0.14 ± 0.2	0.87	0.4	-0.07 ± 0.11	0.93	0.5	0.07 ± 0.09	1.08	0.4	-0.03 ± 0.14	0.98	0.9	-0.09 ± 0.08	0.92	0.3
Rejection of good host	0.33 ± 0.26	1.4	0.05	0.01 ± 0.01	1.01	0.4	0.04 ± 0.02	1.04	0.09	-0.003 ± 0.02	0.99	0.9	-0.02 ± 0.01	0.98	0.2
Rejection of bad host	-0.02 ± 0.02	0.98	0.3	0.01 ± 0.01	1.01	0.3	0.003 ± 0.008	1.003	0.7	-0.007 ± 0.007	0.99	0.3	0.004 ± 0.008	1.004	0.6
Total rejection	-0.01 ± 0.02	0.99	0.4	0.01 ± 0.01	1.01	0.2	0.006 ± 0.007	1.006	0.4	-0.005 ± 0.006	0.99	0.4	-0.004 ± 0.008	0.99	0.6
Number of patch exit	-0.5 ± 0.49	0.61	0.09	0.006 ± 0.03	1.006	0.8	0.07 ± 0.03	1.07	0.04 *	-0.03 ± 0.02	0.97	0.06	-0.02 ± 0.05	0.98	0.6
Oviposition rate	27.2 ± 45	6.63 x 10^{11}	0.5	83.1 ± 26.1	1.2 x 10^{36}	≤ 0.001 ***	82.9 ± 18.5	1.09 x 10^{36}	≤ 0.001 ***	103.5 ± 23	9.08 x 10^{44}	≤ 0.001 ***	23.9 ± 10.7	2.53 x 10^{10}	0.02 *
Rejection rate	1.45 ± 3.6	4.25	0.7	4.71 ± 1.55	110.5	≤ 0.001 ***	3.11 ± 1.07	22.51	0.004 **	3.68 ± 1.2	39.46	0.001 ***	1.13 ± 0.72	3.1	0.1

Table 5-1: Effects of different behavioural components on residence time of *Anaphes listronoti* females at different temperatures when exploiting *Listronotus oregonensis* egg patches. Estimated regression coefficients β ± se, hazard ratios exp(β), and p-values were calculated from Cox regression models and likelihood ratio tests, respectively.

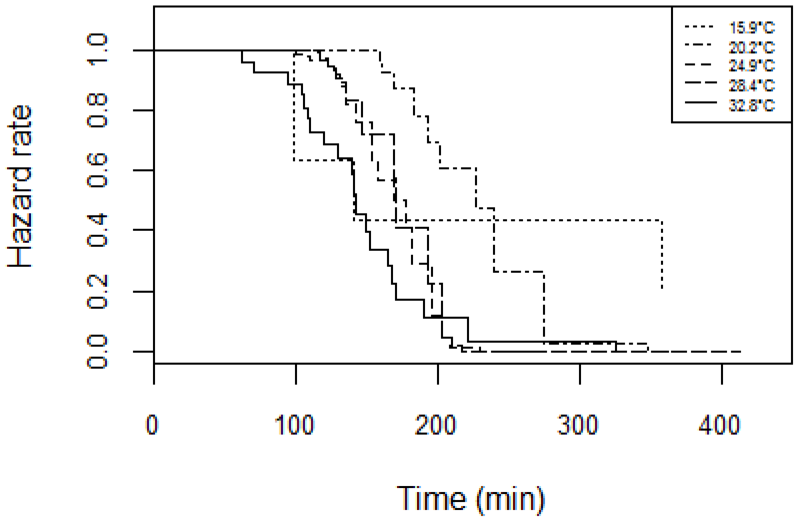

Figure 5-3: Patch-leaving hazard rate of *Anaphes listronoti* females when exploiting *Listronotus oregonensis* egg masses at different temperatures.

Offspring number and sex ratio

Females parasitized fewer eggs at high and low temperatures (2nd degree polynomial regression, $p \leq 0.001$, $R^2 = 0.50$) than at intermediate temperatures (Figure 5-4). Percent parasitism was higher when estimated from video sequences than when calculated from parasitoid emergence and host egg dissection (Mann-Whitney test, $p = 0.009$): 13.6 ± 16.9% of observed parasitized eggs yielded no offspring. This effect was greater at 32.8°C (29.7 ± 23.6%) than at 24.9°C and 28.4°C (Tukey – quasibinomial GLM, $p = 0.04$ and $p = 0.003$ – Figure 5-5). Temperature had no significant effect on offspring sex ratio (linear regression: $p = 0.35$, mean sex-ratio: 0.16 ± 0.11) and clutch size (linear regression: $p = 0.08$, mean clutch size: 1.26 ± 0.22). However, when the 15.9°C treatment was removed from analysis, clutch size significantly decreased with temperature (linear regression: p = 0.02)

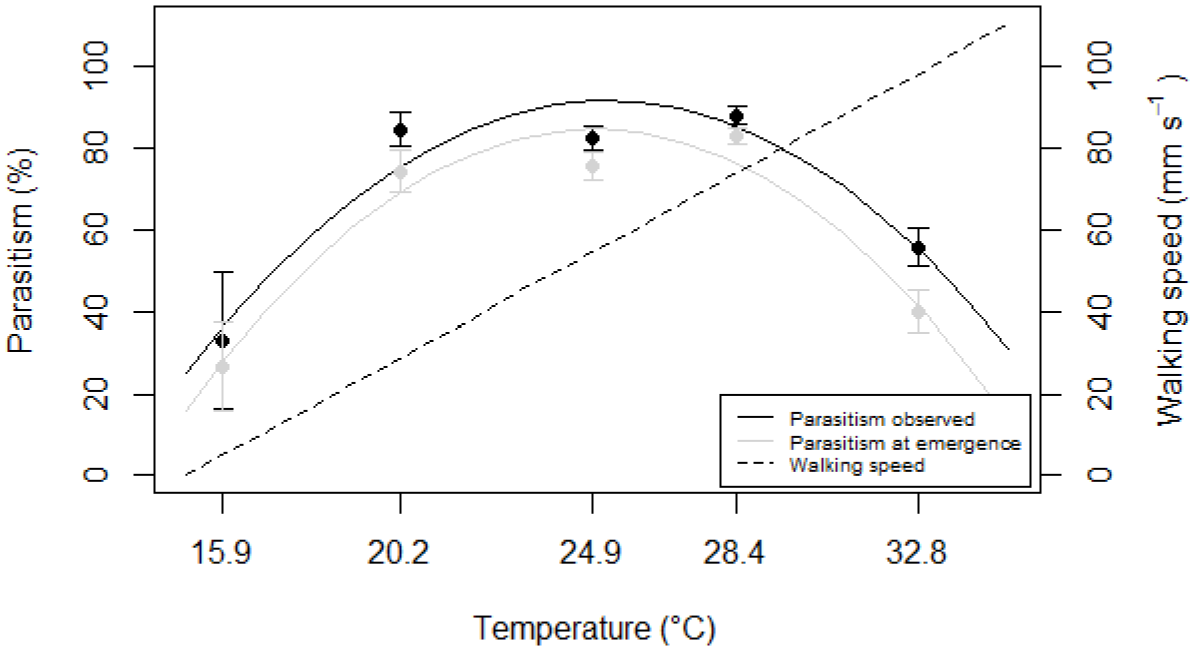

Figure 5-4: Percentage of *Anaphes listronoti* parasitism of *Listronotus oregonensis* eggs ($\overline{X}$ ± SE), calculated from either video sequences (black) or offspring emergence (grey), and walking speed calculated from formula 1; (see text)

Null model

Anaphes litronoti performance, expressed by percent parasitism, was maximum at 28.4°C (Figure 5-4). It was higher than expected under the null kinetic model at all sub-optimal temperatures and lower than expected at the supra-optimal temperature. Duration of antennal rejection and patch residence time were the only variables proportional to walking speed. For other variables, most significant responses followed a bell curve or a reverse bell curve along the thermic range and thus differed from the kinetic null model.

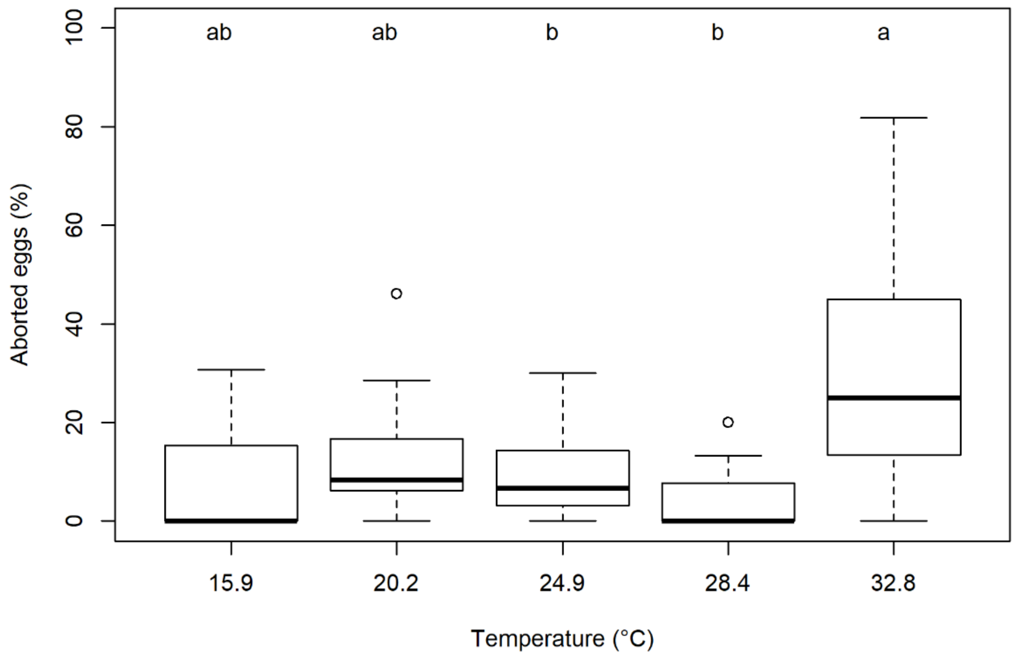

Figure 5-5: Percentage of *Listronotus oregonensis* aborted eggs in patches exploited by *Anaphes listronoti* females at different temperatures. Boxes represent the 25th and 75th percentiles, the heavy line represents the median, whiskers represent 1.5 × interquartile range of the data, and data points represent outliers. Different letters represent significant differences between temperatures.

5.5 / Discussion

Temperature significantly influenced host patch exploitation by *A. listronoti* females under laboratory conditions, with maximum parasitism observed at 28.4°C. The females spent less time on the patch with increasing temperatures, and parasitism rate was lower at low and high temperatures, but there was no difference in offspring sex ratio or clutch size. Time budget during patch exploitation differed between temperatures, especially at 32.8°C, where females switched from antennal to ovipositor rejections while using the same cues for patch-leaving decisions, i.e. oviposition and rejection rate. The null model showed that *A. listronoti* performance was higher than expected under kinetic constraint only for sub-optimal temperatures, but lower than expected at supra-optimal temperatures.

Patch acceptance

At all tested temperatures except 28.4°C, only half or less of the females exploited the host patch (Figure 5-1), probably resulting from the artificial experimental conditions. *Anaphes listronoti* tendency to leave the host patch without exploiting it was significantly affected by temperature. Fournier and Boivin (2000) showed that the dispersal capacity of two *Trichogramma* species was influenced by environmental conditions, mostly wind, solar radiation and temperature. In parasitoids, warm temperatures are usually associated with higher dispersal through increases in walking and mostly flying capacities (Forsse et al., 1992; Langer et al., 2004; Gaudon et al., 2018). In a previous study, we found that *A. listronoti* females walked a greater distance at intermediate temperature (20°C to 30°C) than at lower and higher temperatures (Augustin et al., 2020). However, here we report the highest patch departure rates at the lowest and highest temperatures tested. Reduced patch acceptance could be related to a lower capacity of parasitoid females to detect chemical host-associated cues. In an aphid-ladybeetle system, Sentis et al. (2015) showed that temperature modified both the nature and quantity of infochemicals emitted by the prey, as well as the capacity of the predator to perceive these signals. Thus, high levels of *A. listronoti* patch departure at the lowest and highest temperatures may result from a lack of kairomones detection, or their misreading by searching females.

Time allocation to different behaviours

The duration of antennal rejections closely followed the kinetic response, as inferred by walking speed; the higher the temperature, the faster the metabolism due to protein conformation and binding to substrate (Neven, 2000). However, the durations of ovipositor rejection and oviposition increased at 32.8°C, suggesting a constraint to host handling at high temperature. Sentis et al. (2013) found that handling rate in ladybeetles follows a bell curve, being lower than expected at high temperature as predicted by the metabolic theory of ecology (MTE) (Brown et al., 2004). *Anaphes listronoti* females likely experienced difficulties handling host eggs with their ovipositor at high temperatures, resulting in longer interactions with the host despite higher metabolic rate. Females spent more time completing ovipositor rejection and less time performing antennal rejection at 32.8°C. *Anaphes* females mark the host egg after oviposition by touching its surface with the antennae while walking over it (Van Baaren et al., 1995). Females can learn to associate these external marking cues, detected with antennae, with the presence of a parasitoid egg inside the host. *Anaphes listronoti* females can learn to detect cues from self, conspecifics and females from other species (Van Baaren and Boivin, 1998). Yet, after exposure to cold at the pupal stage, they are less efficient in assessing host status with external examination only and they need to insert their ovipositor in the host to assess whether it was already parasitized (Van Baaren et al., 2005). In general, thermal stress affects both memory consolidation and the rate of the active forgetting process (Abram et al., 2015 and references therein). However, in our case, it is not clear whether thermal stress causes an impairment in detection or learning of chemical cues. The observed changes in behaviour could thus arise from: (1) alterations in the female's host marking behaviour right after oviposition; (2) changes in the nature and/or quantity of marking pheromones as a result of temperature, occurring between host marking and the next encounter; (3) changes in the female's capacity to recognize kairomones; (4) a combination of some or all of the above. In a previous study, we found that *A. listronoti* males failed to exhibit courtship and females refused to mate as frequently at low and high temperatures than at the optimum temperature (J. Augustin, unpublished data). This could also result from thermal-induced impairment of the capacity of females to detect/recognize chemical cues.

Opposite to *A. listronoti*, *Trichogramma euproctidis* females performed more ovipositor rejection at low temperature (14°C) than at intermediate and high ones (24 and 34°C) (Moiroux et al., 2016). The authors suggested that the external discrimination abilities of *T. euproctidis* females are altered at low temperature. While the low number of females exploiting the patch at 15°C does not allow us to draw conclusions about host rejection mechanism at this temperature, the differences in host rejection behaviour at high temperatures between *T. euproctidis* (34°C) and *A. listronoti* (32.8°C) is interesting. *Anaphes listronoti* has only been observed in Canada, where temperature during the summer rarely exceed 30°C. At the opposite, the *T. euproctidis* strain used by Moiroux et al. (2016) originated from individuals sampled in Egypt. The different thermic conditions experienced by the two species in their environment could explain the different thermic adaptations and discrimination abilities. While *T. euproctidis* females has a wider thermal range for host patch exploitation, they appear to be better adapted to elevated temperature. Conversely, *A. listronoti* females are much less likely to encounter temperatures higher than 30°C, and their sensory organs may not be adapted to such conditions. Consequently, their discrimination abilities are lessened at 32.8°C compared to more intermediate temperatures.

Patch exploitation strategy

Anaphes listronoti residence time decreased with temperature, suggesting that host patch exploitation is at least partially linked to the metabolic rate of the individual. Females used the same patch-leaving rules, except at 15.9°C, where we identified no behavioural components affecting patch-leaving rates of females (probably because of the low N). For all other temperatures, oviposition rate significantly increased patch-leaving rates. Rejection rates also significantly increased patch leaving at 20.2°C, 24.9°C, and 28.4°C, but not at 32.8°C. Number of rejections and ovipositions are correlated, suggesting that they are both used as patch-leaving rules at almost all temperature. At the highest temperature, females may have difficulties assessing whether the host was parasitized or not (see above). Parasitoid females entering a host patch have an initial tendency to remain on it (Waage, 1979). This propensity decreases with time until it reaches a threshold, at which females leave the patch. When a host encounter, a rejection or an oviposition increases patch residence time, the underlying mechanism is defined as incremental. Conversely, when these interactions with the host increase patch-leaving rates, the mechanism is decremental (Waage, 1979). *Anaphes listronoti* females operate under a decremental mechanism because ovipositions and host rejections increase patch leaving tendency. Decremental mechanisms are considered optimal for species whose host patches are homogeneous in quality through the environment (Iwasa et al., 1981; Wajnberg, 2006). Under these conditions, it could be adaptive for females to rely on the same patch-leaving rules, as we observed in this study, despite changes in temperature conditions. In addition, as seen in Figure 5-4, at low temperature, *A. listronoti* performance was higher than expected under the null model. However, at the hottest temperature, performance is lower than expected. It might be that females lost time when assessing host quality because they perform ovipositor rejection, which takes on average 14.1 times longer than antennal rejection, to discriminate non-parasitized vs. parasitized hosts. As a result, unlike for other temperatures, females do not rely on host rejection rate as a patch-leaving rule; their decision is only based on oviposition rate.

Changes in residence time in relation to temperature followed changes in walking speed, but they were not directly proportional; a two-fold increase in walking speed resulted in a one-fold decrease in residence time, suggesting that metabolic rate is not the only mechanism responsible for residence time in *A. listronoti*. We hypothesized that females should spend less time on the patch as temperature increases, and this effect should be stronger than metabolic rate alone in the case of an integrated response. However, we observed something different: the magnitude of changes in residence time is less than those in metabolic rate. Using the same patch-leaving rules could provide a buffer effect to homogenize residence time when female parasitoids experience different conditions. This could also be explained by the alteration of the female time perception by temperature: for ectotherms, time subjectively passing by faster at high than at low temperature (Parent, 2016). Thus, at high temperature, from a female's perspective, relatively more time was spent on the patch. Accordingly, a female's perception time would affect her oviposition and rejection rate. In addition, despite the 1-hour acclimation before females were released in the patch, it remains possible that observed behaviours are not a response to the experienced temperature during patch exploitation, but rather a response to the increase or decrease in temperature compared to the pre-trial temperature (Amat et al., 2006). Indeed, it could be advantageous for females to adjust patch exploitation (residence time and number of ovipositions) after experiencing a drop in environmental temperature (that could indicate adverse environmental conditions such as rain or wind). In all cases, females spent less time on the patch as temperature increased, and this effect cannot be explained by the kinetic response alone. Unfortunately, our data do not allow a definite identification of the mechanisms or strategies involved.

Offspring number and sex ratio

Females laid fewer offspring at low and high temperatures, through a decrease in parasitism rate. This can be explained by reduced activity and differences in searching behaviour (McCutcheon and Simmons, 2001; Langer et al., 2004). Clutch size is similar to other reports for *A. listronoti* at 23°C: Our study, 1.26 ± 0.22 eggs per host; Collins and Grafius (1986), 1.29 ± 0.47. Similarly, temperature did not affect clutch size of the egg parasitoid *Trichogramma dendrolimi* (Schmidt and Pak, 1991). There was a small incidence of parasitoid-induced host egg abortion (*sensu* Abram et al., 2016) from 15.9°C to 28.4°C, with parasitism leading to failed parasitoid offspring development and host egg abortion. Percentage of egg abortion was significantly higher at 32.8°C (29.7% of eggs aborted) compared to other temperatures (Figure 5-5).

Interestingly, offspring sex ratio did not vary with temperatures experienced by *A. listronoti* females when exploiting a patch. In contrast, Moiroux et al. (2014) showed that *Trichogramma euproctidis* offspring sex ratio increases at both low and high temperatures experienced by foraging females. Female parasitoids allocate a sex ratio that increases their own fitness or their offspring's fitness (Mousseau and Fox, 1998). For example, they produce more males at high temperature because size decreases with increasing temperatures during development (Atkinson, 1994; Colinet et al., 2007), and being large is more important for parasitoid female fitness than for male fitness (Charnov et al., 1981; Honěk, 1993). Sex allocation by females can be constrained by defect egg fertilization (Moiroux et al., 2014) or sperm depletion (King, 2000). Sex-specific survival (Wilkes, 1959; Colinet et al., 2006) or dispersal capacity (Roy et al., 2003) under adverse temperatures can also affect secondary sex ratio. No difference in secondary sex ratio was observed in *A. listronoti*, either because females did not adjust sex allocation under the range of tested temperatures, there was no difference in mortality between sexes during parasitoid development, or because females did change sex allocation, but differential embryonic or larval mortality between sexes resulted in a similar secondary sex ratio at all temperatures. As the duration of the tests only differed by about 3 hours between thermal treatments, and subsequent development occurred under the same rearing conditions for about 12 days, we expect sex-specific mortality rate to be the same for all treatments. Therefore, we privilege the first explanation, i.e. no differential sex allocation related to temperature.

Adaptive vs. constrained responses

The responses of *A. listronoti* females to temperature during patch exploitation are partially driven by kinetic response. An absolute kinetic response would result in females behaving the same at all temperatures, but slower or faster as temperatures decreased or increased. This is not the case for *A. listronoti* because females had fewer host contacts at low and high temperatures than at intermediate temperatures, and patch exploitation strategies differed between temperatures. As parasitoid performance was lower than expected at high temperature, we suggest three potential constraints: increased handling time due to impaired coordinated movement (Sentis et al., 2013), weakening of the muscular contraction of the spermatheca, leading to lower egg fertilization (Moiroux et al., 2014), and reduced detection of chemical cues (Sentis et al., 2015). The first and the third constraints were obvious at 32.8°C, with females spending more time interacting with host eggs than expected, rejection rate not being used as a patch leaving rule, and females switching from antennal rejections to ovipositor rejections for host quality assessment. The second constraint, the impairment of the muscular contraction of the spermatheca during oviposition, was not observed; sex ratio remained constant along the tested thermic range. At low temperatures, performance was higher than expected under the kinetic null model. This could either be an adaptive response of the females to temperature or, as suggested earlier, a buffering effect due to use of the same patch-leaving rules.

Our results highlight the complexity of parasitoid behavioural responses to temperature. The frequency and duration of behaviours may (1) simply result from changes in metabolic rate due to the kinetic effect of temperature on insects, (2) be indirect consequences of the insect's metabolic rate, such as handling time, or (3) result from constraints arising from other sources, such as kairomones emission and perception at sub-optimal temperatures (Van Baaren et al., 2005; Sentis et al., 2015). *Anaphes listronoti* females behave better than expected at sub-optimal temperatures, but worse than expected at supra-optimal temperatures. This could have serious consequences under ongoing climate warming for such a short-lived species (2 to 3 days at 29°C [Collins and

Grafius, 1986]). Females would have less time to find and exploit hosts, and offspring will be smaller following the temperature–size rule (Atkinson, 1994; Colinet et al., 2007), and thus have a lower fitness (Honěk, 1993). In contrast, these results suggest that populations from temperate climates may perform better than predicted under the kinetic null model at low temperature. This could be an interesting hypothesis to test in future research.

5.6 / Acknowledgements

This work was supported by internal funding from Agriculture and Agri-Food Canada. We thank D. Thibodeau, J. Frenette and J. Vaillancourt for their technical assistance, and E. Duquette for linguistic revision. All applicable institutional and/or national guidelines for the care and use of animals were followed. The authors declare that there are no conflicts of interest. There are no disputes over the ownership of the data presented in the paper, and all contributions have been attributed appropriately, via co-authorship or acknowledgement, as appropriate to the situation.

5.7 / References

Abram, P. K., Cusumano, A., Peri, E., Brodeur, J., Boivin, G., and Colazza, S. (2015). Thermal stress affects patch time allocation by preventing forgetting in a parasitoid wasp. Behav. Ecol., *26*, 1326-1334.

Abram, P. K., Brodeur, J., Burte, V., and Boivin, G. (2016). Parasitoid-induced host egg abortion: an underappreciated component of biological control services provided by egg parasitoids. Biol. Control, *98*, 52-60.

Abram, P. K., Boivin, G., Moiroux, J., and Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biol. Rev. *92*, 1859–1876.

Amat, I., Castelo, M., Desouhant, E., and Bernstein, C. (2006). The influence of temperature and host availability on the host exploitation strategies of sexual and asexual parasitic wasps of the same species. Oecologia, *148*, 153-161.

Angilletta, M. J. (2006). Estimating and comparing thermal performance curves. J. Therm. Biol. *31*, 541–545.

Atkinson, D. (1994) Temperature and organism size – a biological law for ectotherms? Adv. Ecol. Res. *25,* 1– 58.

Augustin, J., Boivin, G., Brodeur, J., and Bourgeois, G. (2020), Effect of temperature on the walking behaviour of an egg parasitoid: disentangling kinetic response from integrated response. Ecol Entomol. *45*, 741-750

Berrigan, D., and Lighton, J. R. B. (1994). Energetics of pedestrian locomotion in adult male blowflies, *Protophormia terraenovae* (Diptera: Calliphoridae). Physiol. Zool. *67*, 1140–1153.

Berrigan, D., and Partridge, L. (1997). Influence of temperature and activity on the metabolic rate of adult *Drosophila melanogaster*. Comp. Biochem. Physiol. A. *118*, 1301–1307.

Boivin, G. (1988). Laboratory rearing of *Anaphes sordidatus* (Hym.: Mymaridae) on carrot weevil eggs (Col.: Curculionidae). BioControl *33*, 245–248.

Boivin, G., and Martel, V. (2012). Size-induced reproductive constraints in an egg parasitoid. J. Insect Physiol. *58*, 1694–1700.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B. (2004). Toward a metabolic theory of ecology. Ecology *85*, 1771–1789.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. Theor. Popul. Biol. *9*, 129–136.

Charnov, E. L., Los-den Hartogh, R. L., Jones, W. T., and van den Assem, J. (1981). Sex ratio evolution in a variable environment. Nature *289*, 27-33.

Colinet, H., Renault, D., Hance, T., and Vernon, P. (2006). The impact of fluctuating thermal regimes on the survival of a cold-exposed parasitic wasp, *Aphidius colemani*. Physiol. Entomol. *31*, 234–240.

Colinet, H., Boivin, G., and Hance, T. (2007). Manipulation of parasitoid size using the temperature-size rule: fitness consequences. Oecologia *152*, 425–433.

Collins, R. D., and Grafius, E. (1986). Biology and life cycle of *Anaphes sordidatus* (Hymenoptera: Mymaridae), an egg parasitoid of the carrot weevil (Coleoptera: Curculionidae). Environ. Entomol. *15*, 100–105.

Cox, D. R. (1972). Regression models and life-tables. J. R. Stat. Soc. Ser. B Methodol. *34*, 187–220.

Fauvergue, X., Lo Genco, A., and Lo Pinto, M. (2008). Virgins in the wild: mating status affects the behavior of a parasitoid foraging in the field. Oecologia *156*, 913–920.

Forsse, E., Smith, S. M., and Bourchier, R. S. (1992). Flight initiation in the egg parasitoid *Trichogramma minutum*: Effects of ambient temperature, mates, food, and host eggs. Entomol. Exp. Appl. *62*, 147–154.

Fournier, F., and Boivin, G. (2000). Comparative dispersal of *Trichogramma evanescens* and *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) in relation to environmental conditions. Environ. Entomol. *29*, 55–63.

Gaudon, J. M., Allison, J. D., and Smith, S. M. (2018). Factors influencing the dispersal of a native parasitoid, *Phasgonophora sulcata*, attacking the emerald ash borer: implications for biological control. BioControl *63*, 751–761.

Honěk, A. (1993). Intraspecific variation in body size and fecundity in insects: A general relationship. Oikos *66*, 483-492.

Huey, R. B., and Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. *19*, 357–366.

Iwasa, Y., Higashi, M., and Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. Am. Nat. *117*, 710–723.

Jorgensen, S. E.; Fath, Brian. (2008). Encyclopedia of ecology. Amsterdam: Elsevier.

King, B. H. (2000). Sperm depletion and mating behavior in the parasitoid wasp *Spalangia cameroni* (Hymenoptera: Pteromalidae). Gt. Lakes Entomol. *33*, 117-127.

Langer, A., Boivin, G., and Hance, T. (2004). Oviposition, flight and walking capacity at low temperatures of four aphid parasitoid species (Hymenoptera: Aphidiinae). Eur. J. Entomol. *101*, 473–480.

Lauzière, I., Pérez-Lachaud, and Brodeur, J. (2000). Behavior and activity pattern of *Cephalonomia stephanoderis* (Hymenoptera: Bethylidae) attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). J. Insect Behav. *13*, 375-396.

McCutcheon, G. S., and Simmons, A. M. (2001). Relationship between temperature and rate of parasitism by *Eretmocerus* sp. (Hymenoptera: Aphelinidae), a parasitoid of *Bemisia tabaci* (Homoptera: Aleyrodidae). J. Agric. Urban Entomol. *18*, 97–104.

Moiroux, J., Brodeur, J., and Boivin, G. (2014). Sex ratio variations with temperature in an egg parasitoid: behavioural adjustment and physiological constraint. Anim. Behav. *91*, 61–66.

Moiroux, J., Abram, P. K., Louâpre, P., Barrette, M., Brodeur, J., and Boivin, G. (2016). Influence of temperature on patch residence time in parasitoids: physiological and behavioural mechanisms. Sci. Nat. *103*, 1-10.

Mousseau, T. A., and Fox, C. W. (1998). The adaptive significance of maternal effects. Trends Ecol. Evol. *13*, 403–407.

Neven, L. G. (2000). Physiological responses of insects to heat. Postharvest Biol. Technol. *21*, 103–111.

Parent, J. P. (2016). La perception du temps et sa modulation par la température chez les guêpes parasitoïdes. PhD thesis, Département de sciences biologiques, Université de Montréal, Montreal, Quebec, Canada

Roy, M., Brodeur, J., and Cloutier, C. (2003). Temperature and sex allocation in a spider mite. Oecologia *135*, 322-326.

Schmidt, J. M., and Pak, G. A. (1991). The effect of temperature on progeny allocation and short interval timing in a parasitoid wasp. Physiol. Entomol. *16*, 345–353.

Sentis, A., Hemptinne, J.-L., and Brodeur, J. (2013). Parsing handling time into its components: implications for responses to a temperature gradient. Ecology *94*, 1675–1680.

Sentis, A., Ramon-Portugal, F., Brodeur, J., and Hemptinne, J.-L. (2015). The smell of change: warming affects species interactions mediated by chemical information. Glob. Change Biol. *21*, 3586–3594.

Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M. M. B., Allen, S. K., Boschung, J., Naeuls, A., Xia, Y., Bex, V., and Midgley, P. M. (2013). Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Traoré, L., Pilon, J. G., Fournier, F., & Boivin, G. (2006). Adaptation of the developmental process of *Anaphes victus* (Hymenoptera: Mymaridae) to local climatic conditions across North America. Ann. Entomol. Soc. Am. *99*, 1121-1126.

Van Baaren, J., and Boivin, G. (1998). Genotypic and kin discrimination in a solitary hymenopterous parasitoid: Implications for speciation. Evol. Ecol. *12*, 523–534.

Van Baaren, J., Boivin, G., and Nénon, J.-P. (1994). Intra-and interspecific host discrimination in two closely related egg parasitoids. Oecologia *100*, 325–330.

Van Baaren, J., Nénon, J.-P., and Boivin, G. (1995). Comparison of oviposition behavior of a solitary and a gregarious parasitoid (Hymenoptera: Mymaridae). J. Insect Behav. *8*, 671–686.

Van Baaren, J., Outreman, Y., and Boivin, G. (2005). Effect of low temperature exposure on oviposition behaviour and patch exploitation strategy in parasitic wasps. Anim. Behav. *70*, 153–163.

Van Baaren, J., Boivin, G., and Outreman, Y. (2006). Deleterious effects of low temperature exposure on learning expression in a parasitoid. Int. J. Comp. Psychol. *19*.

Vannier, G. (1994). The thermobiological limits of some freezing intolerant insects: the supercooling and thermostupor points. Acta Oecol. *15*, 31–42.

Waage, J. K. (1979). Foraging for patchily-distributed hosts by the parasitoid, *Nemeritis canescens*. J. Anim. Ecol. *48*, 353-371.

Wajnberg, É. (2006). Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. Behav. Ecol. Sociobiol. *60*, 589–611.

Wajnberg, É., Gonsard, P.-A., Tabone, E., Curty, C., Lezcano, N., and Colazza, S. (2003). A comparative analysis of patch-leaving decision rules in a parasitoid family. J. Anim. Ecol. *72*, 618–626.

Wilkes, A. (1959). Effects of high temperatures during postembryonic development on the sex ratio of an arrhenotokous insect, *Dahlbominus fuliginosus* (Nees) (Hymenoptera: Eulophidae). Can. J. Genet. Cytol. *1*, 102–109.

Chapitre 6 : Low and high temperatures decrease the mating success of an egg parasitoid and the proportion of females in the population

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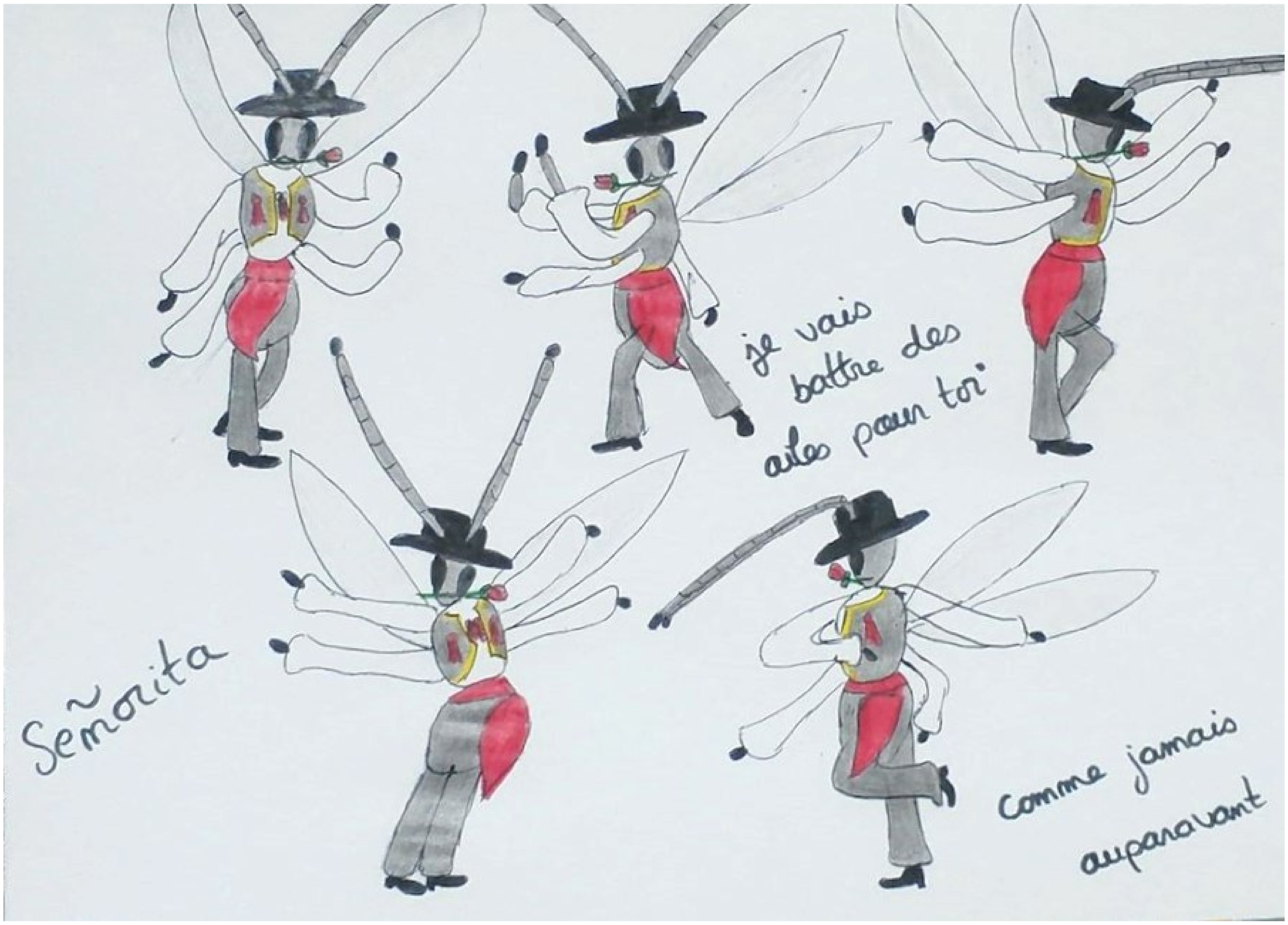

Laurie Blanchemain

6.1/ Abstract

Temperature influences all aspects of insect physiology and behaviour, including reproduction. Adverse temperatures can decrease mating success and sperm transfer, leading to increased sex ratio in haplodiploid organisms. We tested the effect of five temperatures on the reproduction of the egg parasitoid *Anaphes listronoti*. Temperatures inferior and superior to 24.5°C decreased mating success by 30% to 40%, with a decrease of up to 80% at 35°C. Mating failures can arise from lack of encounters between sexes, absence of courting by the male, or male rejection by the female. These behavioural malfunctions at low or high temperatures may result from either a change in activity level or a disruption in chemical communication between sexes. Both courtship and copulation duration decreased with increasing temperature. For mated females, there was no effect of mating temperature on offspring number and sex ratio. However, the increased number of virgin females at adverse temperatures did modify the simulated population sex ratio of the next generation, which increased from 0.2 at 24.5°C to 0.4, 0.5, 0.4 and 0.8 at 15.7°C, 20°C and 30°C and 35°C, respectively. The effect of temperature on courtship and copulation success of *A. listronoti* could lead to a decrease of the number of females in the population.

Keywords: Mating success; Temperature; Sex ratio; *Anaphes listronoti*

6.2 / Introduction

For haplodiploid organisms, males develop from unfertilized haploid eggs and females from fertilized diploid eggs (Heimpel and de Boer, 2008). The population sex ratio of haplodiploid hymenopteran parasitoids tends to be biased toward females (Hamilton, 1967) and is influenced by several factors (reviewed by Godfray 1994). These factors can be divided into three categories: (1) structural and physiological defects of either sex, (2) impaired mating, and (3) environmental factors affecting sex allocation of foraging mated females. This last aspect has been largely studied in hymenopteran haplodiploid parasitoids (Ode and Hunter, 2002). Sex allocation can only occur when mating is successful and females have spermatozoids in their spermatheca to fertilize eggs.

Temperature governs all aspects of poikilotherm life (Bale et al., 2002; Hance et al., 2007), including reproduction. Egg and sperm production, fecundity, fertility and embryogenesis are strongly affected by temperature (Walsh et al., 2019). While the effects of temperature on individual development are well known (Régnière et al., 2012), its consequences on behaviour have received less attention (Abram et al., 2017). For instance, insect mating behaviour follows a complex sequence of mate finding, courting behaviour and assessment of partner quality (Alexander et al., 1997; Johansson and Jones, 2007). Each step is usually mediated by acoustic, tactile or visual signals, as well as sexual pheromones (Ayasse et al., 2001; Candolin, 2003). Temperature has been shown to affect mating through pheromone-related disruption: quantity, quality, recognition (Sentis et al., 2015) or emission rate (Zhu et al., 2015; Bouwer et al., 2017). Temperature can also affect mating through physiological disruption of behaviour, as female acceptance relies on proper courtship behaviour by the male (Matthews, 1982). For example, Fasolo and Krebs (2004) found that heat stress affects both male courtship and female receptivity in *Drosophila mojavensis*. Females can also rely on male motor performance when choosing their mate (Byers et al., 2010), a trait affected by temperature (Montgomery and Macdonald, 1990). Exposure to adverse temperatures during arthropod development and host patch exploitation can influence female ovigeny (Moiroux et al., 2018) and offspring sex ratio (Roy et al. 2003; Colinet and Boivin, 2011; Moiroux et al., 2014). However, the impact of adverse conditions on mating frequency and the subsequent consequences on individual fitness and population dynamics remain partially explored. They can be important for short-lived species that cannot afford to delay mating until more favourable climatic conditions.

Anaphes listronoti (Huber) (Hymenoptera: Mymaridae) is an egg parasitoid of the carrot weevil *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae). Both females and males can mate several times (polygamy), although one mating is sufficient for fertilization of all oocytes (Boivin and Martel, 2012). Females emit long-range volatile pheromones to attract males (Cormier et al., 1998). Courtship and mating behaviour of *A. listronoti* have been described by Collins and Grafius (1986a) as follows. Upon encountering a female, the male increases its activity and starts wing fanning. Wing fanning increases the likelihood of securing a mate (Benelli et al., 2012) by enhancing the rate at which pheromones (Loudon and Koehl, 2000) and acoustic signals (Villagra et al., 2011) are perceived by females. When approaching the female, the male touches her abdomen with his antennae. Non-receptive females walk or fly away, while receptive females remain stationary and allow the male to mount and copulate.

The main goal of this study was to examine the effect of temperature on *A. listronoti* mating behaviour and to estimate the consequence on sex ratio of the subsequent generation. Our first objective was to assess whether and how courtship and mating behaviour of *A. listronoti* males and females are disrupted at the low and high limits of the thermal range of the species. We first hypothesized that sub-optimal temperatures impair male courtship through changes in metabolic rate or disruption of chemical communication between sexes. We thus predicted that females increasingly refuse to mate as temperature diverges from the optimum, i.e. the temperature at which mating success is maximum. Impaired mating could also arise from the male not recognizing the female because of impaired pheromonal and visual components (Jachmann and Van den Assem, 1993; Ayasse et al., 2001). We also determined whether sub-optimal temperatures during mating affect the sex ratio of the female's offspring and the mechanism involved: lower mating success or impaired sperm transfer. We hypothesized that under suboptimal mating conditions, sperm transfer is constrained by either reduced sperm motility at low temperature (Richards, 1963) or shorter copulation at high temperature (Simmons and Marti Jr., 1992; Katsuki and Miyatake, 2009). As a consequence, we predicted that *A. listronoti* sex ratio would be higher (more sons) at extreme temperatures than under optimal thermal reproductive conditions, i.e. a sex ratio of 0.16 at 24°C after one mating (Boivin and Martel, 2012). We then aimed to assess the effect of disrupted mating on *A. listronoti* population dynamics by calculating the next generation sex ratio, assuming that females only had one mating opportunity. Sex ratio at the scale of the population results from two main factors: sex allocation by individual females and proportion of virgin females in the population (as they only produce male offspring). We hypothesized that mating under adverse temperatures contributes to increased sex ratio in the subsequent population mainly through an increase in the proportion of virgin females. *Anaphes listronoti* sex ratio is higher under field conditions (Collins and Grafius, 1986b) than when reared in the laboratory (Boivin and Martel, 2012), possibly because of higher proportions of unmated females in nature (Collins and Grafius, 1986b).

6.3 / Material and methods

Parasitoids

Anaphes listronoti was reared on carrot weevil eggs in the laboratory at 24 °C ± 2 °C, 50% relative humidity (RH) and 16L:8D photoperiod following Boivin (1988). The strain originated from an Agriculture and Agri-Food Canada untreated carrot field in Sainte-Clotilde (45°09′ N, 73°41′ W) (1991), Quebec, Canada. The first individuals were sampled in 1984, and new individuals from the field were added to the rearing every year.

Listronotus oregonensis eggs were obtained following Martel et al. (1975).

Mating success

The objective of this experiment was to measure the mating success of *A. listronoti* couples when exposed to a range of temperatures, and to document causes of failure. We tested temperatures within the active thermal range of the species: 10 °C to 35 °C (J. Augustin, personal observation). However, because no individuals mated during pre-test at 10°C, the lowest temperature tested was 15.7°C. Virgin males and females, aged 0 to 24 h, were maintained individually in 300 µL Beem® polyethylene capsules and placed in a growth chamber (Sanyo, model MLR351H) for one hour prior to the test to acclimate to one of the five experimental temperatures: 15.7 °C, 20 °C, 24.5 °C, 30 °C and 35 °C (with maximum variation of 1.4 °C and relative humidity of 50.7% ± 13.4). A total of 177 couples were tested, with a minimum of 24 couples at 24.5 °C. All individuals developed at 24 °C ± 2 °C prior to the mating experiment. Temperature during the mating experiment was monitored using a HOBO Temp Logger (model H08-001-02) placed beside the experimental arena in the growth chamber. To control for parasitoid size, which can have an impact on mate choice and sex allocation (Godfray 1994), only individuals born singly from the host egg were used, since they are all of similar size (Boivin and Martel, 2012). Tested females were introduced in a glass vial (2 cm in height and 2 cm in diameter) placed over a filter paper, and the male was added next. Couples were videotaped using a USB digital Dino-Lite AM5212NZT camera (Koonlung Inc., model E600) throughout the duration (see below) of the test or until the end of mating.

Insects are poikilotherms, and their metabolic rate increases with temperature. According to the physiological time concept (Taylor, 1981), the increase in metabolic rate implies that time passes faster for an ectotherm as temperature increases. As tests consisted of a success/failure criterion of the mating encounter, test durations needed to be comparable between thermic treatments, to ensure that all individuals had the same opportunities. Thus, in order to control for physiological time, we adjusted the test duration to the tested temperature using degree-minutes. Test duration was set at 10 min at 24 °C, the rearing temperature. For other temperatures, test durations were calculated using degree-minutes, with a base temperature of 7 °C (Zhao et al., 1991), established after the base temperature of the host (Simonet and Davenport, 1981). Physiological test duration at 24 °C was thus $(T_{test} - T_{base})$ * Test duration = (24 °C – 7 °C) * 10 min = 170 degree-minutes. We then used this physiological time to calculate test durations for other temperatures. For example, at 15 °C, test duration was 170 degree-minutes / $(T_{test} - T_{base})$ = 170 / (15 °C – 7 °C) = 21.25 min. Resulting test times were 21, 13, 9, 7 and 6 min at 15 °C, 20 °C, 25 °C, 30 °C and 35 °C, respectively. After each trial, vials were washed with distilled water, and the filter paper was changed. Each individual was only tested once. Experiments were run between 10:00 and 12:30.

Mating behaviour

Courtship and copulation durations were measured using video sequences from the previous experiment. Courtship in *A. listronoti* starts with an increase in male activity, including wing fanning, and stops when the male touches the female abdomen with its antennae. Copulation starts when the couple remains motionless after the male has taken the characteristic mating position, and ends when the two individuals part. Absence of mating may result from either: (1) no encounter between the individuals, (2) no courtship behaviour by the male when encountering the female, or (3) the female refusing to mate (she would keep walking, not allowing the male to adopt the copulation position, until she succeeded in dismounting the male or he gave up). Mating success, expressed in percentages, was calculated for each temperature. When mating did not occur, the reason was noted.

To assess whether courtship and copulation behaviours resulted from metabolic rate or other physiological and behavioural components on mating success, we compared their durations to the duration required for females to walk a given distance under a specific temperature. Walking speed increases with temperature in *A. listronoti* (Augustin et al. 2020), and females require less time to cover the same distance at higher temperatures. If mating behaviours are affected by temperature at a rate similar to the effect of temperature on walking speed, we can consider that the effect mostly results from changes in metabolic rate. We used data from Augustin et al. (2020) to calculate walking speed and duration (in seconds) for a 20-mm distance (arena diameter) according to temperature.

(1) $Walking\ speed\ (T) = 0.012\,T + 0.655$

in mm/s, where T is the temperature (°C)

(2) $Walking\ duration\ (T) = \frac{20}{Walking\ speed\ (T)}$

Daughter numbers (sperm number proxy)

We used the number of daughters produced by mated females (21, 21, 24, 22 and 13 mated females at 15.7°C, 20°C, 24.5°C, 30°C and 35°C, respectively) to estimate the number of spermatozoids transferred during mating (Martel et al., 2008) at different temperatures. In order to make sure that the females had emptied their spermatheca (a mean of 38.3 spermatozoids per female following one mating at room temperature [≈ 22°C] with a single male) (Boivin and Martel, 2012), we provided each female with 100 fresh host eggs over the course of their life, i.e. 5 days (Collins and Grafius, 1986b). Females were placed in a Petri dish (54 mm diameter) containing a first batch of 60 fresh carrot weevil eggs (≤ 24 hours old) on humidified filter paper, for 48 h. Next, they were provided with a second batch containing 40 fresh eggs to exploit for another 48 h. Most females were dead by the end of these two oviposition sequences. For those remaining alive, we offered them an additional batch of 10 eggs, but we never observed any offspring emerging from the third batch. *Anaphes listronoti* females were thus given more than twice the amount of host eggs they can parasitize, since they have a lifetime production of about 43 oocytes (Boivin and Martel, 2012). Oviposition took place at rearing conditions (24°C, 50% RH, 16L:8D), with temperature treatments only differing during mating. Carrot weevil eggs were placed in individual 300 µL Beem®

polyethylene capsules and kept under rearing conditions (24°C, 50% RH, 16L:8D) until an adult wasp or a weevil larva emerged. After 21 days, the remaining eggs were dissected to determine whether they contained a dead parasitoid or a dead carrot weevil larva. If they contained neither, they were considered “aborted” (*sensu* Abram et al., 2016). Dead parasitoids were included in female offspring calculation.

Population sex ratio

To determine the effects of mating temperature on the sex ratio (proportion of males) of the next generation, we estimated the number of sons and daughters produced within a hypothetical population of 100 females for each mating temperature when considering their mating status. The total number of daughters and sons, and the resulting population sex ratio were calculated using formulas (3), (4) and (5), respectively. Number of daughters corresponds to the number of daughters laid by mated females. Number of sons corresponds to the number of sons laid by mated females + total number of progenies laid by virgin females. Virgin *A. listronoti* females lay the same number of progenies as mated females (Collins and Grafius, 1986b).

(3) $\text{N daugthers}_T = \text{Ni females} * \text{Percentage of mated females}_T * \text{Mean number of progeny}_T * (1 - \text{SR}_T)$

(4) $\text{N sons}_T = (\text{Ni females} * \text{Percentage of mated females}_T * \text{Mean number of progeny}_T * \text{SR}_T) + \text{Ni}$
$\text{females} * (1 - \text{Percentage of mated females}_T) * \text{Mean number of progeny}_T$

(5) $\text{SR pop}_T = \text{N sons}_T / (\text{Ndaugthers}_T + \text{N sons}_T)$

with Ni being the number of initial females in the population (here 100), T the mating temperature, and SR the sex ratio laid by females mated at temperature T.

Data analyses

Linear and polynomial regressions were used to assess the effect of temperature on courtship and mating duration, and offspring data. Generalized linear regressions (GLM) (Nelder and Wedderburn, 1972) followed by a Tukey post-hoc test were used to determine differences between temperatures for mating success and reasons for unsuccessful mating. Wasps that laid less than 10 eggs (N = 3) were removed from the offspring analysis. All analyses were conducted with the R software (RC Team, 2016).

6.4 / Results

Mating success

Compared to 25°C, lower and higher temperatures significantly decreased the percentage of encounters between males and females in the arena (GLM, quasibinomial, $p \leq 0.001$) and the percentage of males that exhibited courtship behaviour when interacting with females (GLM, quasibinomial, $p \leq 0.001$).

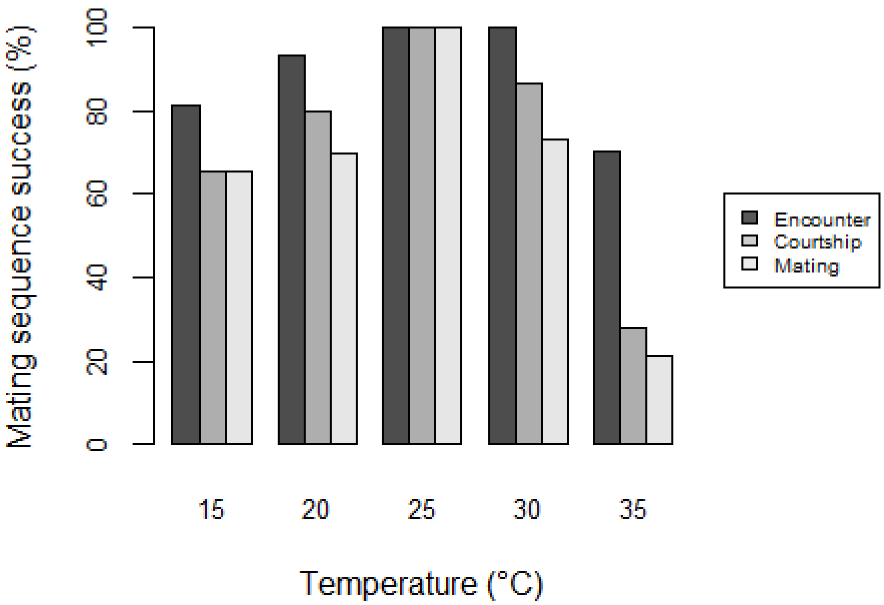

Figure 6-1: Effect of temperature on encounter, courtship and mating success of *A. listronoti* couples. Behaviours are sequential, and percentages are expressed accordingly (encounter, then courtship, and finally mating). N = 177

Mating was also significantly reduced at low and high temperatures (GLM, quasibinomial, $p \leq 0.001$; Figure 6-1); it was maximum at 25°C (100%) and decreased to 20% at 35°C. Mating success at 35°C was significantly different from all other temperatures, except 15°C. Mating failure was due either to an absence of encounter between the two individuals, the male not exhibiting courtship or the female refusing to mate when the male exhibited courtship. The relative proportions of those failures differed between temperatures. At 15°C, all females accepted mating, and mating failure was due to the lack of encounter between mates (55.2 %) and males not courting (44.8%). At 20°C, mating failure was due to the male not courting (44.3%), a lack of encounter (22.3%) and female rejection (33.3%). At 30°C, all couples had an encounter in the arena but they did not mate because the male did not exhibit courtship behaviour (50% of the time) or the female refused to mate (50% of the time). At 35°C, mating failure was due to the male not executing courtship (54.1%), the lack of encounter between the mates (37.5%), and the female refusing to mate (8.4%).

Courtship and copulation durations

Courtship duration was significantly affected by temperature (2nd degree polynomial, $p = 0.02$, $R^2 = 0.06$; Figure 6-2.A): the higher the temperature, the shorter the duration of courtship from 20°C to 35°C. However, at 15°C the duration of courtship was shorter than at 20°C. There was no relation between courtship duration and walking duration (Wilcoxon test, $p < 0.001$), even when only comparing the linear part of the courtship duration (Wilcoxon test, $p < 0.001$); the slope for courtship duration was much steeper than that of walking duration. As walking duration is used as an approximation of metabolic rate, there is no relation between courtship duration and metabolic rate. Copulation duration significantly decreased with temperature (linear regression, $p \leq 0.001$, $R^2 = 0.29$; Figure 6-2.B). Copulation duration decreased almost proportionally with walking duration, although the copulation duration slope is steeper (copulation; $y = -1.57x + 77.65$ compared to walking; $y = 30.22441 - 0.45758x + 0.00357x^2$). The two slopes were significantly different (Wilcoxon test, $p \leq 0.001$).

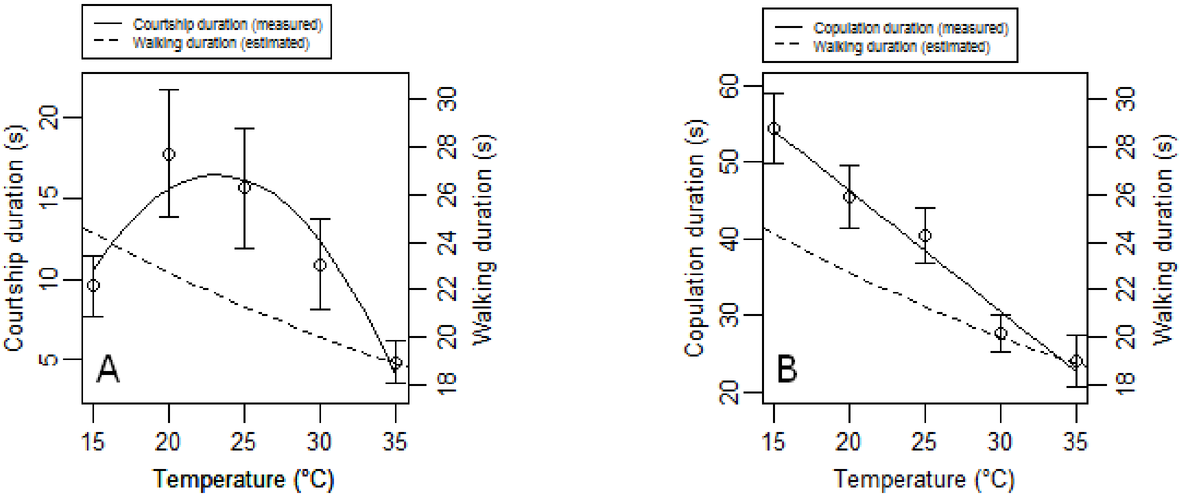

Figure 6-2: Effect of temperature on estimated walking duration (dashed line) and (A) measured courtship duration (full line), and (B) measured copulation duration (full line) of *A. listronoti* males. Means ± SE. N = 177

Offspring

The temperature at which females mated had no impact on offspring number (2nd degree polynomial regression, $p = 0.99$, $R^2 = 0.03$) including the number of non-emerged parasitoids (parasitoids that were recognizable as such after dissection of the egg, but died before emergence) (ANOVA, $F_{4,76} = 1.67$, $P = 0.183$). Over the 8190 carrot weevil eggs incubated, 1312 were dissected; 25.1% of those dissected eggs contained non-emerged parasitoids, 18.3% contained dead carrot weevil larvae and 56.6% were classified as aborted (no parasitoid or carrot weevil larvae detected). There was no effect of temperature on the number of dissected eggs (2nd degree polynomial regression, $p = 0.31$, $R^2 = 0.004$).

Number of daughters (proxy for number of spermatozoids transferred)

Temperature during mating (2nd degree polynomial regression: $p= 0.93$, $R^2 = 0.02$), duration of copulation (linear regression: $p = 0.57$, $R^2 = 0.008$) and their interaction (ANOVA, $F_{1,85} = 1.19$, $p = 0.28$) did not affect the number of daughters produced by females (Figure 6-3.A and B).

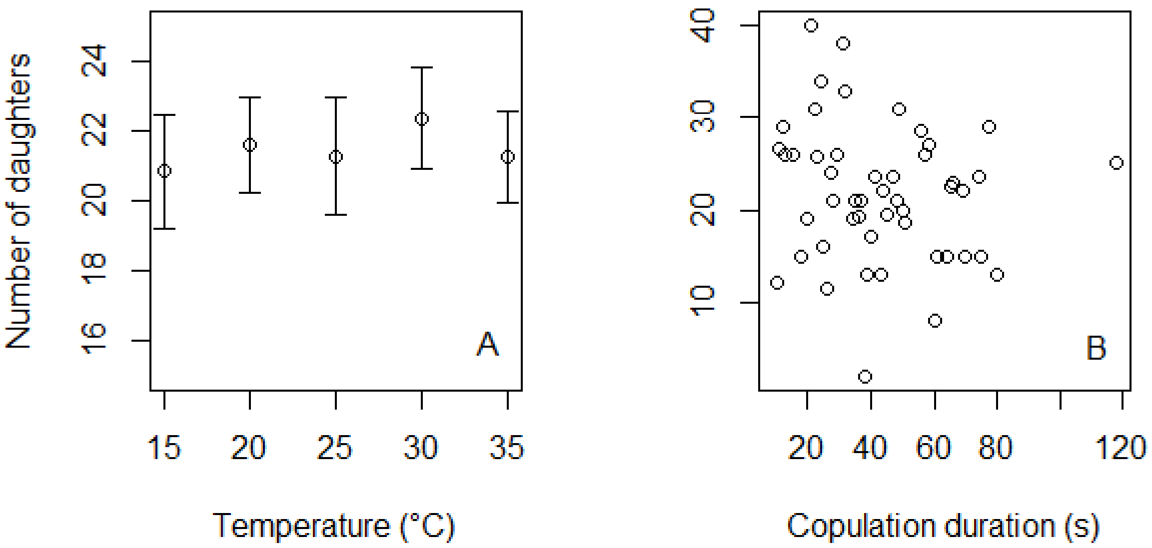

Figure 6-3: Effect of mating temperature (A) (Mean ± SE) and copulation duration (B) on the number of daughters produced by mated *A. listronoti* females. N = 177

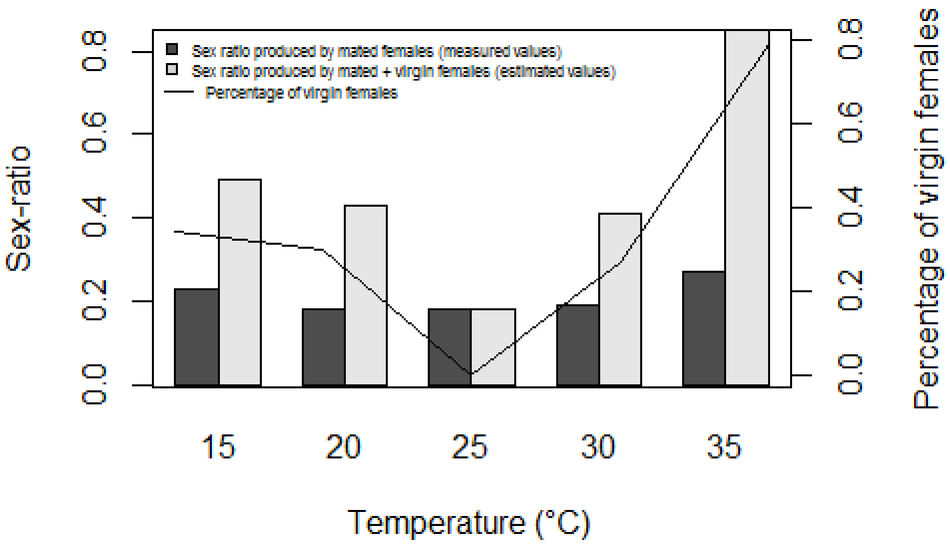

Figure 6-4: Effect of temperature on offspring sex-ratio and the percentage of virgin females in the population. In dark grey, the measured offspring sex-ratio produced by mated females (N = 82). In light grey, the calculated offspring sex ratio of mated + virgin females (calculated using the proportion of virgin and mated females in the population at a given temperature and the offspring sex-ratio of mated females at the same temperature). As virgin females produce the same number of progenies as mated females, but only sons, the estimated sex ratio (proportion of males) increases with the proportion of virgin females in the population.

Population sex ratio

Population sex ratio increased between two and four-fold at sub-optimal temperatures because the number of virgin females is greater in the population at extreme temperatures (Figure 6-4).

6.5 / Discussion

Sub-optimal temperatures significantly decreased mating success of *A. listronoti*, mainly by reducing encounter rates between males and females. Temperature during mating had a significant effect on mating behaviours and their durations, but had no effect on offspring sex ratio of mated females, contrary to our second hypothesis. However, mating temperature did have an effect on theoretical sex ratio at the scale of the population through an increase in the proportion of virgin females.

Mating success

Our data show that *A. listronoti* mating success decreases as temperature departs from the optimum, as reported in other insect species (e.g. Kanno and Sato, 1979; Simmons and Marti Jr., 1992; Cook, 1994). Mating success decreased by 30% to 40% with a 5°C change from the optimal temperature (25°C). This effect was greater at 35°C, with a decrease of 80% in mating success (Figure 6-1). Considering that males and females were confined in a small experimental arena and did not have to find each other over a distance, mating success would be even lower under natural conditions. However, this effect could be mitigated by the capacity of parasitoids to select suitable climatic conditions to initiate mating behaviours. For example, the aphid parasitoid *Aphidius nigripes* exhibits a diel periodicity in female pheromone emission and male receptivity, peaking at sunrise and sunset (McNeil and Brodeur, 1995), when temperature is usually lower. A similar diel periodicity is observed in *A. listronoti* female pheromone release and subsequent male response (Cormier et al., 1998).

Low encounter rates at 15.7°C, 20°C and 35°C resulted from reduced activity of both mates. Male parasitoids recognize females through visual and chemical cues (Jachmann and Van den Assem, 1993; Ayasse et al., 2001). As temperature is not likely to affect visual cues, the absence of courtship behaviour when in presence of a mate suggests that temperature disrupted chemical communication. Either the female capacity to release sexual pheromones was impaired (less pheromones emitted or of different nature) (Sentis et al., 2015) or the male was less able to detect or recognize chemical cues from the females (Linn et al., 1988; Bourdais et al., 2012). At 15°C, males initiated courtship behaviour only when they had contacted the female with their antennae or when they were very close to the mate (~1 mm; J. Augustin, personal observation). Low temperature has been shown to impair the emission (Zhu et al., 2015; Bouwer et al., 2017) and dispersion rate (Boullis et al., 2016) of semiochemicals. Reduced mating success under non-optimal temperatures could also be related to the energy required for courtship. For instance, increased running speed, as observed in *A. listronoti* male courtship behaviour (Cormier et al., 1998), is linked to increased metabolic rate (Fleming and Bateman, 2007). Extreme temperatures could then prevent high activity of males through decreased endurance (Full, 1987). At 35°C, *A. listronoti* males would frequently stop their courtship after a few unsuccessful attempts (J. Augustin, personal observation); however, this is also observed in aphid parasitoids without any effect of temperature (Mackauer and Fraser, 1969). One last option is that, at the low and high end of the range, individuals were more motivated to find a thermal refuge than to search for a mate, hence the low encounter rate.

Few females refused to copulate, probably resulting from a behavioural impairment at sub-optimal temperatures (not being able to push back the males), as observed in aphids trying to avoid parasitism (Le Lann et al., 2014; Moiroux et al., 2015). This would increase mating success for males, but lower mate selection for females. At more suitable temperatures, females can refuse to mate because they (1) do not recognize the male as a potential mate or (2) refuse a low-quality partner (Ruther et al., 2009). The temperature-coupling hypothesis states that temperature could affect the signal preference between mates (Ritchie et al., 2001). For *A. listronoti*, there is likely a mismatch modulated by temperature between signal emission and preference between mates.

These results on thermal effects during mating may also result to some extent from the experimental procedure, i.e. a sudden change in thermal conditions with tested individuals maintained at 22°C being placed at 15.7°C or 35°C without acclimatization. However, our data does not allow us to disentangle these two effects.

Courtship and copulation duration

Courtship and copulation durations (Figure 6-2) were negatively correlated to temperature, as observed for other insect species (Kanno and Sato, 1979; Cook, 1994; Katsuki and Miyatake, 2009). For copulation, it likely results from an increased metabolic rate with temperature (Figure 6-2.B). Males can adjust their ejaculate in the presence of competitors to optimize their mating success (Martel et al., 2008). Do they also adjust copulation duration to ensure complete sperm transfer based on temperature during mating? Our results (Figure 6-2.B) suggest such a pattern, because copulation duration did not closely follow metabolic rate. The number of spermatozoids transferred, estimated through the number of daughters produced, did not change with temperature, indicating some type of adjustment by the male. The copulation duration slope is steeper than the walking distance slope, suggesting that males need to adjust copulation duration at low temperature, but not at high temperature.

Offspring number and sex ratio

There was no significant effect of temperature or copulation duration on the number of daughters (as proxy of number of sperm transferred) produced by *A. listronoti* females (Figure 6-3.A and B). Depending on the species, the relation between the number of spermatozoids in the spermatheca and the number of daughters laid by a female can be linear (Martel et al., 2008) or not (Chirault et al., 2019). Therefore, this method cannot inform us on the exact number of spermatozoids transferred during copulation. However, as there was no difference in the number of daughters between thermal treatments, we can conclude that temperature experienced during mating did not limit females in the number of spermatozoids received during ejaculation. Gilbert and Richmond (1982) suggested that copulation duration in *Drosophila melanogaster* increases at low temperature because sperm motility is reduced. Similarly, sperm velocity decreases with decreasing temperatures in cockroaches (Richards, 1963). Contrary to other coleopteran species (Richards, 1963; Katsuki and Miyatake, 2009), the number of spermatozoids transferred with the ejaculate did not appear to change with temperatures in *A. listronoti*. This can be explained by the structure of the reproductive tract: in males of the Hymenoptera *Dahlbominus fuscipennis*, bundles containing a similar number of spermatozoids form in the vesicular pockets of the male reproductive tract. These bundles are discharged once directly into the vagina of the female during copulation (Wilkes, 1965). As a result, a uniform number of spermatozoids is transferred during copulation, unrelated to copulation duration.

We hypothesized that sperm transfer would be impaired at sub-optimal temperatures, as observed in *Trichogramma euproctidis* (Moiroux et al., 2014), where sperm velocity is reduced at low temperature. However, in *A. listronoti*, copulation always resulted in sperm transfer at all tested temperatures, and females obtained enough spermatozoids to produce the same ratio of males and females. For parasitoids, sex ratio usually increases at extreme temperatures because of lower mating success, fewer spermatozoids transferred (King, 1987), disrupted egg fertilization during oviposition or an adaptive response from the female to the environmental conditions (Moiroux et al., 2014). Our data show that the increase in *A. listronoti* population sex ratio (especially at high temperature) would result from the lower proportion of mated females, and not from reduced sperm transfer during copulation. Reduced mating success could, however, be balanced by subsequent mating opportunities during the female life. But *A. listronoti* lives for only 3 to 4 days at 26°C (Collins and Grafius, 1986b), and re-mating could be scarce in nature.

We showed that temperature can affect sex ratio by preventing mate encounter and possibly disrupting recognition between sexes. The consequences of an excess of males in a population resulting from the reproduction of virgin females, as well as the increased sex ratio usually observed at higher temperatures, need to be investigated thoroughly at the population level. In some Lepidosauria reptiles, male-skewed sex ratio can cause a decline and even extinction of the population (Galliard et al., 2005; Grayson et al., 2014). In turtles, significant increases in temperature, such as those expected under climate change, may decimate populations because of high mortality of immature stages and no male production (Janzen, 1994; Hays et al., 2017). For insects, recent studies have shown that diploid sterile males do increase the proportion of males in the population (Zayed and Packer, 2005; Fauvergue et al., 2015). This increases the probability of extinction in small populations due to both the loss of successful mating opportunities and the reduction in the number of daughters produced by mated females (Zayed and Packer, 2005; Fauvergue et al., 2015). The effect of extreme temperatures on sex allocation needs to be better understood at the population level, especially in the context of climate change and biological control.

6.6 / Acknowledgements

We thank J. Vaillancourt, D. Thibodeau, and J. Frenette for their technical assistance. We thank E. Duquette for language review. This work was supported by internal funding from Agriculture and Agri-Food Canada.

6.7 / References

Abram, P.K., Brodeur, J., Burte, V., and Boivin, G. (2016). Parasitoid-induced host egg abortion: an underappreciated component of biological control services provided by egg parasitoids. Biol. Contr., 98, 52-60.

Abram, P.K., Boivin, G., Moiroux, J., and Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biol. Rev., 92, 1859-1876.

Alexander, R.D., Marshall, D.C., and Cooley, J.R. (1997). Evolutionary perspectives on insect mating. In: The Evolution of Mating Systems in Insects and Arachnids, J.C. Choe, and B.J. Crespi, eds. (Cambridge: Cambridge University Press), pp. 4–31.

Augustin, J., Boivin, G., Brodeur, J., and Bourgeois, G. (2020). Effect of temperature on the walking behaviour of an egg parasitoid: disentangling kinetic response from integrated response. Ecol. Entomol. *45*, 741-750

Ayasse, M., Paxton, R.J., and Tengö, J. (2001). Mating behavior and chemical communication in the order Hymenoptera. Annu. Rev. Entomol. 46, 31–78.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., et al. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Change Biol. 8, 1–16.

Benelli, G., Bonsignori, G., Stefanini, C., and Canale, A. (2012). Courtship and mating behaviour in the fruit fly parasitoid *Psyttalia concolor* (Szépligeti) (Hymenoptera: Braconidae): the role of wing fanning. J. Pest Sci. 85, 55–63.

Boivin, G. (1988). Laboratory rearing of *Anaphes sordidatus* [Hym.: Mymaridae] on carrot weevil eggs [Col.: Curculionidae]. BioContr. 33, 245–248.

Boivin, G., and Martel, V. (2012). Size-induced reproductive constraints in an egg parasitoid. J. Insect Physiol. 58, 1694–1700.

Boullis, A., Detrain, C., Francis, F., and Verheggen, F.J. (2016). Will climate change affect insect pheromonal communication? Curr. Opin. Insect Sci. 17, 87–91.

Bourdais, D., Vernon, P., Krespi, L., and van Baaren, J. (2012). Behavioural consequences of cold exposure on males and females of *Aphidius rhopalosiphi* De Stephani Perez (Hymenoptera: Braconidae). BioContr. 57, 349–360.

Bouwer, M.C., Slippers, B., Wingfield, M.J., Allison, J.D., and Rohwer, E.R. (2017). Optimization of pheromone traps for *Coryphodema tristis* (Lepidoptera: Cossidae). J. Econ. Entomol. 110, 1603–1610.

Byers, J., Hebets, E., and Podos, J. (2010). Female mate choice based upon male motor performance. Anim. Behav. 79, 771–778.

Candolin, U. (2003). The use of multiple cues in mate choice. Biol. Rev. 78, 575-595.

Chirault, M., Bressac, C., Goubault, M., and Lécureuil, C. (2019). Sperm limitation affects sex allocation in a parasitoid wasp *Nasonia vitripennis*. Insect Sci., 26, 853-862.

Colinet, H., and Boivin, G. (2011). Insect parasitoids cold storage: A comprehensive review of factors of variability and consequences. Biol. Contr. 58, 83–95.

Collins, R.D., and Grafius, E. (1986a). Courtship and mating behavior of *Anaphes sordidatus* (Hymenoptera: Mymaridae), a parasitoid of the carrot weevil (Coleoptera: Curculionidae). Ann. Entomol. Soc. Am. 79, 31–33.

Collins, R.D., and Grafius, E. (1986b). Biology and life cycle of *Anaphes sordidatus* (Hymenoptera: Mymaridae), an egg parasitoid of the carrot weevil (Coleoptera: Curculionidae). Environ. Entomol. 15, 100–105.

Cook, D.F. (1994). Influence of temperature on copula duration and mating propensity in *Lucilia cuprina* Wiedemann (Diptera: Calliphoridae). Austral Entomol. 33, 5–8.

Cormier, D., Royer, L., Vigneault, C., Panneton, B., and Boivin, G. (1998). Effect of female age on daily cycle of sexual pheromone emission in gregarious egg parasitoid *Anaphes listronoti*. J. Chem. Ecol. 24, 1595–1610.

Fasolo, A.G., and Krebs, R.A. (2004). A comparison of behavioural change in Drosophila during exposure to thermal stress. Biol. J. Linn. Soc. 83, 197–205.

Fauvergue, X., Chuine, A., Vayssade, C., Auguste, A., and Desouhant, E. (2015). Sterile males in a parasitoid wasp with complementary sex determination: from fitness costs to population extinction. BMC Ecol. 15, 13.

Fleming, P.A., and Bateman, P.W. (2007). Just drop it and run: the effect of limb autotomy on running distance and locomotion energetics of field crickets (*Gryllus bimaculatus*). J. Exp. Biol. 210, 1446–1454.

Full, R.J. (1987). Locomotion energetics of the ghost crab: I. Metabolic cost and endurance. J. Exp. Biol. 130, 137–153.

Galliard, J.-F.L., and Fitze, P.S. (2005). Sex ratio bias, male aggression, and population collapse in lizards. Proc. Natl. Acad. Sci. 102, 18231–18236.

Gilbert, D.G., and Richmond, R.C. (1982). Esterase 6 in *Drosophila melanogaster*: reproductive function of active and null males at low temperature. Proc. Natl. Acad. Sci. 79, 2962–2966.

Godfray, H.C.J. (1994). Parasitoids: behavioral and evolutionary ecology. Princeton University Press.

Grayson, K.L., Mitchell, N.J., Monks, J.M., Keall, S.N., Wilson, J.N., and Nelson, N.J. (2014). Sex ratio bias and extinction risk in an isolated population of tuatara (*Sphenodon punctatus*). PLoS ONE 9, e94214.

Hamilton, W.D. (1967). Extraordinary sex ratios. Science 156, 477–488.

Hance, T., van Baaren, J., Vernon, P., and Boivin, G. (2007). Impact of extreme temperatures on parasitoids in a climate change perspective. Annu. Rev. Entomol. 52, 107–126.

Hays, G.C., Mazaris, A.D., Schofield, G., and Laloë, J.-O. (2017). Population viability at extreme sex ratio skews produced by temperature-dependent sex determination. Proc. R. Soc. B Biol. Sci. 284, 20162576.

Heimpel, G.E., and de Boer, J.G. (2008). Sex determination in the Hymenoptera. Annu. Rev. Entomol. 53, 209–230.

Jachmann, F., and Van den Assem, J. (1993). The interaction of external and internal factors in the courtship of parasitic wasps (Hym., Pteromalidae). Behaviour 125, 1–19.

Janzen, F.J. (1994). Climate change and temperature-dependent sex determination in reptiles. Proc. Natl. Acad. Sci. 91, 7487–7490.

Johansson, B.G., and Jones, T.M. (2007). The role of chemical communication in mate choice. Biol. Rev. 82, 265–289.

Kanno, H., and Sato, A. (1979). Mating behaviour of the rice stem borer moth, *Chilo suppressalis* WALKER (Lepidoptera: Pyralidae) II. Effects of temperature and relative humidity on mating activity. Appl. Entomol. Zool. 14, 419–427.

Katsuki, M., and Miyatake, T. (2009). Effects of temperature on mating duration, sperm transfer and remating frequency in *Callosobruchus chinensis*. J. Insect Physiol. 55, 113–116.

King, B.H. (1987). Offspring sex ratios in parasitoid wasps. Q. Rev. Biol. 62, 367–396.

Le Lann, C., Lodi, M., and Ellers, J. (2014). Thermal change alters the outcome of behavioural interactions between antagonistic partners. Ecol. Entomol., 39, 578-588.

Linn, C.E., Campbell, M.G., and Roelofs, W.L. (1988). Temperature modulation of behavioural thresholds controlling male moth sex pheromone response specificity. Physiol. Entomol. 13, 59–67.

Loudon, C., and Koehl, M.A.R. (2000). Sniffing by a silkworm moth. J. Exp. Biol. 203, 2977–2990.

Mackauer, M. and Fraser, S. (1969). Sexual behaviour of and hybridization between 3 species of *Aphidius* Nees parasitic on pea aphid (Hymenoptera aphidiidae). Proc. Entomol. Soc. Wash. 71, 339–351.

Martel, P., Svec, H. J., & Harris, C. R. (1975). Mass rearing of the carrot weevil, *Listronotus oregonensis* (Coleoptera : Curculionidae), under controlled environmental conditions. Can. Entomol. 107, 95–98.

Martel, V., Damiens, D., and Boivin, G. (2008). Strategic ejaculation in the egg parasitoid Trichogramma turkestanica (Hymenoptera: Trichogrammatidae). Ecol. Entomol. 33, 357–361.

Matthews, R.W. (1982). Courtship in parasitic wasps. In P. W. Price (ed.), Evolutionary Strategies of Parasitic Insects and Mites, p. 66-86. Plenum Press, New York.

McNeil, J. N., and Brodeur, J. (1995). Pheromone-mediated mating in the aphid parasitoid, *Aphidius nigripes* (Hymenoptera: Aphididae). J. Chem. Ecol., 21, 959-972.

Moiroux, J., Brodeur, J., and Boivin, G. (2014). Sex ratio variations with temperature in an egg parasitoid: behavioural adjustment and physiological constraint. Anim. Behav. 91, 61–66.

Moiroux, J., Boivin, G., and Brodeur, J. (2015). Temperature influences host instar selection in an aphid parasitoid: support for the relative fitness rule. Biol. J. Linn. Soc. 115, 792–801.

Moiroux, J., Boivin, G., and Brodeur, J. (2018). Ovigeny index increases with temperature in an aphid parasitoid: Is early reproduction better when it is hot? J. Insect Physiol., 109, 157-162.

Montgomery, J. C., and Macdonald, J. A. (1990). Effects of temperature on nervous system: implications for behavioral performance. Am. J. Physiol. Regul. Integr. Comp. Physiol., 259, R191-R196.

Nelder, J.A., and Wedderburn, R.W.M. (1972). Generalized Linear Models. J. R. Stat. Soc. Ser. Gen. 135, 370.

Ode, P.J., and Hunter, M.S. (2002). Sex ratios of parasitic Hymenoptera with unusual life-histories. In Sex Ratios, I.C.W. Hardy, ed. (Cambridge: Cambridge University Press), pp. 218–234.

Régnière, J., Powell, J., Bentz, B., and Nealis, V. (2012). Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling. J. Insect Physiol. 58, 634–647.

Richards, A.G. (1963). The rate of sperm locomotion in the cockroach as a function of temperature. J. Insect Physiol. 9, 545–549.

Ritchie, M.G., Saarikettu, M., Livingstone, S., and Hoikkala, A. (2001). Characterization of female preference functions for *Drosophila montana* courtship song and a test of the temperature coupling hypothesis. Evolution 55, 721–727.

Roy, M., Brodeur, J., and Cloutier, C. (2003). Temperature and sex allocation in a spider mite. Oecologia, 135, 322-326.

Ruther, J., Matschke, M., Garbe, L.-A., and Steiner, S. (2009). Quantity matters: male sex pheromone signals mate quality in the parasitic wasp *Nasonia vitripennis*. Proc. R. Soc. B Biol. Sci. 276, 3303–3310.

Sentis, A., Ramon-Portugal, F., Brodeur, J., and Hemptinne, J.-L. (2015). The smell of change: warming affects species interactions mediated by chemical information. Glob. Change Biol. 21, 3586–3594.

Simmons, A.M., and Marti Jr., O.G. (1992). Mating by the fall armyworm (Lepidoptera: Noctuidae): Frequency, duration, and effect of temperature. Environ. Entomol. 21, 371–375.

Simonet, D.E., and Davenport, B.L. (1981). Temperature requirements for development and oviposition of the carrot weevil. Ann. Entomol. Soc. Am. 74, 312–315.

Taylor, F. (1981). Ecology and evolution of physiological time in insects. Am. Nat. 117, 1–23.

Team, R.C. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Villagra, C.A., Pinto, C.F., Penna, M., and Niemeyer, H.M. (2011). Male wing fanning by the aphid parasitoid *Aphidius ervi* (Hymenoptera: Braconidae) produces a courtship song. Bull. Entomol. Res. 101, 573–579.

Walsh, B.S., Parratt, S.R., Hoffmann, A.A., Atkinson, D., Snook, R.R., Bretman, A., and Price, T.A. (2019). The impact of climate change on fertility. Trends Ecol. Evol**.** 34, 249-259.

Wilkes, A. (1965). Sperm transfer and utilization by the arrhenotokous wasp *Dahlbominus fuscipennis* (Zett.) (Hymenoptera: Eulophidae). Can. Entomol. 97, 647–657.

Zayed, A., and Packer, L. (2005). Complementary sex determination substantially increases extinction proneness of haplodiploid populations. Proc. Natl. Acad. Sci. 102, 10742–10746.

Zhao, D.X., Boivin, G., and Stewart, R.K. (1991). Simulation model for the population dynamics of the carrot weevil, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae**).** Can. Entomol. 123, 63-76.

Zhu, H., Thistle, H.W., Ranger, C.M., Zhou, H., and Strom, B.L. (2015). Measurement of semiochemical release rates with a dedicated environmental control system. Biosyst. Eng. 129, 277–287.

Chapitre 7 : Individual behaviour and population dynamics under climate change: Simulation of an insect parasitoid life cycle

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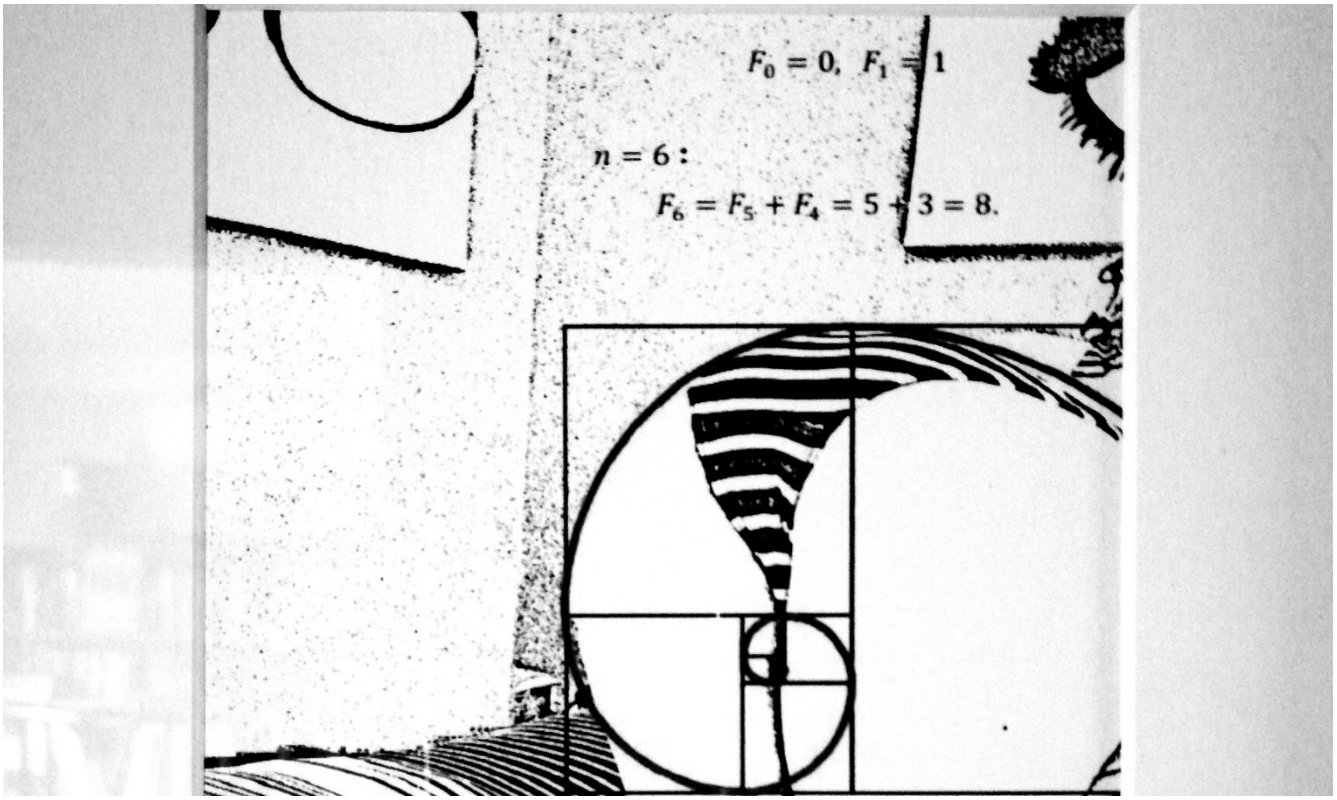


Blaise Laurent

7.1 / Abstract :

In the context of climate change, there is an urgent need for better understanding the effect of temperature on animal behaviour, and for including these effects into predictive population models. In order to evaluate the importance of such an inclusion, we created two population dynamics models. The first was based only on development, mortality and oviposition rate data, and the second included behaviours in addition. Behaviours incorporated in the second model were mating, host searching and host exploitation. In order to assess models efficiency, we compared both their predicted populations to field populations of the modelled biological agent, an egg parasitoid. Sensitivity analyses were carried out in order to evaluate the relative importance of each component of the parasitoid life-cycle (development, mortality and behaviours) on population dynamics. Finally, we used the two models to investigate the importance of including behaviours into population dynamics in the context of climate change's mean increase in temperature. Including behaviours into the population dynamics model did not increase the efficiency for predicting field population: both models were equally efficient. Resulting parasitoid population were however different, with the one modelled with the inclusion of behaviour being higher than the one modelled with physiology processes only. Sensitivity analyses showed that mating probability, probability of being active, searching between plants and host exploitation duration did not affect parasitoid population level. However, host oviposition directly influenced parasitoid populations, as well as changes in parasitoid mortality and parasitism rates. In addition to having different relative impact on the parasitoid population, behaviours and development all had different thermal performance curves, with optimal temperature and tolerance range varying. An addition of 3.1°C to the 2017 temperatures, mimicking climate change's south Quebec mean increase in temperature, resulted in different populations dynamics between the two models. Our analysis shows that, at intermediate temperatures conditions, the inclusion of behaviours already change the dynamics of the simulated population; but behaviours and their duration should specifically be included when studying more extreme conditions, because physiology used alone misses certain effects of temperature on the life cycle of the individuals.

Key-words: Individual-Based-Model – Dynamic modelling - Behaviour - *Anaphes listronoti*

7.2 / Introduction

The effect of temperature on ectotherm physiology has been extensively studied (Neven, 2000; Angilletta et al., 2002; Folguera et al., 2011), leading to the development of several different models, both at the individual, population and community scale. According to Boltzmann-Arrhenius model (Dell et al., 2011), the rate of chemical reactions of an ectotherm is conditioned by two factors, that both depends on temperature: the rate of enzymatic action and their conformation (Neven, 2000). Consequently, the metabolic rate (Clarke and Fraser, 2004) and the developmental rate (Davidson, 1944; Logan et al., 1976; Taylor, 1981; Wagner et al., 1984; Damos and Savopoulou-Soultani, 2012; Régnière et al., 2012) of ectotherms are dependent upon temperature. Temperature-driven models using developmental and physiological data such as reproduction and survival rate, or physiological tolerance such as the critical thermal minimum and maximum (CT_{min} and CT_{max}), are largely used to predict population phenology (Satake et al., 2006; Nietschke et al., 2007; Régnière et al., 2012) and distribution (Addo-Bediako et al., 2000; Jeschke and Strayer, 2008; Keith et al., 2008; Kearney et al., 2009a; Kearney and Porter, 2009; Woodin et al., 2013). However, recent research has put into perspective the significance of behaviour in insect life cycle, and potential consequences on population dynamics (Tenhumberg, 2004). For example, Morales and Ellner (2002) found that spatial spread in the landscape was severely underestimated in their model if they did not include behavioral heterogeneity between individuals and time. Still few predictive models include behaviour (Harmon and Barton, 2013) despite their importance in biological processes. Specifically, in the context of climate change, behaviours may be decisive for species adaptations (Huey and Tewksbury, 2009; Kearney et al., 2009b; Sih et al., 2011; Tuomainen and Candolin, 2011; Andrew et al., 2013; Sih, 2013; Sih et al., 2016) and interactions (Davis et al., 1998; Jiang and Morin, 2004; Van der Putten et al., 2010; Harmon and Barton, 2013). Consequently, bridges between behavioral ecology and population dynamics need to be readily established (Ives, 1995; Levin, 2000; Vet, 2001; Tenhumberg, 2004; Knowlton and Graham, 2010; Wong and Candolin, 2015).

“Process-oriented population models” allow the inclusion of both behaviour and physiology in population dynamics (Stimac, 1982; Bolliger et al., 2005; Hayes et al., 2009). A population is structured by age or phenological stage, and the transition from one stage to the next is conditioned by physiological and behavioural processes. Processes can be fixed values or submodels incorporating ecological data. One issue is that these models calculate processes altogether for all individuals of the same stage: at a given time, all those individuals behave the same. A more powerful approach is to account for the variability in individual behaviours in the population. To this end, instead of working with populations structured in age or phenological stages, the model can be designed at the individual scale (Individual-based model) (Huston et al., 1988; DeAngelis and Mooij, 2005; Grimm et al., 2006). This makes it possible to include variability between individuals and their interactions with their environment (Huston et al., 1988; Judson, 1994; Grimm et al., 2006). Finally, as the model includes a time component, it conforms to a dynamic model. Dynamic models calculate the simulated variables for a time t based on their state and external conditions (e.g. temperature) at t-1 (Hannon and Ruth, 2009). Example of use of individual-based dynamic models include the prediction of the control level by a parasitoid in a greenhouse (van Roermund et al., 1997), or of biomass yield and nutrient fluxes in a mussel farm (Brigolin et al., 2009).

In order to evaluate the importance of including individual behaviours into population dynamics, we developed such a model for *Anaphes listronoti* Huber (Huber et al., 1997), an egg parasitoid of the carrot weevil (*Listronotus oregonensis* (Le Conte)). This multivoltine species (Boivin, 1993) was chosen because data on its life history, thermal biology (Collins and Grafius, 1986a; Traoré et al., 2006; Rhéaume, 2009; Boivin and Martel, 2012) and the effect of temperature on its behaviour (Augustin et al., 2020) are available. Data for its host, *Listronotus oregonensis* (mortality for each stage, and the effect of temperature on development and oviposition rate) is also sufficient to include it in the model (Simonet and Davenport, 1981; Zhao et al., 1991; Boivin, 1999; Rhéaume, 2009). Another important consideration is that we had access to wild populations of both the parasitoid and its univoltine host (Boivin, 1993) on an experimental farm, that allowed to evaluate the model.

Our first objective was to assess the effect of including individual behaviours into a population dynamics model. Accordingly, we created two models, one that included individual behaviours and one that did not, and tested their efficiency to predict a field population. First, we describe the data collection for the A. *listronoti* field population from a Ste-Clotilde experimental farm in 2017. Second, we detail the model not including behavioural components, based on laboratory data of *Anaphes listronoti*, *Anaphes victus* and *Listronotus oregonensis.* Third, we describe the model including behaviour, based on behavioural data for *Anaphes listronoti*. Then, we compare both models to the field population. We then carry out sensitivity analyses of biological processes included in the model, in order to examine the relative importance of behavioural and physiological processes for the population dynamics. Finally, we compare the outcome population of the two models (including and excluding behaviours) for a mean increase in temperature of 3.1°C (climate change simulation).

7.3 / Field data for model validation

Populations and temperature data were collected in 2017 from a first-year carrot plot at the experimental farm of Agriculture and Agri-Food Canada (AAFC) in Sainte-Clotilde (Lat : 45.166196°, Long. : -73.676439°). The plot was 8 m x 20 m, with 9 rows of 100 carrots m^{-1}, for a total of about 16 000 carrots. No pesticides were used in the plot. We introduced 600 adult carrot weevils (300 males, 300 females) into the plot at the beginning of the growing season, between May 30th and June 8th 2017. Part of the carrot weevils were obtained from laboratory rearing at the AAFC research centre in Saint-Jean-sur-Richelieu (N = 500), and part were captured in another carrot plot from the experimental farm using Boivin traps (N = 100). Since the test plot of the experimental farm was not used to grow carrot in previous years, we expected that no initial carrot weevil population would be present. Hourly temperatures were measured using a HOBO Temp Logger (model H08-001-02) placed within the carrot row (Figure 7-1).

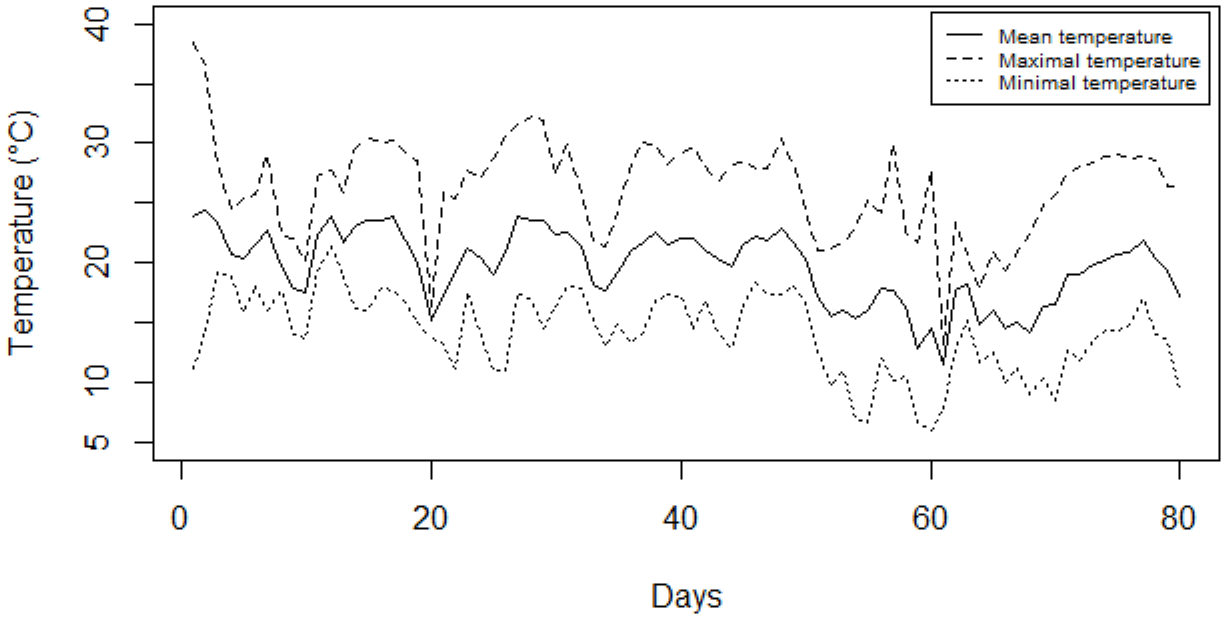


Figure 7-1 : Mean, maximum and minimum field temperatures measured by HOBO Temp Logger (model H08-001-02) placed within the carrot row.

Each week, 25 carrots were sampled from the plot, and the number of carrot weevil eggs was counted and individually put in 300 µL Beem® polyethylene capsules at rearing conditions (25°C ± 2°C, 50% RH and 16L:8D) in order to check emergence for parasitism. Two species of *Anaphes* have been described in Quebec : *Anaphes listronoti* and *Anaphes victus* (Huber et al., 1997), and a third one has recently been found in *Listronotus oregonensis* eggs at the same experimental farm, but has not yet been officially described; it is referred to as *Anaphes* sp. We wanted to include in the model only individuals of *A. listronoti*, so species were discriminated using morphological criterion (Huber et al., 1997) and mating tests. Both males and females of the three species only mate with individuals from their own species. Having rearings of the three species, we tried to mate individuals emerged from the field to individuals from the rearings. If the mating was successful, we assumed that the individual emerged from the field belonged to the species with which it mated.

Number of degree-days (DD) accumulated between field sampling and emergence in the laboratory was calculated for each emerged adult *A. listronoti*. Using these data and field temperatures, we calculated the date at which the adult parasitoid would have emerged in the field. For example, one carrot weevil egg sampled on 27 June led to the emergence of two parasitoids after 6 days at rearing conditions (3 July). During these 6 days, parasitoid accumulated: (rearing temperature – base temperature) * 6 days = (25°C - 6°C) * 6 days = 114 DD. In the field, based on HOBO data, it would have taken 8 days to accumulate 114 DD. Thus, in the field population, they were considered as having emerged on 5 July. Finally, the number of parasitoids obtained from the 25 carrots sampling was adjusted to the 16 000 carrots present in the field by multiplying it by 640, assuming that the 25 carrots randomly sampled were representative of the parasitoid density in the plot.

7.4 / Model description

7.4.1 / Purpose

The purpose of the models was to simulate population dynamics of *A. listronoti* in relation to ambient temperature. Both models include phenological stages, and the second model includes in addition behavioral sequences (e.g. host searching of parasitoid females, as illustrated in Figure 7-2) of the egg parasitoid.

7.4.2 / Variables

Table 7-1 displays the biological variables of the parasitoid and its host included in the model, the environmental variables, and the spatial structure of the habitat. Since development and mortality data are not available for *A. listronoti*, we used *Anaphes victus* data, a sympatric, morphologically (Huber et al., 1997) and genetically (Landry et al., 1993) close species of *A. listronoti*. They both parasitize the carrot weevil in Quebec carrot fields (Cormier et al., 1996), and are raised under the same conditions in the laboratory. We expect both species to share similar developmental duration in relation to temperature, and similar mortality rates. The six developmental stages in *Anaphes* represent the immature stage, adult age 1, adult age 2, adult age 3, adult age 4 and adult age 5 (Rhéaume, 2009). The larval stages of the parasitoid are not separated in the model, as we do not have data on their thermal requirements, but we do have data on the time required to go from oviposition to the adult emergence based on temperature (Traoré et al., 2006). Mortality rates are daily mortality for both the parasitoid and the host populations, caused by factors not explicitly modeled, such as predation (Rhéaume, 2009). Thermal mortality was not added to mortality rate, as temperatures measured in the experimental field in 2017 within carrot rows (maximum measured temperature: 38.5°C, only occurring once) were not high enough to cause temperature-related mortality (mean upper thermal limits for insects = 39.3°C (Hoffmann et al., 2013)). For reproduction processes in the behaviour model, number of oocytes at female emergence, and number of spermatozoids transferred during mating were calculated using the "rnorm" function of the R stats package (R Core Team, 2016), using mean and standard deviation values from Boivin and Martel (2012) (Table 7-1).

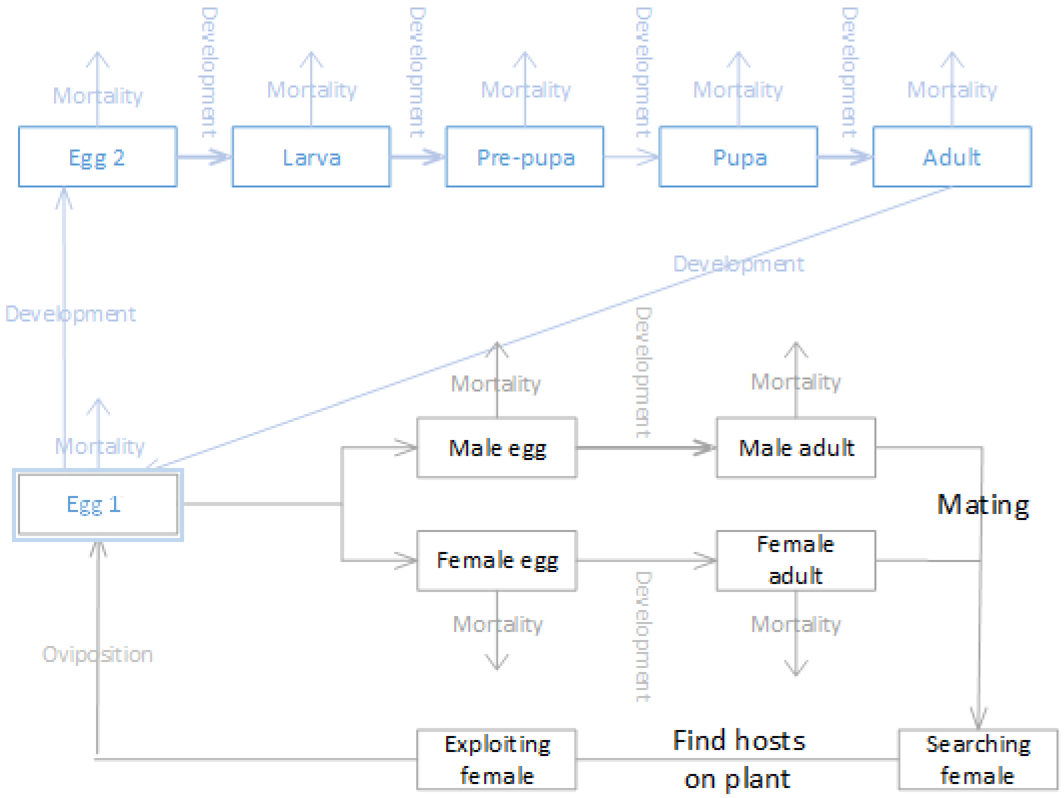


Figure 7-2: Diagram representing the life cycle of *Anaphes listronoti* and its host as included in the model including behaviour. Boxes represent the different stages of the life cycle of the species, and arrows between the boxes represent the events allowing the transition of individuals from one stage to another. *Anaphes listronoti* cycle is represented in grey, and its host cycle, *Listronotus oregonensis*, is represented in blue. Carrot weevil eggs are pale yellow following oviposition (stage “Egg 1”) and turn brown after 24 h (stage “Egg 2”) (Boivin, 1999). *Anaphes listronoti* females prefers the first egg stage.

Parasitoids development was sex specific because thermal base values differ between males and females (Traoré et al., 2006). In contrast, the carrot weevil development values were the same for males and females (Simonet and Davenport, 1981; Rhéaume, 2009), so they were not separated for calculation. The seven stages of carrot weevil represent respectively the yellow egg stage (0 to 24 h, preferred stage of *A. listronoti*), brown egg (24 h to hatching), larva, prepupa, pupa, adult and sexually mature adult (Simonet and Davenport, 1981). Host stage preference of the parasitoid for ≤24h old weevil eggs was implicitly included as only eggs from this stage were available for parasitism in both models. Carrot weevil behaviour was not modelled because *A. listronoti* attacks only the immobile egg stage. The carrot weevil phenological model thus served only to provide a realistic number of hosts to the parasitoid, using total number of carrot weevil females in the population and their reproductive rates, based on Zhao et al. (1991).

Parasitoids			
Development	**Value**	**Species**	**Reference**
Number of developmental stages (♀ + ♂)	6	*A. victus*	Rhéaume, 2009
Minimal temperature for development and accumulation DH (♀) (°C)	6	*A. victus*	Traoré et al., 2006
Minimal temperature for development and accumulation DH (♂) (°C)	9	*A. victus*	Traoré et al., 2006
Maximal temperature for development and accumulation DH (♂ + ♀) (°C)	35	*A. victus*	Traoré et al., 2006
DH requirement for adult emergence from host egg (♂)	3408	*A. victus*	Traoré et al., 2006
DH requirement for adult emergence from host egg (♀)	4728	*A. victus*	Traoré et al., 2006
Mortality			
Daily mortality (%) - Immature stage	1	*A. victus*	Rhéaume, 2009
Daily mortality (%) - 0-day old adult	4.55	*A. victus*	Rhéaume, 2009
Daily mortality (%) - 1-day old adult	9.24	*A. victus*	Rhéaume, 2009
Daily mortality (%) - 2-days old adult	31.6	*A. victus*	Rhéaume, 2009
Daily mortality (%) - 3-days old adult	76.9	*A. victus*	Rhéaume, 2009
Daily mortality (%) - 4-days old adult	100	*A. victus*	Rhéaume, 2009
Biological values			
Lifetime production of oocytes (mean ± sd)	43.0 ± 2.5	*A. listronoti*	Boivin and Martel, 2012
Number of spermatozoids transfered during mating (mean ± sd)	38.3 ± 20.7	*A. listronoti*	Boivin and Martel, 2012
Sex-ratio (♂ / ♂ + ♀)	0.16	*A. listronoti*	Boivin and Martel, 2012
Clutch size (Number of parasitoid/host egg)	1.29 ± 0.47	*A. listronoti*	Collins and Grafius, 1986
Carrot weevil			
Development			
Number of developmental stages	7	*L. oregonensis*	Simonet and Davenport, 1981
Minimal temperature for development and accumulation DH (°C)	7	*L. oregonensis*	Simonet and Davenport, 1981
Maximal temperature for development and accumulation DH (°C)	29.4	*L. oregonensis*	Simonet and Davenport, 1981
DH requirement for development from egg to larva	3120	*L. oregonensis*	Simonet and Davenport, 1981
DH requirement for development from larva to prepua	6144	*L. oregonensis*	Simonet and Davenport, 1981
DH requirement for development from prepupa to pupa	2736	*L. oregonensis*	Simonet and Davenport, 1981
DH requirement for development from pupa to adult	3120	*L. oregonensis*	Simonet and Davenport, 1981
DH requirement for development from adult to sexually mature adult	3144	*L. oregonensis*	Simonet and Davenport, 1981
Mortality			
Daily mortality (%) – egg stages	4.15	*L. oregonensis*	Rhéaume, 2009, Boivin, 1999
Daily mortality (%) – larval stage	5.25	*L. oregonensis*	Rhéaume, 2009, Boivin, 1999
Daily mortality (%) – pre-pupa and pupa stages	11	*L. oregonensis*	Rhéaume, 2009, Boivin, 1999
Daily mortality (%) – adult stages	0.35	*L. oregonensis*	Rhéaume, 2009, Boivin, 1999
Biological values			
Sex-ratio (♂ / ♂ + ♀)	0.5	*L. oregonensis*	Saade et al., 1996
Environment			
Meteorological data			
Temperature (°C)	-	-	HOBO Temp Logger (model H08-001-02)
Habitat			
Carrot plot (m x m)	20 x 8	-	-
Carrot plant (cm x cm)	10 x 10	-	-

Table 7-1: Variables used in the models

In the physiology-only model, time step was of one day. In the behaviour-model, time step was of one minute, in order to account for real duration of parasitoid behaviour (around one minute for mating to dozens of minutes for patch exploitation). Wasps were only active during the photoperiod (from 6h00 to 21h00 based on data from the on-site weather station). The first day of simulation was set on 5 July 2017, based on field population emergence data. The last day of simulation was set at 10 days following the last day of carrot sampling: 22 September 2017, for a total of 80 days of simulation.

7.4.3 / Initialization

Initial values at the beginning of the simulation were identical between both models. Initial number of adult carrot weevils was 600 (300 males + 300 females), based on the number of individuals introduced in the plot. Initial number of adult parasitoids in the model was calculated based on field sampling emergence data: 640 females and 640 males. Initial number for immature stages for both species were 0. Initial values of number of oocytes in adult parasitoid females in the behaviour-model were defined according to the "rnorm" normal probability function from the R stats package (R Core Team, 2016), using biological values from previous studies (Table 7-1).

7.4.4 / Input

We used hourly temperature measured in the field as inputs for temperature in the models. For the physiology-only model (time step of one day), we calculated the minimum, maximum and mean temperature for each day. For the behaviour model (time step of one minute), we duplicated the hour value of temperature to each minute of the hour. For example, if the HOBO measured 15°C at 2PM and 16°C at 3PM, temperature for every minute from 2PM to 3PM was set at 15°C, and for every minute from 3PM to 4PM was set at 16°C.

7.4.5 / Process overview and scheduling

Scheduling of the processes in the model was based on the parasitoid species ecology. *Anaphes listronoti* individuals emerge in the first two hours of the photophase (Collins and Grafius, 1986a), so individuals started being active right after sunrise. Both males and females are ready to mate upon emergence (Collins and Grafius, 1986b). Males emerge earlier and wait for females on the emergence patch (Landry et al., 1993), so mating was the first event of the day. After mating, parasitoid females would start searching for host, and continue searching and exploiting until nightfall (16 hours of daylight). At night, all individuals were inactive. The main differences between the two model were : (1) the time steps, (2) the calculation at the individual level for female parasitoids in the behaviour model, and (3) the “parasitoid oviposition” part of the cycle, that was calculated as a single daily value in the physiology-only model, but calculated using different sequential processes in the physiology + behaviour model (Table 7-2).

7.3.5.1 / Physiology-only model

Anaphes listronoti females, males and carrot weevil were all modelled using separated matrix: one matrix for the parasitoid females, one for the males, and one for the carrot weevils. Each line of the matrices represented a cohort of individuals of the same age (Logan, 1988). Columns contained information for the cohort: cohort number, stage, number of individuals and DH accumulated. For this physiology-only model, processes included, in order, carrot weevil oviposition, parasitoid mating, parasitoid oviposition, and parasitoid and carrot weevil mortality and development.

Carrot weevil oviposition

Number of carrot weevil eggs laid each day by individual females was calculated as a function of temperature T using the formula calculated from Stevenson and Davenport (1981) (Figure 7-3a).

$$(1.1)\quad Oviposition\ (T) = -0.003\,T^3 + 0.154\,T^2 - 2.576\,T + 13.091$$

Carrot weevil females start laying eggs when the plants reach the phenological stage 3 to 4 true leaves (Boivin, 1988), but after that, plant phenological stage does not affect either carrot weevils’ egg-laying or *A. listronoti* exploiting behaviour (Collins and Grafius, 1986c). Plant stage was thus not included in the model. However, female weevil’s age does affect their egg-laying rate, as described in Rhéaume (2009). We considered that female reached maturity at the beginning of our simulation, so days of simulation would represent the day since reaching maturity of the females.

$$(1.2)\ Number\ of\ eggs\ per\ carrot\ weevil\ female\ (day) = \left(\frac{day}{10}\right)^{0.668} * e^{1-\left(\frac{day}{10}\right)^{0.675}}$$

Total number of eggs laid by carrot weevil females on a given day at a given temperature was calculated with formula (1.3).

$$(1.3)\ \text{Number of host eggs} = \text{Number of carrot weevil females} * \text{Oviposition}\ (T) * \text{Number of eggs laid per female (day)}$$

Parasitoid mating and oviposition

Number of mated parasitoid females was calculated every day as a proportion of total population using the “rnorm” function, with the result of equation (2) as the value for mean (Figure 7-3b). Equation (2) was based on data from Chapter 6 :

$$(2)\ Probability\ of\ parasitoid\ female\ mating\ (T) = \frac{-0.481\,T^2 + 22.247\,T - 166.194}{100}$$

Number of parasitoid eggs was then calculated using the “rnorm” function, with mean value calculated with equation (3.1) modified from Rhéaume (2009), and including the effect of temperature on parasitism rate from Chapter 5 : equation (3.2) (Figure 7-3c) :

(3.1) $Number\ of\ parasitoid\ eggs = number\ of\ parasitoid\ females * NOmax * Parasitism\ rate\ (T)$

NO_{max} was the maximum number of eggs oviposited daily by *Anaphes* females : 9.72 eggs (Rhéaume, 2009).

(3.2) $Parasitism\ rate\ (T) = 0.004\,T^2 + 0.201\,T - 1.755$

Sex ratio and clutch size were independent of temperature, based on experimental data (Chapter 5), so they were calculated using fixed values from Table 7-1.

Development

Development represents the transition from one phenological stage to the next. This transition was based on the accumulation of degree-hour (DH) since the reach of the current stage. Calculation was made for cohorts, based on DH, for *A. listronoti* females, males and carrot weevils. When a certain temperature threshold depending on species, sex and stage (Table 7-1) was reached, all the individuals in the cohort grew to the next stage. DH accumulation was calculated according to equation (4).

(4)
$$\begin{gathered} If\ T\ < Tbase\ ; xi = 0 \\ If\ T\ \geq Tbase\ ; xi = T - Tbase \\ Accumulated\ DH\ during\ the\ day = \sum_{i=1}^{24} xi \end{gathered}$$

T_{base} represents the lowest temperature at which development is observed for a given species. It can vary depending on the sex of the individual, as is the case of *Anaphes* (Table 7-1). Development in relation to temperature can be illustrated as a rate of development per day, as shown in (Figure 7-3d).

Mortality

For *Anaphes* females, males and carrot weevils, natural mortality was calculated as a percentage of the number of individuals in each cohort, with different mortality values depending on the stage (Table 7-1).

(5) $Number\ of\ dead\ individual\ of\ stage = number\ of\ individuals * stage\ mortality$

7.3.5.2 / Model including behaviour

As for the physiology-only model, *Anaphes listronoti* females, males and carrot weevil were modelled using separated matrix: one matrix for the parasitoid females, one for the males, and one for the carrot weevils. In the matrix representing the females parasitoid population, lines represented individuals, and each column contained information for this individual (x and y position in the field, cohort, sex, stage, number of oocytes, number of spermatozoids, degree-hours (DH) accumulated, dead or alive). For the *A. listronoti* males and carrot weevil population matrices, as individual biological data was not needed, each line represented a cohort of individuals of the same age. One last matrix contained the host eggs position in the field (x and y position and number of host eggs on the plant). *A. listronoti* males and carrot weevil matrices were the same as the physiology-only model. In this physiology + behaviour model, processes included, in order, carrot weevil oviposition, parasitoid mating, host searching and host exploitation, parasitoid and carrot weevil mortality and development. Parasitoid mating, host searching and host exploitation only applied to *A. listronoti* females (Figure 7-2). Mating represented the probability for the female parasitoid to mate, and the subsequent filling of her spermatheca with a certain number of spermatozoids. Host searching included three aspects: the probability of the female being active, whether she moved from plant to plant, and the time required to do so. Host exploitation included the female parasitism rate, offspring sex-ratio and the time spent exploiting the host patch. All behaviours were affected by temperature.

	Physiology-only model	**Physiology + behaviour model**
Time step*	Day*	Minute*
Matrices*	Anaphes females : cohort* Anaphes males : cohort Carrot weevil : cohort	Anaphes females : individual* Anaphes males : cohort Carrot weevil : cohort
Initial values	Carrot weevil females : 300 Carrot weevil males : 300 Anaphes females : 640 Anaphes males : 640	Carrot weevil females : 300 Carrot weevil males : 300 Anaphes females : 640 Anaphes males : 640
Processes*	Carrot weevil oviposition Anaphes mating Anaphes oviposition*	Carrot weevil oviposition Anaphes mating Host searching* *Probability of being active* *Mouvement duration* Host exploitation* *Patch exploitation duration* *Parasitism rate* *Search duration on empty plant*
	Anaphes mortality Anaphes development Carrot weevil mortality Carrot weevil development	Anaphes mortality Anaphes development Carrot weevil mortality Carrot weevil development

Table 7-2 : Comparison between the physiology-only model and the physiology + behaviour model. Parameters that differ between the two model are indicated with an asterisk (*).

Carrot weevil oviposition

Carrot weevil oviposition was calculated the same way as the physiology-only model, using equation (1.1), (1.2) and (1.3). However, as the behaviour model accounted for female parasitoid movement between host plant, number of host eggs per host plant was calculated in addition. Number of hosts laid in a single plant was calculated by dividing total number of host eggs obtained in equation (1.3) by the total number of host plant in the field (16 000), and then using the R "sample" function on each plant to determine the final number of host eggs on it.

Parasitoid mating

Mating relied on the probability of an individual female to mate given the temperature. Male number in the population or on the female host plant were not included, as field data showed that males would always find and reach virgin females at all observed weather conditions (unpublished data). Probability of female mating at temperature T was calculated according to equation (2). Successful mating results in transmission of spermatozoids from the male to the female spermatheca, allowing the female to lay daughters and sons (haplo-diploidy). Temperature did not affect the number of spermatozoids transferred when mating occurred (Chapter 6), so number of spermatozoids transferred was calculated for every temperature using the "rnorm" function from the R stats package (R Core Team, 2016), using mean and standard deviation values from Boivin and Martel (2012). We assumed that males and their spermatozoids stock were never the limiting factor, so we did not keep account of spermatozoids number left for males. Virgin females had a possibility to mate once every morning, until they were mated. Females of this species can mate several times (Boivin and Martel, 2012), but usually do it only once (Collins and Grafius, 1986b). Measured mating duration (courtship + copulation, successful and unsuccessful) was on average always inferior or equal to 1 min at all temperatures (Chapter 6) thus mating duration in the model was set at one minute for all temperatures.

Host searching

Host searching included the probability of the female being active, whether she moved from plant to plant, and the time required to do so. In order to simulate the female movement between plants, we represented the carrot plot as a matrix of 200 x 80 cell, each cell representing one individual carrot plant.

The probability of female being active was calculated based on data from Augustin et al., (2020) (Figure 7-3e).:

$$(6)\ Probability\ of\ being\ active\ (T) = \frac{-0.025\,T^3 + 1.584\,T^2 - 30.916\,T + 215.096}{100}$$

Whether females were active or not was then defined stochastically with the sample function of R stats pack (R Core Team, 2016), using the probability calculated in equation (6) to weight the probability of the female being active or not. Inactive individuals could not move from one plant to another in search of new patches, and could not oviposit in hosts on their current plant. Active individuals could move from their plant to an adjacent one, randomly (R sample function, 8 potential plants), and oviposit in host present on their current plant. Movement was only allowed from one plant to an adjacent one, one at a time, because we lacked data on movement at greater distance. Flight for parasitoids is possible, depending on the species, from 10 to 32°C (Langer et al., 2004; Yu et al., 2009), but we do not know how the females move from one carrot plant to another in the field. We assumed that, as the season advances, they need less and less to fly because adjacent carrot leaves become entangled, rendering flying, an energetically costly activity (Harrison and Roberts, 2000), unnecessary. Movement duration (min) from one plant to the next depended upon temperature, as walking speed (cm min^{-1}) and distance walked (cm) change according to temperature (Augustin et al., 2020). We first calculated walking speed according to temperature:

$$(7.1)\ Walking\ speed\ (T) = 0.071\, T + 3.928$$

Then we calculated movement duration between two plants (Figure 7-3f).:

$$(7.2)\ Movement\ duration\ (T) = \frac{Distance\ between\ two\ plants}{Walking\ speed\ (T)}$$

The distance between two plants in the model was always 12.07 cm. As plants were represented in the model as 10x10cm squares, distance between the center plant and the four directly adjacent plants was 10cm, and the distance between the four other adjacent plants (diagonals) was 14.14 cm. We used the mean distance between 10 and 14.14 cm as the distance between two plants used in calculating movement duration. The effect of volatiles from the infested host plant or the host on females searching patterns are not known for this species and thus were not included.

Host exploitation

Host exploitation included the parasitism rate, offspring sex-ratio and the time spent exploiting the host patch. Parasitism rate was dependent of ambient temperature (Chapter 5), and calculated using equation (3.2). Sex ratio and clutch size were independent of temperature, based on experimental data (Chapter 6), so, as for the physiology-only model, they were calculated using the fixed values in Table 7-1. Time spent exploiting the host patch (min) depended on temperature. In the field, at the number of eggs present in patches (1-5 eggs), parasitism rate did not vary with patch size (Collins and Grafius, 1986c). We used data from Chapter 5 to calculate the effect of temperature on patch exploitation duration (Figure 7-3g). We then used data from van Baaren et al. (2005a) to adjust this equation to the average number of eggs found on carrot plants in natural conditions: 2 eggs (Boivin, 1999). After patch exploitation, number of oocytes and spermatozoids available to the female were adjusted according to the progeny laid in the patch.

$$(8)\ Patch\ exploitation\ duration\ (T) = -0.286\, T + 18.44$$

If no host was present on the plant, searching time was also dependent on temperature:

$$(9)\ Searching\ duration\ on\ empty\ plant\ (T) = -0.162\, T + 10.452$$

In the same manner as for equation (8), equation (9) was obtained from the effect of temperature on patch exploitation duration, and then adjusted to patches containing no healthy egg (taken as a proxy for plants containing no host) using van Baaren et al. (2005b) data (Figure 7-3h).

Behaviours were calculated each minute during daytime. At 21:00 (nighttime), behaviours stopped. For *A. listronoti* females and males, development and mortality were calculated. For carrot weevil, development, mortality and oviposition were calculated. All these processes were only calculated once a day, at the end of the day.

Development

Development was calculated for *A. listronoti* females, males and carrot weevil the same way as for the physiology-only model, using equation (4).

Mortality

For *Anaphes* females, natural mortality was calculated as a probability for the individual to die, based on mortality rates from Rhéaume (2009) (see Table 7-1). The R sample function was then used to assess whether the individual had died or not, based on the probability from its stage. For *Anaphes* males and carrot weevils, natural mortality was calculated the same as the physiology-only model (Table 7-1), using equation (5).

7.4.6 / Design concept

Adaptive traits such as changes in host searching or patch exploitation behaviour based on learning (van Baaren and Boivin, 1998; van Baaren et al., 2006), patch quality (van Baaren et al., 2005b), or the presence of competition (Hamilton, 1967), were not included in the model. We did not include the effect of egg load and spermatozoid stock on behaviour (Fletcher et al., 1994; Minkenberg et al., 1992), nor of mating status (Fauvergue et al., 2008; Kugimiya et al., 2010; Wajnberg et al., 2006). Individuals did not predict the future conditions they would experience. Females in our model did not learn and did not estimate the future consequences of their decisions, or the future conditions they would experience. Basically, modelled *A. listronoti* females reacted only to the current conditions without adjusting behaviour according to previous or future conditions. This approach was chosen because the effect of temperature on all these aspects are not well-known yet, and thus including them in the model would require several estimations based on untested assumptions.

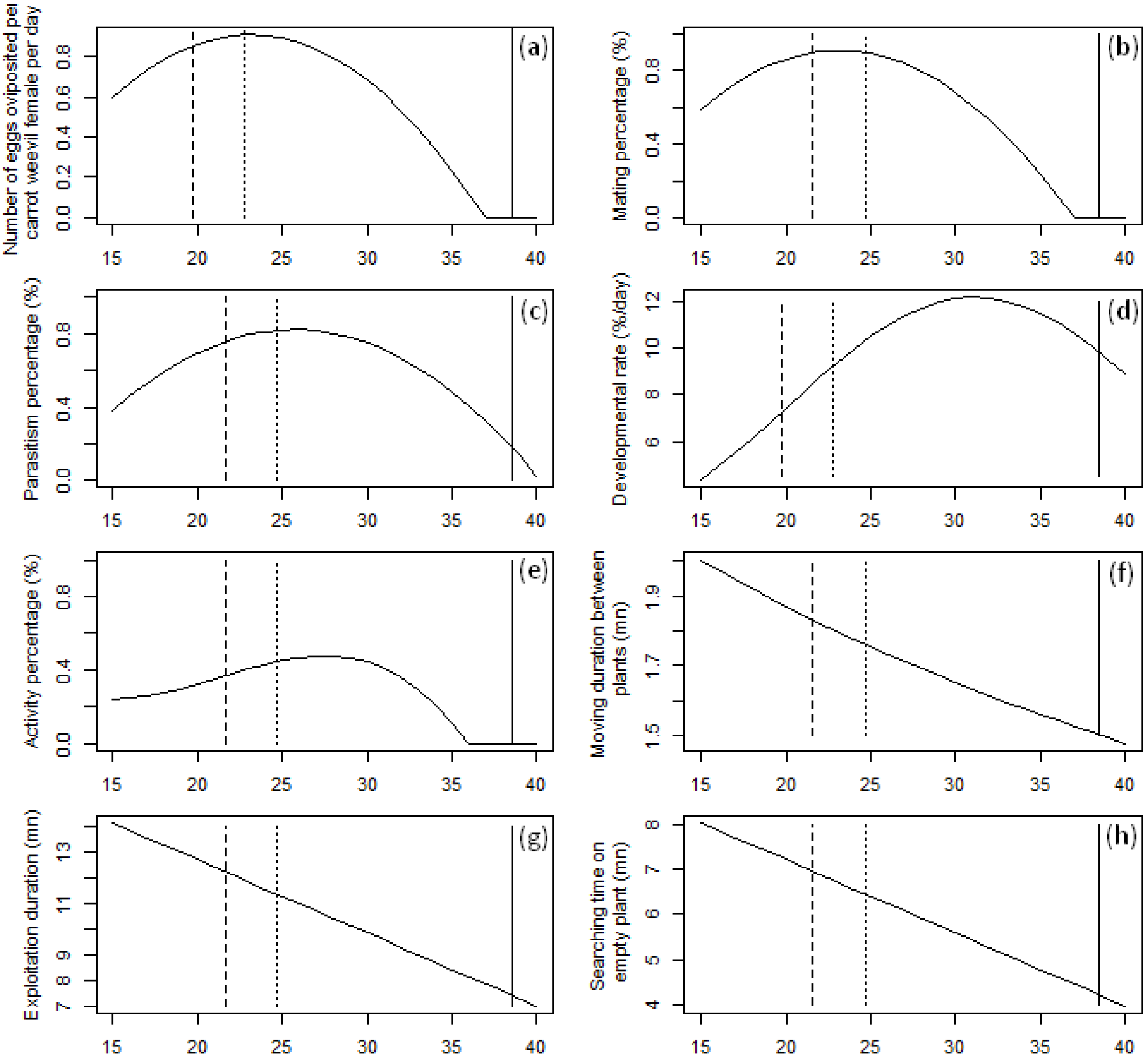


Figure 7-3: Temperature response curves of *Anaphes listronoti* females' behaviour and development. Graphics (a) through (g) respectively correspond to equations (1.1), (2), (3.2), (4), (6), (7.2), (8) and (9). For behaviour, mean temperatures experienced during the active period of females (21.6°C) correspond to vertical dashed lines. For development, mean temperatures were calculated from the 24 h temperatures (19.7°C), and are also indicated as vertical dashed lines on the developmental rate graph. Projected temperatures for climate change (mean temperatures + 3.1°C) are shown by vertical dotted lines. Maximum temperature experienced in 2017 (38.5°C) is indicated with a vertical solid line.

No interaction between individuals was explicitly included. Even for mating, males only were considered as spermatozoid sources, with no real interaction being modelled between males and females. If being on the same plant as another parasitoid (male or female), the female would not change its behaviour. *Anaphes listronoti* is a facultative gregarious species: females can lay 1 to 6 eggs in the same host (Collins and Grafius, 1986a). However, after emergence and mating, they live solitarily. The only interaction usually observed between adult individuals is through the scrambled competition, where females compete for hosts. In the presence of a competitor, females adjust their offspring sex-ratio (Hamilton, 1967), and their residence time (Mohamad et al., 2015). However, we do not know how temperature affects this aspect, which is why it was not included in the model. Stochasticity was included in the model in order to account for the variability of response between individuals when placed in a same situation. The probability of an event occurring was modulated by temperature, being maximum at the optimal temperature of the species for a given behaviour and decreasing as temperature differs from the optimum temperature.

7.4.7 / Statistical analyses

Model comparison

The final parasitoid adult population in the field was used in order to check models efficiency. We compared observed and simulated data using Root Mean Squared Error (RMSE), using the "rmse" function in the R Metrics package (Hamner and Frasco, 2018). Area under the curve of simulated parasitoid population were calculated using with the "auc" function of the R Metrics package (Hamner and Frasco, 2018), and the resulting values were compared between the two models using Mann-Withney tests using the R "wilcox.test" function (RC Team, 2016).

Sensitivity analyses

Sensitivity analyses serve to evaluate how much each input or internal process contributed to the model outputs. In our case, it was used to evaluate how much each process in the model (development, mortality, behaviours, host oviposition) affected the parasitoid populations output. All processes (durations, rates and probabilities) included in the model (parasitoid mating percentage, probability of being active, moving from plant to plant, parasitism rate, exploitation duration, development, and mortality, and carrot weevil oviposition) were increased and decreased of 50% compared to their original value in the model. For example, if for a given temperature the duration to move from one plant to the next was 2 min, it was modified to 3 min for a first simulation (+50%) and to 1 min for a second simulation (-50%). In the case of probabilities, final values were limited to 0 for lowest values and 1 for highest values, even if that did not represent a real 50% increase or decrease. For example, if for a given temperature probability of mating was 0.8, it was set for a first simulation at 1 (+25%, but probabilities were limited at 1), and for a second simulation at 0.4 (- 50%). The impact of these changes was assessed using area under the curve of resulting populations. Percentage of increase or decrease in the population was then calculated in reference to the initial simulated population. Differences between original simulated population and simulated population resulting from increase and decrease in events were calculated using a Mann-Withney test using the "wilcox.test" function in R.

Climate change simulations

We used the projected increase in mean temperature during the summer for the southern Quebec to simulate future weather conditions. CMIP5 (Coupled Modelled Intercomparison Project, that use the projected CO_2 scenarios to run model climates) using the scenario RCP (Representative Concentration Pathways) 4.5 (representing a stabilization of our CO_2 rejections to 650 ppm in the atmosphere), projects a mean increase in temperature of 3.1°C (1.9 to 4.2°C) in 2080 (Ouranos, 2015). We added this value to the temperatures measured in our plot in 2017 to simulate the effect of the mean increase in temperature on populations. Area under the curve of both simulated parasitoid population were calculated using with the “auc” function of the R Metrics package (Hamner and Frasco, 2018), and the resulting values were compared between the two models using Mann-Withney tests using the R “wilcox.test” function (RC Team, 2016).

7.5 / Results

7.5.1 / Physiology + behaviour **vs.** *Physiology only*

There was a significant difference between simulated populations modeled with physiology-only and population modeled with physiology + behaviour (area under the curve, Mann-Whitney test, $p < 0.001$ – Figure 7-4). Populations modelled with behaviour were a little higher than those modelled with physiology-only (area under the curve : 175 450 and 142 373 respectively). The physiology-only model fitted a little better the parasitoid field population (RMSE for physiology + behaviour model = 1479 and RMSE for physiology-only model = 1461). Population levels and peak dates were similar between measured and simulated values, except for around day 30, where a peak occurred in simulated population but not in measured populations. Peaks in measured population are less wide than those of simulated population.

7.5.2 / Sensitivity analyses

Increasing and decreasing mating and activity percentage, moving duration between plants and exploitation duration did not affect *A. listronoti* population number (Figure 7-5). On the other hand, parasitism rate, carrot weevil oviposition, parasitoid DH requirement and mortality significantly affected the resulting number of individuals in the parasitoid population. Increasing the parasitism rate increased the mean parasitoid population by 21%, but the effect was not significant ($p = 0.1$). Decreasing parasitism rate by 50% significantly decreased the parasitoid population by 58% ($p < 0.001$) (Figure 7-5). Increasing carrot weevil oviposition significantly increased the parasitoid population by 48% ($p = 0.006$), and reducing it decreased parasitoid population by 51% ($p < 0.001$) (Figure 7-5). Increasing DH requirement for parasitoid development by 50% led to a decrease in overall parasitoid population of 38% ($p < 0.001$) and decreasing DH requirement increased the mean number of parasitoid adults in simulated populations by 35% ($p = 0.02$). In addition, changes in DH requirement created a lag in parasitoid population dynamics. Population peaked earlier or later when DH requirement decreased and increased respectively (Figure 7-5). Increasing parasitoid mortality rate by 50% led to a significant decrease of 23% in the parasitoid population ($p = 0.03$), while decreasing mortality rate led to a significant increase of 41% in the parasitoid population ($p = 0.005$) (Figure 7-5).

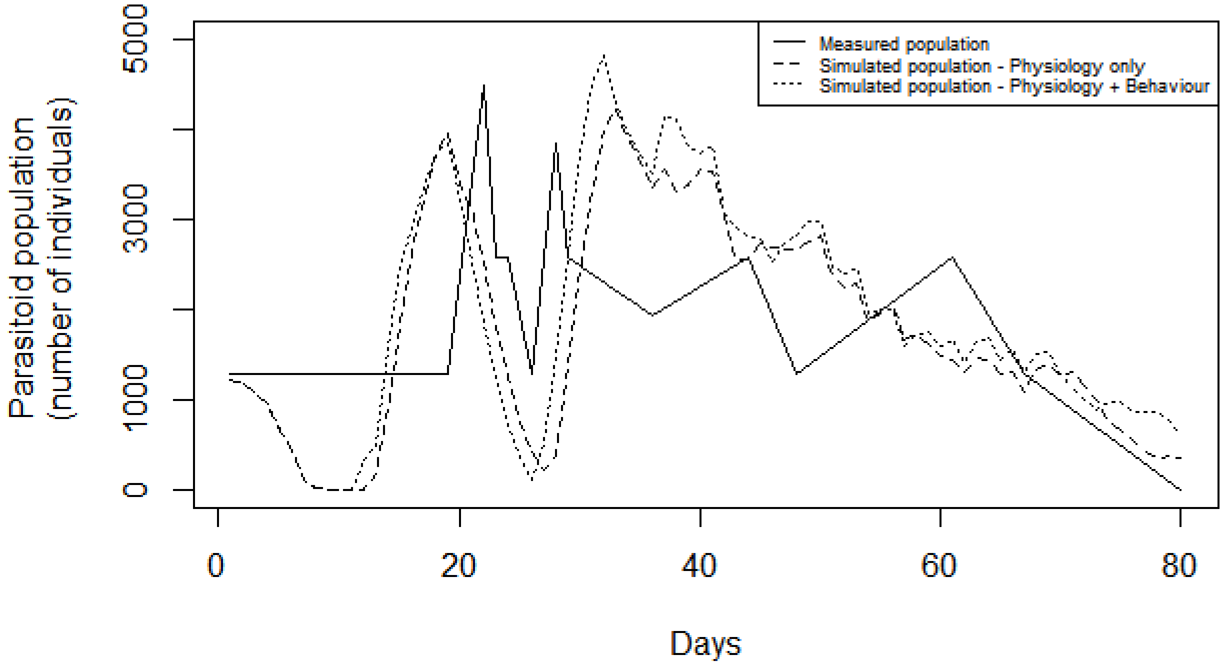


Figure 7-4: Number of *Anaphes listronoti* adult parasitoids in measured and simulated field populations. Simulated populations result from two different models: one including only physiological variables of the insect, and the second including both physiological and behavioral variables. Both simulated populations curves represent the mean of 10 simulations including stochastic process.

7.5.3 / Climate change

When adding 3.1°C to the 2017 temperature data in order to simulate projected future conditions, the parasitoid populations resulting from the two model are also significantly different (area under the curve - $p < 0.001$, Figure 7-6). However, the difference between the two simulated population is not greater than for the 2017 temperatures. Physiology-only populations were higher under the 3.1°C mean increase in temperature than under 2017 thermic conditions (16% increase). On the opposite, populations resulting from the model including behaviour were lower when temperatures increased (11% decrease).

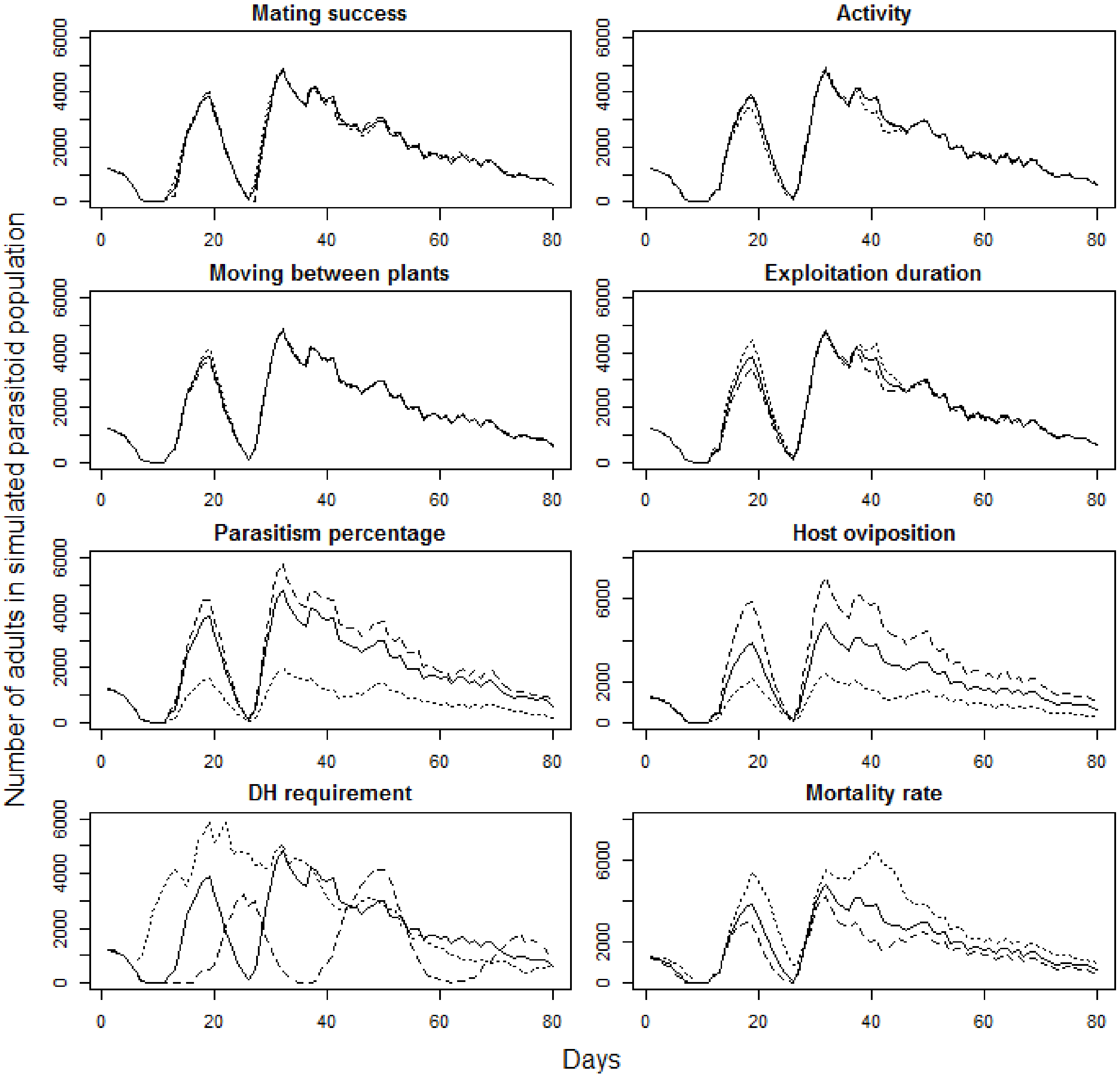


Figure 7-5 : Impact of 50% increase and decrease of behavioural and physiological traits on the simulated *Anaphes listronoti* adult population dynamics. Full lines represent the original simulated population, dashed lines represent the increase of the trait by 50%, and dotted lines the decrease of the trait by 50%.

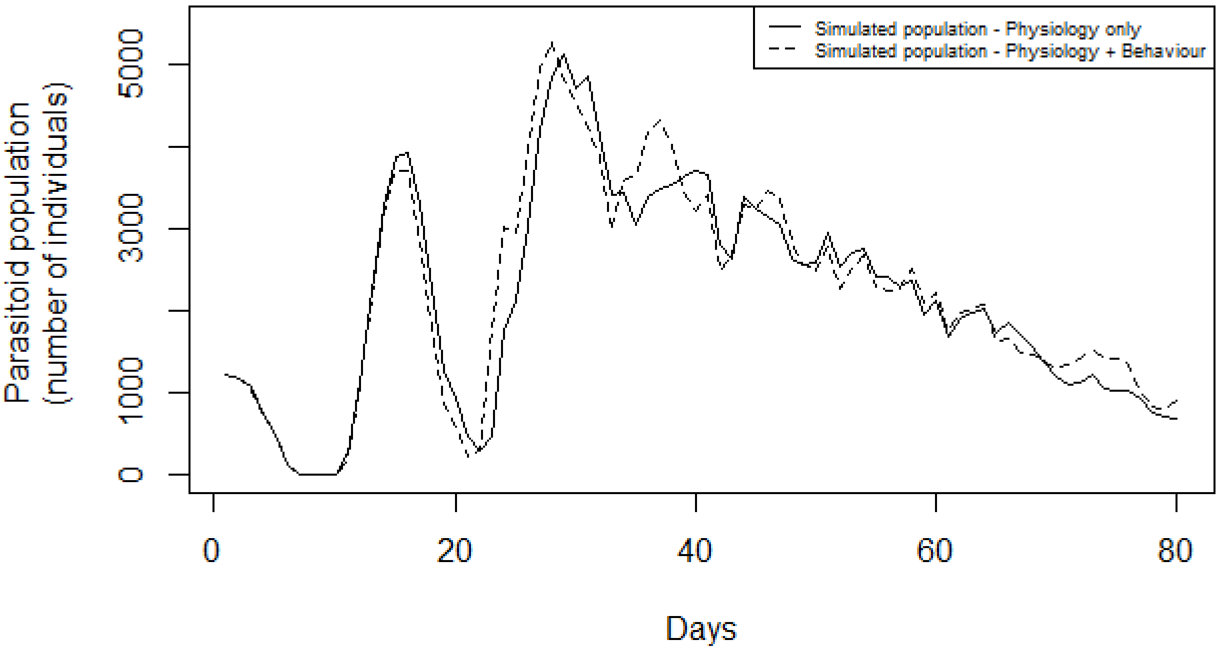


Figure 7-6 : Simulated populations including and excluding behaviour under 3.1°C warmer conditions compared to 2017 measured temperatures. Both simulated populations curves represent the mean of 10 simulations including stochastic process.

7.6 / Discussion

When looking at current field temperatures, there was a small difference between the two models, but both were equally efficient at predicting field parasitoid population. When adding 3.1°C to 2017 measured temperatures, differences persisted between the two simulated populations, but did not increase, contrary to our expectations. Populations simulated with inclusion of behaviour were a little higher than population simulated with physiology only. Behaviour and physiological processes have different relative impact on population dynamics: while variations in most physiological processes lead to a variation of similar amplitude in the population, the impact of variation in behaviour processes was less predictable. For a certain range of temperatures, changes in behaviour had almost no impact on the final population, but outside this range behaviour performance is greatly reduced, with potentially large impact on the parasitoid population. However, we lack information about individual movement, time allocation and mortality in the field, and the impact of temperature on them.

7.6.1 / Physiology + behaviour vs Physiology only

There was no improvement in field population prediction when including behaviours into the model. It could be that, at current weather conditions, that were representative of those in which the host-parasitoid association has evolved, both physiological and behavioural processes allowing the optimal functioning of the species. In this range of temperature, changes in most behaviour performance lead to almost no changes in the population. Thus, using only physiological processes such as oviposition and mortality rates in a prediction model could be efficient, as, based on the sensitivity analyses, population dynamics is more sensitive to them. However, if temperature frequently exceeds the temperature range in which the species has evolved, behaviour performance drastically decreases, with a potential increased weight of the behavioural processes in the population dynamics.

Differences between measured and simulated populations that were observed around 30 days could be explained by weather effects that were not included in the model, such as rain or wind. Winds > 10 km h^{-1} were observed on day 17, 20, 33, 47, 50, 58 and 59. Heavy rains > 10 mm d^{-1} occurred on day 4, 10, 20, 31, 32, 39, 45 and 61. High winds and rain observed on day 20 could account for the lower population around day 30, because females would spend less time moving and searching for hosts in those conditions, so they laid fewer offspring, that take about 11 days to emerge (Collins and Grafius, 1986a). In addition, at the beginning of the season, the crop canopy cover is limited and does not protect the insects from adverse weather conditions. Fournier and Boivin (2000) showed that wind >15 km h^{-1} limited dispersion in two *Trichogramma* species. Similarly, Weisser et al. (1997) showed that females of *Aphidius rosae* stayed on plant leaves during wind or rain. For the same species, winds of 7.2 km h^{-1} were sufficient to significantly decrease oviposition, and oviposition ceased completely in all rain conditions (Fink and Völkl, 1995; Weisser et al., 1997). Rain and wind thus have the potential to have large effects on female foraging and host exploitation, and could explain the differences between measured and simulated populations.

7.6.2 / Sensitivity analyses

Behaviours

Sensitivity analyses allowed the comparison of the relative importance of behaviours in the life cycle of the insect and the consequent population levels. Behaviours linked with host exploitation (host oviposition and parasitism rate) were the most sensitive. Changes of 50% in parasitoid mating percentage, activity, movement between host plant and exploitation duration did not affect parasitoid population levels. However changes in "physiological" processes such as mortality and DH requirements significantly affected population outcome. In models that did not include behaviours, aphid mortality was the biological factor that affected most the peak density of the aphid population model (Parry et al., 2006). Morgan (2000) found that mortality, instar duration, longevity and fecundity all significantly affected the modelled aphid population, with mortality having the greater effect. In a corn rootworm model, oviposition rate and developmental rate both affected significantly the modelled population density (Garcia et al., 2014). However, as none of those models included behaviours, it is not possible to assess their importance for the modelled populations.

A decrease in mating success did increase sex-ratio (proportion of males) in the population (0.18 in original simulated population vs 0.38 in 50% decrease in mating success population; $p < 0.001$), but it did not affect the number of individuals in the population (fewer females would lead to fewer offspring and thus fewer individuals overall). This can result from the females having a chance to mate every morning, and thus, even if they laid only sons for a day or two, they could lay daughters for the rest of their lives after mating. Fauvergue et al., (2008) showed that half of the released virgin *Lysiphlebus testaceipes* parasitoid females were mated by a wild male after only 10 min, so virgin females could be rare in nature. Therefore, in both the model and in nature, proportion of unmated females in the population may be low (Nadel and Luck, 1992; Martel and Boivin, 2004). In addition, virgin females spent more time motionless compared to mated females, thus leaving smaller and more disperse broods (Fauvergue et al., 2008). *Anaphes listronoti* virgin females also tend to start laying eggs later than mated ones (Collins and Grafius, 1986a). Thus, virgin females seem to move and oviposit less than mated ones. Following these two assumptions, the number of virgin females and the resulting increased proportion of males in the population could be of only small effect on the overall population. The increase in mean sex ratio having no effect on the number of individuals in the population can also be explained if the host eggs are the main limiting factor: in the case of a bottom-up system. The parasitoid population would remain the same because the offspring potential of all females is much higher than the offspring that is actually laid in the field. Thus, even a limited number of females would be sufficient to maintain the same level of population for the next generation. In this bottom-up system, parasitism and resulting population would be affected by host density. Both density-dependent and density-independent parasitism exist, and both can be important for the system stability (Hassell, 2000). There is however a strong effect of scale in the relation between parasitism and host density (Norowi et al., 2000); and if a large body of studies documenting the density dependence at the plant scale exists, little is known about effects at larger scale (Rusch et al., 2015).

Probability of being active was assessed every minute, which could explain why changing its value by 50% had no effect on subsequent population level : females had a lot of opportunities to become active. In addition, when they were active, they spent several minutes exploring their current plant, ovipositing in the host and moving to an adjacent plant. This ratio could also be of little importance for the overall offspring number of the female, if another factor is more limiting than time spend active, for example, host density as suggested before. The same is true for the movement between plants, for which 50% changes in value had no effect on resulting population number. Mean duration between plants was 2 min, and changes of 50% resulted in durations of 1 to 3 min for moving between plants. At the scale of the 24 h trial (or even the 16 h active period), this difference is negligible. However, plants in the model were extremely simplified (2D square) and, when host eggs were present, active females on the host plant would always find and oviposit in them. Yet, plant structure and habitat can strongly impact the searching behaviour. Gols et al., (2005) and Gingras et al., (2008) respectively found that plant structure had a clear impact on the time required by parasitoids to find the host, and on the searching behavior of the female on the plant. In addition, plant species composition in the habitat affects the speed at which parasitoids find hosts

(Buckowinsky et al., 2007). As a result, it is likely that time spend searching for host or in transit between host patches is larger in reality than in our model, and that the search is not always successful (Gardner and Dixon, 1985). However, these aspects are little known in the field. In addition to the plant and habitat structure, the spatial distribution of host is another critical factor in host searching (Cain, 1985; Vinatier et al., 2013; Louâpre et al., 2019). This factor did not vary in our model, but it could affect the time parasitoid spent on a given patch and the time spent looking for patches. Overall, searching efficiency in parasitoid is a crucial component of their fitness, and should be integrated in population dynamics models (Vet, 2001). However, data is still lacking about how temperature affects those aspects of the insect life. Movement (walking and flying) is dependent upon temperature (e.g. Langer et al., 2004) and as such can alter host searching. However other factors are disrupted by temperature, like chemical communication (Boullis et al., 2015; 2016; Sentis et al., 2015), and time perception of parasitoid, with consequences on transit time and time spent exploiting a patch (Parent, 2016). Therefore, searching efficiency is certainly affected by changes in temperature regimes, but we cannot yet predict how and to what extent. This is likely one of the factors that limit the lifetime fitness of parasitoid females and, as such, represents one of the main limitations of our behavioural model.

Variations in exploitation duration had no significant impact on predicted population either. Mean value in the original simulated population was 12 min, and decreasing and increasing by 50% its value led to exploitation duration of 19 min and 6 min, respectively. This difference was low at the scale of the trial. However, time is an important factor in parasitoid ecology. Exploitation duration depends on patch characteristics, abiotic conditions and biological state of the female (Wajnberg, 2006). All these factors could then contribute greatly to the final level of population through time spent exploiting a given patch, mostly because most parasitoid species are probably time-limited in field conditions (Bezemer and Mills, 2003). There are time-limited and egg-limited foragers (Heimpel and Rosenheim, 1998; Heimpel et al., 1998; Rosenheim et al., 2008). The former usually does not have enough time in their lifetime to oviposit all their potential offspring (Rosenheim, 1999; Wajnberg et al., 2006), while the latter usually live long enough but does not have enough eggs to exploit host throughout its lifetime. This concept of time as a finite resource (Ydenberg et al., 1994; van Alphen et al., 2003) is particularly important when taking behaviours into account, because this is one of the main differences between our two models, namely the time scale (minutes instead of days). The outcomes of the behaviours are important, but their duration may be as important. Indeed, Le Lann et al. (2014) argued that the impact of temperature on locomotion and host handling duration could decrease oviposition opportunities by females, making them time-limited. In our model, host density was the factor affecting most the parasitoid population. It represented the limiting factor, in that female reproductive success was not limited by their time spent foraging or their number of eggs available, but by the number of hosts they were able to find. Unfortunately, our data does not allow us to know whether this is an artefact of the model structure or a real biological effect in the studied population. However, given the importance of the time-limitation studies of parasitoids in the literature, parasitoid females are likely more time-constrained in reality than in our model. This is another important limitation of our behavioral model.

The increase and decrease in carrot weevil oviposition was directly linked to changes in parasitoid population (50% change in carrot weevil oviposition linked to 50% changes in parasitoid population (Figure 7-5)), while changes in parasitism rate were not as direct. Host number seems to be the main limiting factors for the parasitoid population, as increase and decrease in their number led to the same increase and decrease in parasitoid population. Increasing parasitism rate only led to changes in population of 22%, probably because parasitism rate reached 100%, and then the factor limiting exploitation became the number of host eggs and not the parasitism rate. Decrease in parasitism rate also had a direct effect on population level (decrease of 58% of mean population). This could be caused in nature by several factors, including wind and rain (Fink and Völkl, 1995) or low and high temperatures (Langer et al., 2004; Ayvaz et al., 2008). Mechanisms for this change could include a decrease in walking distance at sub-optimal temperature (Augustin et al., 2020) and possible impairments in host discrimination ability and learning (van Baaren et al., 2005a; 2006).

A 50% decrease and increase in DH requirement respectively increased and decreased significantly the number of adult parasitoids in the population. These changes can be explained either by the lags between emergence dates that arise from the increased development duration, or by mortality during immature stages. The simulation always lasted 80 days, and as a result cohorts were not always at the same stage at day 80 (immature stage or adult) depending on the DH required. The increase in population when less DH are required to complete development can also result from the decreased mortality during immature stages, just because the individuals spent less time at those stages. Mortality was calculated as a daily rate, so less days spent at the immature stages would result in overall less individuals dead. On the opposite, the decrease in population when more DH are required can be explained by the additional individuals that died during the immature stages, because they spent more time at those stages. We would expect this mortality to be even higher in natural conditions because of the predation risk. Egg stages are sensitive to predators and parasitoids because they cannot physically escape or defend themselves: the longer an egg stays in the environment, the higher the chances that a predator or another parasitoid can find and kill it (Benrey and Denno, 1997; Brodeur et Boivin, 2004). In fact, Culler et al. (2015) found that a faster development following warming in the Artic resulted in a reduced mortality from predation in mosquitoes. A decrease in number of individuals reaching adult stage should be compensated by the higher number of offspring that females could lay, because females can live longer in these conditions (an increase in DH requirement to pass from one stage to the other means that for a same temperature, the female will live longer). This is however not what we observed in our simulations, probably because *A. listronoti* females oviposition rate decreases with age (Rhéaume, 2009), so living longer does not necessarily mean an increase in offspring.

Increase and decrease in mortality rate had a significant effect on parasitoid population. Increasing mortality by 50% significantly decreased population by 24%. Fewer individuals got to the adult stage because of increased mortality during the immature stage, and individuals did not live as long and so could lay fewer offspring. This did not translate itself in a 50% decrease in population, probably because there were less females, so they could each lay more offspring (opposite to previous modelling conditions where they seemed to be limited by the number of host available). This effect could compensate some of the increased mortality. On the other hand, decreasing mortality led to an increase in 48% of the population, even though there were no more host eggs available. More individuals survived the immature stages and, even though no more host eggs were available, adults were still present in the population. Mortality rates in our model corresponds to stochastic mortality, representing everything that is not specifically included in the model. Parasitoid can die because of predation or physiological causes, with potential consequence on oviposition strategies (Weisser et al., 1994; Volk and Kroupa, 1997). Despite the importance of these aspects, little is known about the frequency and causes of mortality of insects in the wild, and how it influences individual behaviour (Iwasa et al., 1984).

Temperature and sensitivity

Temperature response curves and sensitivity allow us to extrapolate the effect of temperature on population. An increase of 3.1 °C in temperature led to no change in mating probability, and no significant changes in population based on sensitivity analyses. Increase of 3.1 °C led to an increase of 8% in parasitism rate, that should increase parasitoid population based on sensitivity analyses. Mean increase of 3.1 °C in temperature led to an increase in 22% in developmental rate, that could lead to an earlier emergence of individuals in the season, and an increase in population levels. Increase of 3.1 °C led to increase in 22% for activity, a 4% decrease in movement duration and a 7% decrease in exploitation duration. In order to observe changes of 50% in behaviour performances, temperature would have to go below 14°C for mating, parasitism rate and DH requirements, and to reach 33°C for mating, 35 °C for activity, 37 °C for parasitism rate, and more than 40°C for all other behaviours. Mating success, activity and parasitism rate have the narrowest temperature range, similar to what Moriyama and Numata (2019) found with cicadas, and Kellermann and van Heerwaarden (2019) for Drosophila. For Anaphes behaviour, except for mating rate, as long as temperatures do not reach extreme values (> 35 °C), consequences on parasitoid population should be limited (Figure 7-3). However, as more extreme events, including heat waves, are expected for future years (Stocker et al., 2013), it is possible that those adverse conditions, occurring for several days, could affect parasitoid population. As indicated in the literature, our thermic curves suggest that extreme thermic events will be more problematic for insect populations than the mean increase in temperatures (Bale et al., 2002; Clusella-Trullas et al., 2011; Sergio et al., 2018).

Physiology vs behaviour

When comparing the relative importance of behaviour and physiological components for the population level, a trend appears. Changes in physiology (development, mortality, host oviposition rate) led to a proportional change in parasitoid population, with a predictable direction and a similar magnitude. For example, the increase in mortality led to a decrease in population of about the same magnitude (50% increase in mortality, to 43% decrease in population). On the other hand, changes in behaviour had more unpredictable effects on the final population. Most behaviours were resilient (mating and activity percentage, movement between host plants, exploitation duration): 50% changes in their value had no significant effect on the subsequent population. Only parasitism rate had an effect on the population similar to the physiological components. This demonstrates the importance of studying insect behaviours and, most importantly, their impact on population. However, as previously indicated, durations of behaviours can also have great impacts on individual fitness and the resulting population, and should therefore also be included in models.

7.6.3 / Simulation of climate change conditions

In a given species, physiological and behavioural traits can have different minimum, maximum, and optimum temperatures (Moriyama and Numata, 2019). In conditions under which the species has evolved, it can be expected that both physiological and behavioural traits lead to a high fitness at usually experienced conditions (Huey et al., 2012). However, when conditions change, different traits, with different temperature response curves, could have a different impact on fitness, depending on the shape of the temperature response curve and the level of performance of those traits in previous conditions. If we take for example the behaviours included in this model (probability of being active, mating success, exploitation) and development, they all have different temperature response curve (Figure 7-3). Mating success had the lowest optimum temperature (23°C) compared to other behaviours (parasitism: 26°C, activity: 27°C), and all movement, search and exploitation durations decreased as temperature increased. Development had the highest optimum temperature with 31°C. Behaviours have, for this species, lower optimum temperature than developmental rate. Temperature response curves are relatively wide for this species, with performances that slowly decrease as temperatures move away from the optimum. This allows the species to maintain a high fitness on a large range of temperatures.

Under mean temperature conditions experienced in 2017, all behaviours were sub-optimal. Adding 3.1°C brings most of them closer to the maximum performance, but most still do not reach it. This explains the increase in population observed in Figure 7-6 compared to Figure 7-4. However, things are different when considering extreme temperatures. Maximum measured temperature during our trial period in 2017 was 38.5°C, well above the optimum of all behaviours. This illustrates the importance of accounting for extreme temperatures in population models, and one way to do that is to use time steps in minutes or hours, instead of days. Knowing the temperature range of the behavioural and physiological traits studied is a crucial part of understanding the insect short-term responses to climate change. Many studies have focused on critical thermal limits (CTLs) to try to predict insect responses to climate change (Kellermann and van Heerwaarden, 2019), but *A. listronoti* temperature response curves show that temperatures below the CTLs (mean upper thermal limit for insects = 39.3°C (Hoffmann et al., 2013)) can lead to adverse effects in the population. In our case, temperatures superior to 35°C were always sub-optimal, and even lead to the failure of some behaviours (activity and mating). So the range of temperatures at which a species can live may be lower than the range calculated using CTLs, just because, even if they are not dead, they are not able to behave well enough to maintain their fitness (Kellerman and van Heerwaarden, 2019).

7.6.4 / Model limitations

One of the main constraint of our behavioural model is that it only took into account the effect of temperature, while precipitations, wind and UV can all affect foraging by females and their oviposition behaviour (Fink and Völkl, 1995; Weisser et al., 1997; Fournier and Boivin, 2000; Cochard et al., 2017). The effects of these factors on population and behaviour are however not as well-studied as those of temperature, but could be of great importance in a changing climate that is expected to be more variable and more prone to extreme events (Stocker et al., 2013). These effects would be even greater at the beginning of the season, where crop canopy cover is limited and does not yet protect the insects from adverse weather conditions. We used the micro-environment of insects by placing HOBO sensors directly into the plot, but most predictions model are based on weather station data, that do not reflect exactly those micro-conditions. There was a significant 1.4°C mean difference between our HOBO values and the weather station (Mann-Whitney test: $p < 0.001$). When possible, it is the microclimates that insects experience that should be considered when modelling populations (Potter et al., 2013; Pincebourde and Casas, 2015).

A second limitation is the use of *A. victus* instead of *A. listronoti* data for development and mortality rates. Since the two species are sympatric, morphologically (Huber et al., 1997) and genetically (Landry et al., 1993) close, and attack the same host species (Cormier et al., 1996), we assumed that they have the same mortality rates and development duration in relation to temperature. However, if this is not the case, emergence dates could be shifted compared to the model output because of different responses to temperature during development, or different thresholds between species. Similarly, if mortality rates are different between parasitoid species, the number of individuals in the population would vary accordingly. Those aspects could thus partially explain the differences between simulated and observed populations.

Another limiting aspect is the unsatisfactory estimation of behaviour durations. Behaviour durations can have a great impact on females fitness and populations in field conditions (Bezemer and Mills, 2003; LeLann et al., 2014). They should be included in populations models, but we still lack data on these aspects, especially how temperature affect host searching.

Finally, mortality in our model did not include mortality caused by temperature, heavy rain or desiccation. All those factors can increase mortality pressure to the population. Mortality due to temperature, in particular, was not included in the model, as temperatures did not reach mean CTLs usually established for insect species (Hoffmann et al., 2013), and that most thermal death kinetics studies start at 40°C (Hallman and Denlinger, 1998;

Johnson et al., 2004). This could however be an important factor in population dynamics if temperature reach that level.

7.6.5 / Biological control and pest management

If, as discussed previously, *A. listronoti* populations are limited by factors other than number of host eggs available in the habitat, including time spent searching for and exploiting host patches, reduction in pest populations would be lower than predicted by our simulations. However, our simulations show that *A. listronoti* abundance could be mainly limited by the number of carrot weevil hosts available. In our model, parasitoid populations, when adults are present, were high enough to significantly reduce number of host eggs, without having to proceed with additional parasitoid introductions. According to the simulations, when adult parasitoid females are active in the field, the number of carrot weevil eggs escaping parasitism is close to zero. However, damages by only one carrot weevil larva can make the carrot unmarketable (Collins and Grafius, 1986c). As a result, carrots can still be strongly damaged when parasitoid adults of a given cohort have all died, but the next cohort has not yet emerged. Parasitoid population levels thus seem high enough to control the pest, but their cyclicity (adults are not always present) remains a problem. *Anaphes listronoti* females attack preferentially eggs 0 to 24 h old and are not efficient against older stages of the carrot weevil. Other natural enemies exist, including *A. victus*, that attack older stages of the carrot weevil eggs (Picard et al., 1991), carabid predators that consume eggs, larvae, pupae, and even adults (Baines et al., 1990; Zhao et al., 1990), and nematodes that inhibit the maturation of the females reproductive system (Gagnon et al., 2019). Consequently, other natural enemies could still contribute to reduce carrot weevil populations and prevent damages when *A. listronoti* adults are absent.

In the context of climate change, synchronism between *A. listronoti* and the carrot weevil seems to be conserved, as we did not observe large differences in thermal range, or in performance when 3.1°C was added to the 2017 temperatures. Both species have similar base temperature (Rhéaume, 2009), so they can be expected to maintain their emergence period in the spring synchronized. Our climate change simulations also show that *A. listronoti* still control the carrot weevil populations when temperature is 3.1°C in mean compared to 2017 temperatures. However, if thermal conditions are not only higher in mean but also more variables and extreme as projected under climate change (Stocker et al., 2013), based on the parasitoid thermal performance curve, control of the carrot weevil may decrease.

Several models are used in integrated pest management as decision tools, and the one described here could also be of interest. However, the data required for a behavioural model is extensive, and not necessarily available. Therefore, it seems hardly viable to create such a complex model to predict pest and natural enemy populations for all species of interest. We show here that including behaviour into a population model is not always necessary for predictive purposes, but remains of capital importance for understanding the biology and ecology of both pests and their natural enemies, in addition to identifying gaps in our knowledge of their biology or ecology.

7.7 / Conclusion

Our results show that the use of physiological traits in predicting the temperature range could be sufficient when predicting populations at our current temperature conditions. However, with higher mean temperatures and more extreme events, it may not be the best choice. Simulated populations are different under warmer conditions, because of the failure of behaviours at high temperature (optimum temperature for behaviours : 23-27°C) occurs earlier than physiological failure (optimum temperature: 31°C). Different behaviours have different temperature response curves, but also different relative importance in the final population, so this interaction needs to be considered when including temperature and behaviours into population models. Control of the pest by its naturel enemy thus seem affected mainly by the parasitoid cycle at time t (presence of active adults in the field, or in-between generations), and the frequency and scope of extreme thermic events.

7.8 / References

Abram, P.K., Boivin, G., Moiroux, J., and Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biol. Rev. *92*, 1859–1876.

Addo-Bediako, A., Chown, S.L., and Gaston, K.J. (2000). Thermal tolerance, climatic variability and latitude. Proc. R. Soc. Lond. B Biol. Sci. *267*, 739–745.

van Alphen, J.J.M., Bernstein, C., and Driessen, G. (2003). Information acquisition and time allocation in insect parasitoids. Trends Ecol. Evol. *18*, 81–87.

Andrew, N.R., Hart, R.A., Jung, M.-P., Hemmings, Z., and Terblanche, J.S. (2013). Can temperate insects take the heat? A case study of the physiological and behavioural responses in a common ant, Iridomyrmex purpureus (Formicidae), with potential climate change. J. Insect Physiol. *59*, 870–880.

Angilletta, M.J., Niewiarowski, P.H., and Navas, C.A. (2002). The evolution of thermal physiology in ectotherms. J. Therm. Biol. *27*, 249–268.

Araújo, M.B., and Luoto, M. (2007). The importance of biotic interactions for modelling species distributions under climate change. Glob. Ecol. Biogeogr. *16*, 743–753.

Augustin, J., Boivin, G., Brodeur, J., and Bourgeois, G. (2020). Effect of temperature on the walking behaviour of an egg parasitoid: disentangling kinetic response from integrated response. Ecol. Entomol.

Ayvaz, A., Karasu, E., Karabörklü, S., and Tunçbilek, A.Ş. (2008). Effects of cold storage, rearing temperature, parasitoid age and irradiation on the performance of *Trichogramma evanescens* Westwood (Hymenoptera: Trichogrammatidae). J. Stored Prod. Res. *44*, 232–240.

van Baaren, J., and Boivin, G. (1998). Learning affects host discrimination behavior in a parasitoid wasp. Behav. Ecol. Sociobiol. *42*, 9–16.

van Baaren, J., Outreman, Y., and Boivin, G. (2005a). Effect of low temperature exposure on oviposition behaviour and patch exploitation strategy in parasitic wasps. Anim. Behav. *70*, 153–163.

van Baaren, J., Boivin, G., and Outreman, Y. (2005b). Patch exploitation strategy by an egg parasitoid in constant or variable environment. Ecol. Entomol. *30*, 502–509.

van Baaren, J., Boivin, G., and Outreman, Y. (2006). Deleterious effects of low temperature exposure on learning expression in a parasitoid. Int. J. Comp. Psychol. *19*.

van Baaren, J., Boivin, G., Bourdais, D., and Roux, O. (2007). Antennal sensilla of hymenopteran parasitic wasps: variations linked to host exploitation behavior. Mendez Vilas Diaz Alvarez J Ed. Mod. Res. Educ. Top. Microsc. Badajoz Formatex 345–352.

Baines, D., Stewart, R., and Boivin, G. (1990). Consumption of carrot weevil (Coleoptera: Curculionidae) by five species of carabids (Coleoptera: Carabidae) abundant in carrot fields in southwestern Quebec. Environ. Entomol. *19*, 1146-1149.

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., et al. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Change Biol. *8*, 1–16.

Barton, B. T. (2017). Beyond global warming: Putting the “climate” back into “climate change ecology”. Food webs, *13*, 51-52.

Barton, B. T., Beckerman, A. P., and Schmitz, O. J. (2009). Climate warming strengthens indirect interactions in an old-field food web. Ecology, *90*, 2346-2351.

Beltrà, A., Pekas, A., Soto, A., and Tena, A. (2014). Employing evolutionary theory to improve biological pest control: Causes of non-adaptive sex allocation behavior in parasitoid wasps and implications. Basic Appl. Ecol. *15*, 625–632.

Benrey, B., and Denno, R. F. (1997). The slow-growth–high-mortality hypothesis: a test using the cabbage butterfly. Ecology, *78*, 987-999.

Bezemer, T.M., and Mills, N.J. (2003). Clutch size decisions of a gregarious parasitoid under laboratory and field conditions. Anim. Behav. *66*, 1119–1128.

Boivin, G. (1988). Effect of carrot developmental stages on feeding and oviposition of carrot weevil, *Listronotus oregonensis* (Le Conte) (Coleoptera: Curculionidae). Environ. Entomol. *17*, 330–336.

Boivin, G. (1993). Density dependence of Anaphes sordidatus (Hymenoptera: Mymaridae) parasitism on eggs of Listronotus oregonensis (Coleoptera: Curculionidae). *Oecologia*, *93*, 73-79.

Boivin, G. (1999). Integrated management for carrot weevil. Integr. Pest Manag. Rev. *4*, 21–37.

Boivin, G., and Martel, V. (2012). Size-induced reproductive constraints in an egg parasitoid. J. Insect Physiol. *58*, 1694–1700.

Bolliger, J., Lischke, H., and Green, D. G. (2005). Simulating the spatial and temporal dynamics of landscapes using generic and complex models. Ecol. Complex. *2*, 107-116.

Boullis, A., Francis, F., and Verheggen, F. J. (2015). Climate change and tritrophic interactions: will modifications to greenhouse gas emissions increase the vulnerability of herbivorous insects to natural enemies?. Environ. Entomol., *44*, 277-286.

Boullis, A., Detrain, C., Francis, F., and Verheggen, F. J. (2016). Will climate change affect insect pheromonal communication?. Curr. Opin. insect sci., *17*, 87-91.

Bourgeois, G., Plouffe, D., Chouinard, G., Beaudry, N., Choquette, D., Carisse, O., and DeEll, J. (2008). The apple CIPRA network in Canada : using real-time weather information to forecast apple phenology, insects, diseases and physiological disorders. Acta Hortic. 29–34.

Brigolin, D., Dal Maschio, G., Rampazzo, F., Giani, M., and Pastres, R. (2009). An individual-based population dynamic model for estimating biomass yield and nutrient fluxes through an off-shore mussel (*Mytilus galloprovincialis*) farm. Estuar. Coast. Shelf Sci., *82*, 365-376.

Brodeur, J., and Boivin, G. (2004). Functional ecology of immature parasitoids. Annu. Rev. Entomol., *49*, 27-49.

Bukovinszky, T., Gols, R., Hemerik, L. I. A., Van Lenteren, J. C., and Vet, L. E. (2007). Time allocation of a parasitoid foraging in heterogeneous vegetation: implications for host–parasitoid interactions. J. Anim. Ecol., *76*, 845-853.

Cain, M.L. (1985). Random search by herbivorous insects: a simulation model. Ecology *66*, 876–888.

Clarke, A., and Fraser, K.P.P. (2004). Why does metabolism scale with temperature? Funct. Ecol. *18*, 243–251.

Clusella-Trullas, S., Blackburn, T.M., and Chown, S.L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. Am. Nat. *177*, 738–751.

Cochard, P., Galstian, T., and Cloutier, C. (2017). Light environments differently affect parasitoid wasps and their hosts' locomotor activity. J. Insect Behav., *30*, 595-611.

Collins, R.D., and Grafius, E. (1986a). Biology and life cycle of *Anaphes sordidatus* (Hymenoptera: Mymaridae), an egg parasitoid of the carrot weevil (Coleoptera: Curculionidae). Environ. Entomol. *15*, 100–105.

Collins, R.D., and Grafius, E. (1986b). Courtship and mating behavior of *Anaphes sordidatus* (Hymenoptera: Mymaridae), a parasitoid of the carrot weevil (Coleoptera: Curculionidae). Ann. Entomol. Soc. Am. *79*, 31–33.

Collins, R.D., and Grafius, E. (1986c). Impact of the egg parasitoid, *Anaphes sordidatus* (Hymenoptera: Mymaridae), on the carrot weevil (Coleoptera: Curculionidae). Environ. Entomol. *15*, 469–475.

Cormier, D., Stevenson, A.B., and Boivin, G. (1996). Seasonal ecology and geographical distribution of *Anaphes listronoti* and *A. victus* (Hymenoptera: Mymaridae), egg parasitoids of the carrot weevil (Coleoptera: Curculionidae) in central Ontario. Environ. Entomol. *25*, 1376–1382.

Culler, L. E., Ayres, M. P., and Virginia, R. A. (2015). In a warmer Arctic, mosquitoes avoid increased mortality from predators by growing faster. P. Roy. Soc. B-Biol. Sci., *282*, 20151549.

Damos, P., and Savopoulou-Soultani, M. (2012). Temperature-driven models for insect development and vital thermal requirements. Psyche J. Entomol. *2012*, 1–13.

Davidson, J. (1944). On the relationship between temperature and rate of development of insects at constant temperatures. J. Anim. Ecol. *13*, 26–38.

Davis, A.J., Lawton, J.H., Shorrocks, B., and Jenkinson, L.S. (1998). Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. J. Anim. Ecol. *67*, 600–612.

DeAngelis, D.L., and Mooij, W.M. (2005). Individual-based modeling of ecological and evolutionary processes. Annu. Rev. Ecol. Evol. Syst. *3*, 147–168.

Dell, A.I., Pawar, S., and Savage, V.M. (2011). Systematic variation in the temperature dependence of physiological and ecological traits. Proc. Natl. Acad. Sci. *108*, 10591–10596.

Fauvergue, X., Lo Genco, A., and Lo Pinto, M. (2008). Virgins in the wild: mating status affects the behavior of a parasitoid foraging in the field. Oecologia *156*, 913–920.

Fink, U., and Völkl, W. (1995). The effect of abiotic factors on foraging and oviposition success of the aphid parasitoid, *Aphidius rosae*. Oecologia *103*, 371–378.

Fletcher, J.P., Hughes, J.P., and Harvey, I.F. (1994). Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. Proc. R. Soc. Lond. B Biol. Sci. *258*, 163–167.

Folguera, G., Bastías, D.A., Caers, J., Rojas, J.M., Piulachs, M.-D., Bellés, X., and Bozinovic, F. (2011). An experimental test of the role of environmental temperature variability on ectotherm molecular, physiological and life-history traits: Implications for global warming. Comp. Biochem. Physiol. A. Mol. Integr. Physiol. *159*, 242–246.

Fournier, F., and Boivin, G. (2000). Comparative dispersal of *Trichogramma evanescens* and *Trichogramma pretiosum* (Hymenoptera: Trichogrammatidae) in relation to environmental conditions. Environ. Entomol. *29*, 55–63.

Gagnon, A.-È., Boivin, G., Bélair, G., and Mimee, B. (2019). Prevalence of a nematode castrator of the carrot weevil and impact on fecundity and survival. Parasitology., *146*, 702-707.

Gardner, S. M., and Dixon, A. F. G. (1985). Plant structure and the foraging success of *Aphidius rhopalosiphi* (Hymenoptera: Aphidiidae). Ecol. Entomol., *10*, 171-179.

Garcia, A., Consoli, F. L., Godoy, W. A. C., and Ferreira, C. P. (2014). A mathematical approach to simulate spatio-temporal patterns of an insect-pest, the corn rootworm *Diabrotica speciosa* (Coleoptera: Chrysomelidae) in intercropping systems. Landsc. Ecol., *29*, 1531-1540.

Gingras, D., Dutilleul, P., and Boivin, G. (2008). Effect of plant structure on searching strategy and searching efficiency of *Trichogramma turkestanica*. J. Insect Sci., *8*, 28.

Gols, R., Bukovinszky, T., Hemerik, L., Harvey, J. A., Van Lenteren, J. C., and Vet, L. E. M. (2005). Reduced foraging efficiency of a parasitoid under habitat complexity: implications for population stability and species coexistence. J. Anim. Ecol., *74*, 1059-1068.

Graf, B., Höpli, H.U., Höhn, H., and Blaise, Ph. (2002). SOPRA : a forecasting tool for insect pests in apple orchards. Acta Hortic. 207–214.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S.K., Huse, G., et al. (2006). A standard protocol for describing individual-based and agent-based models. Ecol. Model. *198*, 115–126.

Hallman, G.J., and Denlinger, D.L. (1998). Temperature sensitivity in insects and application in integrated pest management. CRC Press.

Hamilton, W.D. (1967). Extraordinary sex ratios. Science *156*, 477–488.

Hamner, B., and Frasco, M. (2018). Metrics: Evaluation Metrics for Machine Learning. R package version 0.1, 1.

Hannon, B.M., and Ruth, M. (2009). Dynamic modeling of diseases and pests (New York: Springer).

Harmon, J.P., and Barton, B.T. (2013). On their best behavior: how animal behavior can help determine the combined effects of species interactions and climate change. Ann. N. Y. Acad. Sci. *1297*, 139–147.

Harrison, J.F., and Roberts, S.P. (2000). Flight respiration and energetics. Annu. Rev. Physiol. *62*, 179–205.

Hassell, M. P. (2000). Host–parasitoid population dynamics. J. Anim. Ecol., *69*, 543-566.

Hayes, D., Jones, M., Lester, N., Chu, C., Doka, S., Netto, J., Stockwell, J., Thompson, B., Minns, C.K., Shuter, B. and Collins, N. (2009). Linking fish population dynamics to habitat conditions: insights from the application of a process-oriented approach to several Great Lakes species. Rev. Fish Biol. Fish., *19*, 295-312.

Heimpel, G.E. (2019). Linking parasitoid nectar feeding and dispersal in conservation biological control. Biol. Control *132*, 36–41.

Heimpel, G.E., and Rosenheim, J.A. (1998). Egg limitation in parasitoids: a review of the evidence and a case study. Biol. Control *11*, 160–168.

Heimpel, G.E., Mangel, M., and Rosenheim, J.A. (1998). Effects of time limitation and egg limitation on lifetime reproductive success of a parasitoid in the field. Am. Nat. *152*, 273–289.

Hoffmann, A.A., Chown, S.L., and Clusella-Trullas, S. (2013). Upper thermal limits in terrestrial ectotherms: how constrained are they? Funct. Ecol. *27*, 934–949.

Huber, J.T., Côté, S., and Boivin, G. (1997). Description of three new *Anaphes* species (Hymenoptera: Mymaridae), egg parasitoids of the carrot weevil, *Listronotus oregonensis* (Leconte) (Coleoptera: Curculionidae), and redescription of *Anaphes sordidatus* Girault. Can. Entomol. *129*, 959–977.

Huey, R.B., and Tewksbury, J.J. (2009). Can behavior douse the fire of climate warming? Proc. Natl. Acad. Sci. *106*, 3647–3648.

Huey, R.B., Kearney, M.R., Krockenberger, A., Holtum, J.A.M., Jess, M., and Williams, S.E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. Philos. Trans. R. Soc. B Biol. Sci. *367*, 1665–1679.

Huston, M., DeAngelis, D., and Post, W. (1988). New computer models unify ecological theory. BioScience *38*, 682–691.

Ives, A.R. (1995). Spatial heterogeneity and host-parasitoid population dynamics: Do we need to study behavior? Oikos *74*, 366–376.

Iwasa, Y., Higashi, M., and Yamamura, N. (1981). Prey distribution as a factor determining the choice of optimal foraging strategy. Am. Nat. *117*, 710–723.

Iwasa, Y., Suzuki, Y., and Matsuda, H. (1984). Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. Theor. Popul. Biol., *26*, 205-227.

Johnson, J.A., Valero, K.A., Wang, S., and Tang, J. (2004). Thermal death kinetics of red flour beetle (Coleoptera: Tenebrionidae). J. Econ. Entomol. *97*, 6.

Jeschke, J.M., and Strayer, D.L. (2008). Usefulness of Bioclimatic Models for Studying Climate Change and Invasive Species. Ann. N. Y. Acad. Sci. *1134*, 1–24.

Jiang, L., and Morin, P.J. (2004). Temperature-dependent interactions explain unexpected responses to environmental warming in communities of competitors. J. Anim. Ecol. *73*, 569–576.

Judson, O.P. (1994). The rise of the individual-based model in ecology. Trends Ecol. Evol. *9*, 9–14.

Kearney, M., and Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecol. Lett. *12*, 334–350.

Kearney, M., Porter, W.P., Williams, C., Ritchie, S., and Hoffmann, A.A. (2009a). Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. Funct. Ecol. *23*, 528–538.

Kearney, M., Shine, R., and Porter, W.P. (2009b). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. Proc. Natl. Acad. Sci. *106*, 3835–3840.

Keith, D.A., Akçakaya, H.R., Thuiller, W., Midgley, G.F., Pearson, R.G., Phillips, S.J., Regan, H.M., Araújo, M.B., and Rebelo, T.G. (2008). Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biol. Lett. *4*, 560–563.

Kellermann, V., and van Heerwaarden, B. (2019). Terrestrial insects and climate change: adaptive responses in key traits. Physiol. Entomol. *44*, 99–115.

Knowlton, J.L., and Graham, C.H. (2010). Using behavioral landscape ecology to predict species' responses to land-use and climate change. Biol. Conserv. *143*, 1342–1354.

Kruidhof, H.M., Kostenko, O., Smid, H.M., and Vet, L.E.M. (2019). Integrating parasitoid olfactory conditioning in augmentative biological control: potential impact, possibilities, and challenges. Front. Ecol. Evol. *7*, 1-7.

Kugimiya, S., Shimoda, T., Wajnberg, E., Uefune, M., and Takabayashi, J. (2010). Host-searching responses to herbivory-associated chemical information and patch use depend on mating status of female solitary parasitoid wasps. Ecol. Entomol. *35*, 279–286.

Landry, B.S., Dextraze, L., and Boivin, G. (1993). Random amplified polymorphic DNA markers for DNA fingerprinting and genetic variability assessment of minute parasitic wasp species (Hymenoptera: Mymaridae and Trichogrammatidae) used in biological control programs of phytophagous insects. Genome *36*, 580–587.

Langer, A., Boivin, G., and Hance, T. (2004). Oviposition, flight and walking capacity at low temperatures of four aphid parasitoid species (Hymenoptera: Aphidiinae). Eur. J. Entomol. *101*, 473–480.

Le Lann, C., Lodi, M., and Ellers, J. (2014). Thermal change alters the outcome of behavioural interactions between antagonistic partners: Thermal change alters species interactions. Ecol. Entomol. *39*, 578–588.

Levin, P.S. (2000). Integrating individual behavior and population ecology: the potential for habitat-dependent population regulation in a reef fish. Behav. Ecol. *11*, 565–571.

Linn, C.E., Campbell, M.G., and Roelofs, W.L. (1988). Temperature modulation of behavioural thresholds controlling male moth sex pheromone response specificity. Physiol. Entomol. *13*, 59–67.

Logan, J.A. (1988). Toward an expert system for development of pest simulation models. Environ. Entomol. *17*, 359–376.

Louâpre, P., Lann, C., and Hance, T. (2019). When parasitoids deal with the spatial distribution of their hosts:

consequences for both partners. Insect Sci. *26*, 923–931.

Martel, V., and Boivin, G. (2004). Premating dispersion in the egg parasitoid Trichogramma (Hymenoptera: Trichogrammatidae). Environ. Entomol., *33*, 855-859.

Mills, N.J., and Heimpel, G.E. (2018). Could increased understanding of foraging behavior help to predict the success of biological control? Curr. Opin. Insect Sci. *27*, 26–31.

Mills, N.J., and Kean, J.M. (2010). Behavioral studies, molecular approaches, and modeling: Methodological contributions to biological control success. Biol. Control *52*, 255–262.

Minkenberg, O.P.J.M., Tatar, M., and Rosenheim, J.A. (1992). Egg load as a major source of variability in insect foraging and oviposition behavior. Oikos *65*, 134–142.

Morales, J. M., and Ellner, S. P. (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behavior. Ecology, *83*, 2240-2247.

Morgan, D. (2000). Population dynamics of the bird cherry-oat aphid, Rhopalosiphum padi (L.), during the autumn and winter: a modelling approach. Agr. Forest Entomol., *2*, 297-304.

Moriyama, M., and Numata, H. (2019). Ecophysiological responses to climate change in cicadas. Physiol. Entomol. *44*, 65–76.

Mohamad, R., Wajnberg, E., Monge, J. P., and Goubault, M. (2015). The effect of direct interspecific competition on patch exploitation strategies in parasitoid wasps. Oecologia, *177*, 305-315.

Nadel, H., and Luck, R. F. (1992). Dispersal and mating structure of a parasitoid with a female-biased sex ratio: implications for theory. Evol. Ecol., *6*, 270-278.

Neven, L.G. (2000). Physiological responses of insects to heat. Postharvest Biol. Technol. *21*, 103–111.

Nietschke, B.S., Magarey, R.D., Borchert, D.M., Calvin, D.D., and Jones, E. (2007). A developmental database to support insect phenology models. Crop Prot. *26*, 1444–1448.

Norowi, H. M., Perry, J. N., Powell, W., and Rennolls, K. (2000). The effect of spatial scale on interactions between two weevils and their parasitoid. Ecol. Entomol., *25*, 188-196.

Ouranos (2015). Vers l'adaptation. Synthèse des connaissances sur les changements climatiques au Québec. Partie 1 : Évolution climatique au Québec. Édition 2015. Montréal, Québec : Ouranos, 114 p.

Parent, J. P. (2016). La perception du temps et sa modulation par la température chez les guêpes parasitoïdes. PhD thesis, Département de sciences biologiques, Université de Montréal, Montreal, Quebec, Canada

Parry, H. R., Evans, A. J., and Morgan, D. (2006). Aphid population response to agricultural landscape change: a spatially explicit, individual-based model. Ecol. Model., *199*, 451-463.

Picard, C., Auclair, J. L., and Boivin, G. (1991). Response to host age of the egg parasitoid *Anaphes n. sp.* (Hymenoptera: Mymaridae). Biocontrol Sci. Technol., *1*, 169-176.

Pincebourde, S., and Casas, J. (2015). Warming tolerance across insect ontogeny: influence of joint shifts in microclimates and thermal limits. Ecology *96*, 986–997.

Potter, K.A., Arthur Woods, H., and Pincebourde, S. (2013). Microclimatic challenges in global change biology.

Glob. Change Biol. *19*, 2932–2939.

Pruess, K.P. (1983). Day-degree methods for pest management. Environ. Entomol. *12*, 613–619.

R Core Team (2016). R: A Language and Environment for Statistical Computing (Vienna, Austria: R Foundation for Statistical Computing).

Ramirez-Romero, R., Sivinski, J., Copeland, C.S., and Aluja, M. (2012). Are individuals from thelytokous and arrhenotokous populations equally adept as biocontrol agents? Orientation and host searching behavior of a fruit fly parasitoid. BioControl *57*, 427–440.

Régnière, J., Powell, J., Bentz, B., and Nealis, V. (2012). Effects of temperature on development, survival and reproduction of insects: Experimental design, data analysis and modeling. J. Insect Physiol. *58*, 634–647.

Rhéaume, A.-J. (2009). Modélisation d'un écosystème agricole tritrophique: la carotte cultivée, le charançon de la carotte (*Listronotus oregonensis*) et *Anaphes victus*, un parasitoïde des œufs. Mémoire. Faculté des sciences de l'agriculture et de l'alimentation. Université Laval. Québec

Rosenheim, J.A. (1999). The relative contributions of time and eggs to the cost of reproduction. Evolution *53*, 376.

Rosenheim, J.A., Jepsen, S.J., Matthews, C.E., Smith, D.S., and Rosenheim, M.R. (2008). Time limitation, egg limitation, the cost of oviposition, and lifetime reproduction by an insect in nature. Am. Nat. *172*, 486–496.

Rusch, A., Delbac, L., Muneret, L., and Thiéry, D. (2015). Organic farming and host density affect parasitism rates of tortricid moths in vineyards. Agr., Ecosyst. Environ., *214*, 46-53.

Samietz, J., Graf, B., Höhn, H., Schaub, L., and Höpli, H.U. (2007). Phenology modelling of major insect pests in fruit orchards from biological basics to decision support: the forecasting tool SOPRA. EPPO Bull. *37*, 255–260.

Satake, A., Ohgushi, T., Urano, S., and Uchimura, K. (2006). Modeling population dynamics of a tea pest with temperature-dependent development: predicting emergence timing and potential damage. Ecol. Res. *21*, 107–116.

Sentis, A., Ramon-Portugal, F., Brodeur, J., and Hemptinne, J.-L. (2015). The smell of change: warming affects species interactions mediated by chemical information. Glob. Change Biol. *21*, 3586–3594.

Sergio, F., Blas, J., and Hiraldo, F. (2018). Animal responses to natural disturbance and climate extremes: a review. Glob. Planet. Change *161*, 28–40.

Shaffer, P.L., and Gold, H.J. (1985). A simulation model of population dynamics of the codling moth, Cydia pomonella. Ecol. Model. *30*, 247–274.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: a conceptual overview. Anim. Behav. *85*, 1077–1088.

Sih, A., Ferrari, M.C.O., and Harris, D.J. (2011). Evolution and behavioural responses to human-induced rapid environmental change: Behaviour and evolution. Evol. Appl. *4*, 367–387.

Sih, A., Trimmer, P.C., and Ehlman, S.M. (2016). A conceptual framework for understanding behavioral responses to HIREC. Curr. Opin. Behav. Sci. *12*, 109–114.

Simonet, D.E., and Davenport, B.L. (1981). Temperature requirements for development and oviposition of the carrot weevil. Ann. Entomol. Soc. Am. *74*, 312–315.

Stimac, J.L. (1982). History and Relevance of Behavioral Ecology in Models of Insect Population Dynamics. Fla. Entomol. *65*, 9.

Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M.M.B., Allen, S.K., Boschung, J., Naeuls, A., Xia, Y., Bex, V., and Midgley, P.M. (2013). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Cambridge, United Kingdom and New York, NY, USA).

Taylor, F. (1981). Ecology and evolution of physiological time in insects. Am. Nat. *117*, 1–23.

Tenhumberg, B. (2004). Predicting predation efficiency of biocontrol agents: linking behavior of individuals and population dynamics. (Osnabrück, Germany).

Traoré, L., Pilon, J.-G., Fournier, F., and Boivin, G. (2006). Adaptation of the developmental process of *Anaphes victus* (Hymenoptera: Mymaridae) to local climatic conditions across North America. Ann. Entomol. Soc. Am. *99*, 1121–1126.

Tuomainen, U., and Candolin, U. (2011). Behavioural responses to human-induced environmental change. Biol. Rev. *86*, 640–657.

Van der Putten, W.H., Macel, M., and Visser, M.E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos. Trans. R. Soc. B Biol. Sci. *365*, 2025–2034.

Van Roermund, H. J. W., Van Lenteren, J. C., and Rabbinge, R. (1997). Biological control of greenhouse whitefly with the Parasitoid *Encarsia formosa* on tomato: an individual-based simulation approach. Biol. Control, *9*, 25-47.

Vet, L. E. (2001). Parasitoid searching efficiency links behaviour to population processes. Appl. Entomol. Zool., *36*, 399-408.

Vinatier, F., Gosme, M., and Valantin-Morison, M. (2013). Explaining host–parasitoid interactions at the landscape scale: a new approach for calibration and sensitivity analysis of complex spatio-temporal models. Landsc. Ecol., *28*, 217-231.

Vinson, S.B. (1976). Host selection by insect parasitoids. Annu. Rev. Entomol. *21*, 109–133.

Völkl, W., and Kroupa, A. S. (1997). Effects of adult mortality risks on parasitoid foraging tactics. Anim. Behav., *54*, 349-359.

Wagner, T.L., Wu, H.-I., Sharpe, P.J.H., Schoolfield, R.M., and Coulson, R.N. (1984). Modeling insect development rates: a literature review and application of a biophysical model. Ann. Entomol. Soc. Am. *77*, 208–220.

Wajnberg, E. (2006). Time allocation strategies in insect parasitoids: from ultimate predictions to proximate behavioral mechanisms. Behav. Ecol. Sociobiol. *60*, 589–611.

Wajnberg, E., Bernhard, P., Hamelin, F., and Boivin, G. (2006). Optimal patch time allocation for time-limited foragers. Behav. Ecol. Sociobiol. *60*, 1–10.

Weisser, W. W., Houston, A. I., and Völkl, W. (1994). Foraging strategies in solitary parasitoids: the trade-off between female and offspring mortality risks. Evol. Ecol., *8*, 587-597.

Weisser, W.W., Volkl, W., and Hassell, M.P. (1997). The importance of adverse weather conditions for behaviour and population ecology of an aphid parasitoid. J. Anim. Ecol. *66*, 386.

Wong, B.B.M., and Candolin, U. (2015). Behavioral responses to changing environments. Behav. Ecol. *26*, 665–673.

Woodin, S.A., Hilbish, T.J., Helmuth, B., Jones, S.J., and Wethey, D.S. (2013). Climate change, species distribution models, and physiological performance metrics: predicting when biogeographic models are likely to fail. Ecol. Evol.

Ydenberg, R.C., Welham, C.V.J., Schmid-Hempel, R., Schmid-Hempel, P., and Beauchamp, G. (1994). Time and energy constraints and the relationships between currencies in foraging theory. Behav. Ecol. *5*, 28–34.

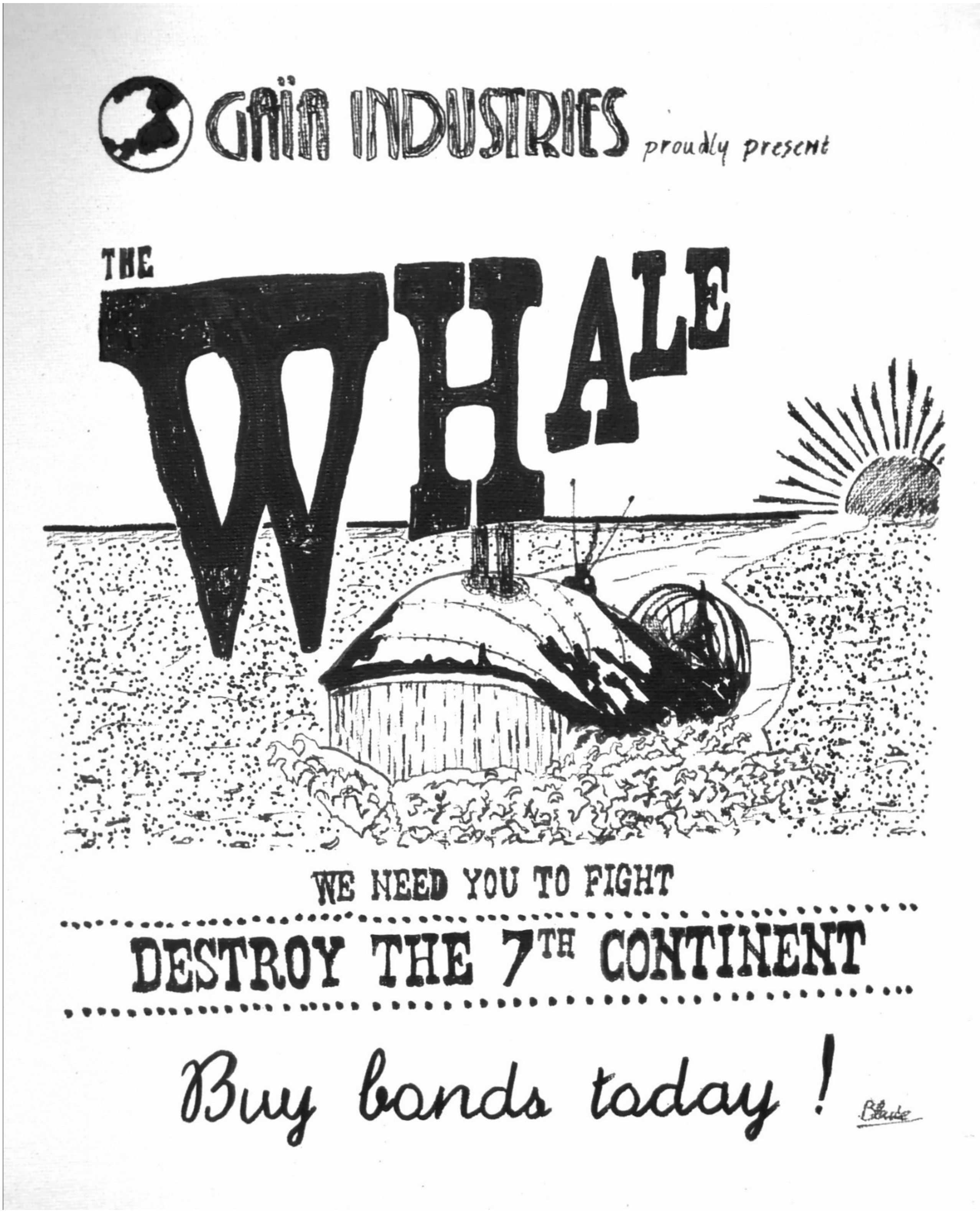
Yu, H., Zhang, Y., Wu, K., Wyckhuys, K.A.G., and Guo, Y. (2009). Flight potential of *Microplitis mediator*, a parasitoid of various lepidopteran pests. BioControl *54*, 183–193.

Zambrano-Bigiarini, M. (2017). hydroGOF: Goodness-of-fit functions for comparison of simulated and observed hydrological time series. R package version 0.3-8.

Zhao, D.X., Boivin, G., and Stewart, R.K. (1990). Consumption of carrot weevil, *Listronotus oregonensis*, [Coleoptera: Curculionidae] by four species of carabids on host plants in the laboratory. Entomophaga *35*, 57-60.

Zhao, D.X., Boivin, G., and Stewart, R.K. (1991). Simulation model for the population dynamics of the carrot weevil, *Listronotus oregonensis* (LeConte) (Coleoptera: Curculionidae). Can. Entomol. *123*, 63–76.

Chapitre 8 : Discussion générale



Blaise Laurent

La température affecte directement la physiologie des ectothermes et a des conséquences sur leurs comportements. Les réponses comportementales des insectes à la température peuvent être complexes et ont des répercussions à l'échelle de la population. Les principales contributions de cette thèse sont : (1) la description du comportement de marche d'*Anaphes listronoti* en termes de réponses kinétiques et intégrées à la température; (2) la démonstration que les stratégies d'exploitation d'agrégats à basses températures permettent une performance plus élevée qu'anticipé par la réponse kinétique seule, mais une performance moins élevée à haute température; (3) la démonstration que les températures basses et élevées durant l'accouplement diminuent le succès d'accouplement de *A. listronoti*, mais n'ont pas de conséquences sur le sex-ratio de la descendance résultant d'un accouplement réussi; (4) la création d'un modèle de dynamique des populations qui intègre l'effet de la température sur les comportements des femelles *A. listronoti*.

Cette thèse illustre la complexité de l'étude des réponses comportementales à la température, et l'importance d'en connaître les mécanismes et l'adaptativité. Elle démontre également l'intérêt d'analyser les liens entre comportements individuels et conséquences sur la population. Enfin, la thèse précise nos connaissances sur les divers types de réponses des ectothermes aux changements climatiques. Ces résultats ouvrent la porte à plusieurs champs de recherche.

8.1 / Impact de la température sur le comportement et les populations d'*Anaphes listronoti*

Pour les femelles *Anaphes listronoti*, la température module les comportements de marche (Chapitre 4), d'exploitation d'un agrégat (Chapitre 5) et d'accouplement (Chapitre 6). Si certains de ces comportements résultent d'un mécanisme kinétique d'accélération ou de ralentissement du métabolisme (vitesse de marche, temps de résidence sur une masse d'œufs), la plupart d'entre eux semblent plutôt résulter d'un mécanisme intégré de réponse à la température (ex. : évitement des conditions thermiques non optimales à basse température (Chapitre 4), conservation de l'énergie à haute température (Chapitre 4), ajustement de la durée de copulation (Chapitre 6)). Ces réponses peuvent se révéler adaptatives, par exemple lors de l'accouplement, le mâle ajuste la durée de la copulation selon la température (Chapitre 6). À l'inverse, certains comportements sont affectés, non seulement par la kinétique (vitesse de marche, Chapitre 4), mais également par des contraintes supplémentaires dues à la température, par exemple la reconnaissance de signaux indicateurs de la qualité de l'hôte lors de la ponte (Chapitre 5), ou la reconnaissance du partenaire sexuel (Chapitre 6). L'étude des comportements s'avère ainsi complexe, d'autant que les deux mécanismes (kinétique et intégré) ne sont pas exclusifs. Puisque la température affecte les comportements individuels, des effets s'observent au niveau de la population, par exemple la diminution du parasitisme (Chapitres 4 et 5) ou du nombre de femelles dans la population (Chapitre 6).

L'inclusion des comportements de reproduction d'*A. listronoti* dans un modèle de simulation dynamique a permis de prédire l'effet de la température sur la génération suivante. Le modèle a également permis de mesurer l'importance relative des différents comportements sur le nombre d'individus dans la population (Chapitre 7). L'intégration dans le modèle des comportements selon la température n'améliore pas significativement son efficacité prédictive sous les conditions météorologiques actuelles. Cependant, pour des températures plus variables et atteignant plus fréquemment les extrêmes, telles que projetées par les changements climatiques, les courbes thermiques comportementales suggèrent que la capacité d'*A. listronoti* à maintenir l'intégralité et la fonctionnalité de ses comportements sera compromise. Il demeure ainsi d'autant plus important de comprendre les mécanismes sous-jacents aux comportements des insectes en fonction de la température. La température n'affecte pas de la même manière les composantes physiologiques et comportementales du cycle de vie, les traits n'ayant pas tous les mêmes courbes thermiques. Tout comme chez *Drosophila melanogaster*, les traits liés à la survie, au développement et la reproduction suivent des courbes thermiques différentes (Kellermann et van Heerwaarden, 2019). Iltis et al. (2019) ont obtenu des résultats similaires chez les chenilles de *Lobesia botrana*, la température affectant différemment certains traits de l'histoire de vie. De plus, certains comportements ont davantage d'importance pour la valeur adaptative de l'insecte que d'autres, notamment ceux qui sont liés à une perte d'opportunité pour l'insecte (accouplement, incidence du parasitisme).

8.2 / Impacts de la température sur le comportement

Le comportement des insectes s'étudie depuis des décennies, ses causes et ses conséquences, aussi bien dans une perspective évolutive, génétique que comparative (Matthews et Matthews, 2009). Cependant, depuis quelques années, on observe un regain d'intérêt dans des domaines plus appliqués, dont la lutte biologique (Ramirez-Romero et al., 2012; Beltrà et al., 2014; Mills et Heimpel, 2018; Heimpel, 2019; Kruidhof et al., 2019), de la gestion des espèces invasives (Holway et Suarez, 1999) ou des changements climatiques et des atténuations potentielles (Huey et Tewksbury, 2009; Sih et al., 2011; Tuomainen et Candolin, 2011; Andrew et al., 2013; Harmon et Barton, 2013; Sih, 2013; Sih et al., 2016). L'une des principales problématiques de l'étude du comportement concerne le manque de connaissances associées à la chaîne causale depuis la réception des informations environnementales et l'expression d'un comportement, notamment au niveau des informations thermiques. La question de l'adaptativité des comportements, en particulier dans le cadre de la réponse à la température, représente un aspect important de leur étude (Abram et al., 2017). Une réaction à un stimulus découle-t-elle d'une contrainte physiologique ? Ou correspond-elle à une réaction adaptée à la situation qui permet d'augmenter la valeur adaptative de l'individu malgré des conditions non-optimales ? Plusieurs considèrent les réponses comportementales d'un animal comme un tampon face aux conditions environnementales (Candolin et Wong, 2012) et donc, une adaptation à court terme aux changements climatiques (Huey et Tewksbury, 2009;

Andrew et al., 2013; Harmon et Barton, 2013). Ainsi, la thermorégulation comportementale permet aux individus d'éviter les températures trop élevées, par exemple en cherchant de l'ombre (Huey et Tewksbury, 2009; Harmon et Barton, 2013). Néanmoins, si dans les conditions futures les informations environnementales perdent leur fiabilité pour les individus, des pièges évolutifs pourraient se produire (Van Dyck et al., 2015; Faldyn et al., 2018). Les organismes utilisent des indices tels que la température et la photopériode pour prédire les conditions à venir et déterminer une réponse, par exemple entrer ou non en diapause à l'automne. Van Dyck et al. (2015) ont ainsi montré qu'en présence de températures plus élevées à la fin de l'été, les chenilles du lépidoptère *Lasiommata megera* continuent à se développer au lieu d'initier la diapause hivernale. On constate alors l'existence d'une 'génération perdue', pour laquelle le cycle n'est pas terminé et qui subira une forte mortalité.

8.2.1 / Réponses kinétique vs intégrée

L'utilisation d'un modèle kinétique nul tel que suggéré par Abram et al. (2017) nous a permis chez *A. listronoti* de distinguer les réponses kinétiques à la température des réponses intégrées, pour les trois types de comportements étudiés, soit la vitesse de marche, l'exploitation d'agrégats et l'accouplement. Certains suivent la réponse kinétique pour la gamme de températures testées (ex. : la vitesse de marche). D'autres relèvent d'une réponse kinétique pour une partie de la courbe thermique seulement (ex. : la distance parcourue ou le pourcentage de parasitisme). La distinction entre ces deux cas de figure demeure complexe lorsqu'on quantifie uniquement les réponses comportementales. Une des solutions à ce problème consiste en l'utilisation d'individus mutants au sein d'une population (Abram et al., 2017). Soto-Padilla et al. (2018) ont ainsi démontré que le mouvement de drosophiles mutantes, dont on avait rendu inactifs les gènes de thermo-réception, n'était pas affecté par la température. Les drosophiles réagissent à la température par un contrôle cognitif, dont le résultat sur le comportement se rapproche des modèles de kinétique enzymatique.

8.2.2 / Comportement adaptatif vs contraint

Les chapitres 4, 5 et 6 ont permis de mettre en évidence plusieurs comportements potentiellement adaptatifs en réponse à la température (par exemple, la durée de copulation (Chapitre 6)). À l'inverse, des comportements contraints se produisent, certains liés à des difficultés physiques, comme ceux observés lors de la manipulation de l'hôte ou de la parade nuptiale. Cependant, la plupart des contraintes observées étaient vraisemblablement liées à la détection des messages chimiques (Chapitres 5 et 6). Ainsi, à hautes températures, les femelles *A. listronoti* utilisent significativement plus les rejets suite à l'insertion dans l'hôte de l'ovipositeur que les rejets antennaires, puisqu'elles ne sont plus capables de détecter ou d'apprendre les stimuli chimiques associés au superparasitisme (van Baaren et al., 2005b; van Baaren et al., 2006; Chapitre 5). De la même manière, la diminution du succès d'accouplement à basse température peut résulter d'un manque de diffusion et de perception des phéromones sexuelles et, à haute température, par une mauvaise reconnaissance des deux partenaires (Chapitre 6). Les femelles parasitoïdes utilisent généralement des phéromones à longue et courte distances lors de la recherche d'hôte (Vinson, 1976; Fatouros et al., 2008). De même, les messages chimiques constituent une composante cruciale de l'accouplement. Ainsi la recherche (McNeil et Brodeur, 1995; McClure et al., 2007; Metzger, 2008), la reconnaissance (Singer, 1998; Howard et Blomquist, 2005; Ruther et al., 2011; Ablard, 2012) et le choix du partenaire sexuel (Johansson et Jones, 2007) impliquent, au moins partiellement, des phéromones sexuelles. Or, la température affecte non seulement les taux d'émission (Zhu et al., 2015; Bouwer et al., 2017) et de dispersion (Boullis et al., 2016) des composés chimiques, mais également la capacité de reconnaissance des messages par les individus récepteurs (Sentis et al., 2015).

8.2.3 / Individu vs population

Différentes températures provoquent des changements comportementaux à l'échelle de l'individu qui, dans le cas des températures supra-optimales les plus élevées, diminuent la performance de tous les comportements observés. Ainsi, à 35°C le succès d'accouplement diminue de 80%, le taux de parasitisme de 30% et la distance parcourue par femelle parasitoïde de 50% comparé à 25°C. En plus des baisses de performance, des pertes de temps (ex. : plus de temps passé à exploiter l'agrégat pour une production moindre de descendants à basse température), d'énergie et d'opportunités (ex. : rencontre de partenaire sexuel, disponibilité des hôtes) se produisent. Cependant, selon nos résultats, les individus ne « gâchent » pas vraiment d'opportunité. Ainsi, malgré les températures sous-optimales, les femelles n'ont pas fait de super-parasitisme, ce qui ne diminuent donc pas les probabilités de survie des œufs déjà pondus. Pour les espèces solitaires, une femelle pondant plusieurs fois dans le même hôte épuise ses ressources sans augmenter sa descendance (Harvey et al., 2013). De même, tous les accouplements ont résulté en un transfert de spermatozoïdes. À basse température, les femelles *A. listronoti* n'ont montré aucun comportement spécifique de sélection d'un partenaire sexuel, ce qui est avantageux pour les mâles mais pas pour les femelles. Ces dernières peuvent cependant s'accoupler avec plusieurs partenaires (Boivin et Martel, 2012). De plus, les femelles vierges ont tendance à retarder la ponte ou à explorer les agrégats différemment afin de maximiser leur valeur adaptative (Fauvergue et al., 2008). Également, la diminution de 50% d'activité et donc de déplacement provoquée par les basses et hautes températures n'avait pas d'effet significatif sur la population finale, tout comme le temps d'exploitation des hôtes et de déplacement (Chapitre 7). Il semble donc, pour la plupart des comportements, qu'il soit possible de compenser les effets délétères des températures sous-optimales lorsque l'individu rencontre subséquemment des conditions proches de son optimum thermique. L'ajustement des périodes d'activités permet également d'exprimer ces comportements en situation plus optimale.

Par exemple, les comportements qui se déroulent aux moments où les conditions sont plus clémentes, comme l'accouplement qui se produit préférentiellement au début de la photophase (McNeil et Brodeur, 1995; Cormier et al., 1998).

En plus de ces mécanismes individuels d'adaptation et de compensation, les différences comportementales observées en laboratoire semblent « compensées » au niveau de la population. Selon les conditions expérimentales modélisées, le nombre d'hôtes disponibles s'avère le principal facteur limitant chez *A. listronoti* (Chapitre 7), plus que la capacité de recherche et d'exploitation des hôtes des femelles. Le comportement d'une femelle maximise son succès reproducteur, et non l'accroissement de la population. Ainsi, s'il existe une grande variabilité phénotypique au sein de la population, une femelle A, qui se déplace peu ou lentement, arrivera sur un agrégat après la femelle B, laquelle aura déjà parasité les œufs. Les comportements de la femelle A affectent le nombre de ses descendants. Cependant, à l'échelle de la population et à court terme, il importe peu que ce soit la femelle A ou B qui ponde dans l'agrégat, tant qu'une génération suivante survient. Cette diversité de comportement entre les deux femelles peut découler de différences génétiques (Wajnberg et al., 1999; Gu et Dorn, 2000) ou développementales (van Baaren et al., 2005b; Colinet et Boivin, 2011), ainsi que de l'état physiologique des femelles : si elles sont accouplées ou non (Fauvergue et al., 2008), de leur réserve d'œufs (Rosenheim et Rosen, 1991; Minkenberg et al., 1992), de leur âge (Wajnberg, 2006), de leur expérience (Rosenheim et Rosen, 1991; van Baaren et al., 2005a) ou encore du microclimat (Woods et al., 2015). Tous ces facteurs affectent l'histoire de vie de l'individu mais, tel que démontré au Chapitre 7, lorsque le facteur limitant la population est le nombre d'hôtes, l'impact demeure réduit à l'échelle de la population. Ainsi, chez les geckos, Grimm-Seyfarth et al. (2018) ont démontré que l'effet de la température à l'échelle individuelle n'a pas forcément de conséquences au niveau de la population. Les auteurs expliquent ce phénomène par un effet tampon dû à une compensation (*trade-off*) au niveau des traits individuels. Ces différences entre les opportunités individuelles et les conséquences populationnelles renforcent le besoin pressant de créer des ponts entre ces disciplines (Ives, 1995; Levin, 2000; Tenhumberg, 2004; Wong et Candolin, 2015).

8.3 / Changements climatiques

Les changements climatiques entraîneront d'ici la fin du siècle des températures plus chaudes en moyenne de 3.1°C pendant l'été dans le sud du Québec (Ouranos, 2015), ainsi que des conditions climatiques (dont la température) plus extrêmes et variables (Stocker et al., 2013). La plupart des études brossent un portrait plutôt pessimiste du devenir des organismes en général (Roberts, 1988; Barnosky et al., 2011; Bellard et al., 2012), et en particulier des insectes (Hallmann et al., 2017; Carnicer et al., 2019; Sánchez-Bayo et Wyckhuys, 2019; Wepprich et al., 2019; Cardoso et al., 2020), les changements climatiques étant identifiés en 4$^{\text{ème}}$ position des causes d'extinctions (Thomas et al., 2004; Sánchez-Bayo et Wyckhuys, 2019). Il est dès lors nécessaire d'analyser plus en détails les conséquences du réchauffement climatique sur les individus, les populations et les écosystèmes.

8.3.1 / Augmentation moyenne de la température et variabilité

En se basant sur les courbes thermiques d'*A. listronoti*, l'augmentation de 3.1°C des températures par rapport aux conditions actuelles se révèle bénéfique, aussi bien pour la physiologie que pour les comportements. En effet, les températures moyennes actuelles au Québec se situent dans la zone infra-optimales d'*A. listronoti*, et cette augmentation de température de 3.1°C s'approcherait de leurs optimums thermiques. Cependant les conditions plus variables et plus extrêmes, en particulier les températures supérieures à 30°C, causent une diminution, voire un arrêt total de la plupart des comportements (déplacement, parasitisme, accouplement). Le maintien de telles températures pendant plusieurs jours pourrait ainsi provoquer de fortes diminutions d'effectifs dans la population, d'autant que la longévité des individus diminue lorsque la température augmente (7 jours à 23°C vs 4 jours à 26°C pour *A. listronoti*) (Collins et Grafius, 1986). Cet effet est d’autant plus important pour les espèces à vie courte. De plus, la limite thermique supérieure, permettant la survie chez les insectes, se trouve en moyenne autour de 39.3°C (Hoffmann et al., 2013) et la plupart des études portant sur la kinétique de la mort thermique ne considèrent que des températures supérieures ou égales à 40°C (Hallman et Denlinger, 1998; Johnson et al., 2004). Ce seuil de 40°C est encore rarement atteint au Québec, mais la situation pourrait changer dans les années futures. Une mortalité due à la chaleur pourrait ainsi venir s'ajouter aux effets physiologiques et comportementaux déjà présents à partir de 30°C. Nos résultats concordent ainsi avec les nombreuses études indiquant l'importance majeure de l'augmentation de variabilité et d'occurrence des phénomènes extrêmes comparée à l'augmentation moyenne des températures (Bale et al., 2002; Drake, 2005; Clusella-Trullas et al., 2011; Folguera et al., 2011; Paaijmans et al., 2013; Estay et al., 2014; Vasseur et al., 2014; Sergio et al., 2018; Zhu et al., 2019).

8.3.2 / Autres facteurs météorologiques

Outre la température, d'autres facteurs météorologiques se verront modifiés par les changements climatiques, mais leurs effets sur les insectes restent moins étudiés : concentrations de gaz à effet de serre, vent, épisodes de sécheresse, précipitations, rayonnement solaire (Stocker et al., 2013). Les concentrations de gaz à effet de serre (en particulier le CO_2) altèrent la croissance, la qualité (notamment le ratio C:N) (Roth et Lindroth, 1995; Agrell et al., 2000), les mécanismes de défense (Johnson et Züst, 2018) et, globalement, la survie des plantes (Caulfield et Bunce, 1994; Agrell et al., 2000). Par conséquent, la performance des herbivores en est affectée (Roth et Lindroth, 1995). La communication chimique entre l'insecte herbivore et la plante hôte (Stange, 1997), et entre les individus se trouve altérée (Boullis et al., 2015; 2016; 2017), ainsi que la composition des communautés et le fonctionnement des écosystèmes (Jones, 1998). Le vent affecte la capacité de dispersion des parasitoïdes *Trichogramma evanescens*, de *T. pretiosum* (Fournier et Boivin, 2000) et d'*Eretmocerus eremicus* (Bellamy et Byrne, 2001), ainsi que le comportement de recherche de l'hôte chez *Aphidius rosae* (Fink et Völkl, 1995). De plus, il influence la communication chimique (McNeil, 1991). À vitesse élevée notamment, il augmente la distance à laquelle les messages chimiques sont portés (Marchand et McNeil, 2000) mais diminue la capacité de vol des individus (Goldansaz et McNeil, 2006).

Les insectes détectent l'humidité relative et adaptent leurs comportements en conséquence (Chown et al., 2011). Le stress hydrique résultant des changements climatiques aura donc un effet considérable sur les populations d'insectes. Les pertes d'eau se produisent majoritairement au niveau de la transpiration respiratoire et de la cuticule (Addo-Bediako et al., 2001; Bazinet et al., 2010). Les composantes cuticulaires, en particulier les CHC (*Cuticular Hydrocarbons*), jouent donc un rôle crucial dans l'évitement des pertes d'eau (Gibbs, 2002; Chown et al., 2011). Les insectes peuvent également adopter la stratégie d'éviter les conditions de sécheresse et de températures élevées (Gibbs et al., 1998). Lorsque plusieurs facteurs de stress sont combinés, par exemple dans le cas d'une sécheresse associée à des températures élevées, la capacité des parasitoïdes à contrôler les populations de leurs hôtes diminue (Romo et Tylianakis, 2013). À l'autre extrême du spectre de stress hydrique, les précipitations intenses ont également un effet important sur les insectes. Il existe ainsi un lien entre les précipitations annuelles et la limite thermique maximale (CT_{max}) (Kellermann et Sgrò, 2018) ainsi que la résistance à la sécheresse (Kellermann et al., 2018). En plus des capacités d'adaptation, la pluie diminue voire interrompt complètement le comportement de recherche de l'hôte et de ponte chez certains parasitoïdes (Fink et Völkl, 1995). Elle peut également affecter la survie des herbivores en modifiant la qualité de la plante hôte (Thacker et al., 1997).

Si la plupart des études liées aux changements climatiques portent sur les conditions estivales et les périodes d'activité des insectes, les conditions hivernales affectent aussi l'écologie saisonnière des individus, notamment la diapause, la survie hivernale et le synchronisme des émergences printanières en fonction des ressources (Bale et Hayward, 2010). Ainsi, la diminution anticipée de la couverture nivale au Québec (Ouranos, 2010) pourrait augmenter la mortalité des insectes exposés à des températures plus extrêmes (Bale et Hayward, 2010). Les conditions de photopériode ne changeront pas pour une latitude donnée, mais les conditions thermiques seront différentes. Ces deux facteurs agissants et interagissant comme paramètre pour l'entrée et la sortie de diapause, des comportements maladaptatifs pourraient subvenir, par exemple des entrées ou des sorties de diapause alors que les conditions ne permettent pas la survie des organismes (Van Dyck et al., 2015), bien que les populations puissent s'adapter aux nouvelles conditions (Tougeron et al., 2019).

8.3.3 / La vie trouve toujours un chemin

Finalement, pour répondre à la question posée par Roberts (1988) : “Y a-t-il de la vie après les changements climatiques?” (“*Is there life after climate change?*”). La réponse ne peut-être que positive. Les insectes possèdent des capacités impressionnantes d'adaptation aux conditions environnementales, que ce soit au niveau physiologique (acclimatation, choc thermique, thermorégulation exogène ou endogène, etc.), comportemental (sélection d’habitat, conservation de l'énergie, décalage des périodes d'activité) ou évolutif (temps de génération court permettant une évolution rapide des populations) (Chapitre 2). Ce dernier point importe dans le contexte des changements climatiques à cause de la rapidité des changements observés, qui s’avère plus problématique pour les organismes ayant de longs cycles de vie (Etterson et Shaw, 2001; Svenning, 2003; Visser, 2008; Quintero et Wiens, 2013). Les capacités d'adaptation à court terme pourraient, selon les cas, permettre aux populations de survivre assez longtemps pour s’adapter par évolution, ou dans le cas contraire, ralentir l'évolution en diminuant la pression sélective exercée (Buckley et al., 2015; Wong et Candolin, 2015). Ces capacités d'adaptation diffèrent selon les conditions, constantes ou variables, que rencontrent les populations en fonction de leur zone géographique (Parmesan, 2006; Deutsch et al., 2008; Huey et al., 2009; Kingsolver, 2009; Bonebrake et Mastrandrea, 2010; Bonebrake et Deutsch, 2012; Diamond et al., 2012; Koltz et al., 2018). Les écosystèmes actuels se modifient (Koltz et al., 2018) et de nouveaux équilibres se forment. Il reste en revanche difficile de prédire la nature et l'échelle temporelle de ces changements. Les précédents changements climatiques liés aux différentes ères géologiques ont provoqué des modifications de répartition géographique (Coope, 1970; Graham et Grimm, 1990; Davis et Shaw, 2001), des variations de composition des communautés (Wilf et Labandeira, 1999), des adaptations au nouveau climat (Parmesan et al., 2000), mais également des extinctions (Graham et Grimm, 1990). La situation se présente différemment aujourd'hui, notamment à cause de la multiplicité des perturbations (Parmesan et al., 2000; Molina-Montenegro et al., 2009; Rohr et Palmer, 2013; Macfadyen et al., 2018), mais ces changements historiques peuvent ainsi nous aider à prédire non seulement l'ampleur des transformations subies par les communautés, mais également le moment approximatif d'un retour à la stabilité (Nolan et al., 2018). De plus, de nombreuses stratégies sont proposées ou mises en œuvre pour tempérer les effets des changements climatiques et protéger les populations végétales et animales (Samways et al., 2020), laissant entrevoir un peu d'espoir de limiter les dommages et de retrouver plus rapidement un nouvel équilibre. Les auteurs suggèrent d’améliorer l’image des insectes auprès du public, ainsi que de mieux communiquer leur importance auprès des preneurs de décisions. Cela permettrait la mise en place de stratégies globales de protection des habitats, assurant le maintien d’une complexité biotique (zones protégées, maintien de l’hétérogénéité des habitats, diminution de l’utilisation de pesticides) et de la connectivité fonctionnelle (corridors de conservation).

8.4 / Perspectives de recherche

Tel que suggéré tout au long de ce chapitre, plusieurs perspectives de recherche émergent des résultats présentés dans cette thèse, aussi bien dans le contexte des changements climatiques et des possibilités d’adaptation des organismes que de la lutte biologique.

8.4.1 / La communication chimique

En premier lieu, nous manquons de connaissances relatives à l'impact de la température sur la communication chimique intra- et interspécifique (Yuan et al., 2009; Boullis et al., 2016). Les composés chimiques constituent la majorité des informations utilisées par les insectes, que ce soit pour trouver des ressources (Fatouros et al., 2008; Beyaert and Hilker, 2014) ou leur partenaire sexuel (Johansson et Jones, 2007). La température affecte directement ces composés : les taux d'émission (Zhu et al., 2015; Bouwer et al., 2017) et de dispersion (Boullis et al., 2016), mais également leur composition (Sentis et al., 2015) et leur demi-vie (McDonough et al., 1991) et donc modifie l'information qu'ils véhiculent; avec des conséquences sur la communication chimique (Laws, 2017). La température altère également les capacités de détection et de reconnaissance des composés chimiques, que ce soit lors de l'exposition directe aux conditions thermiques (McNeil, 1991; Reddy et al., 2002; Sentis et al., 2015), ou lorsque les individus ont été exposés durant leur développement (Colinet et Boivin, 2011; Bourdais et al., 2006; 2012). De plus, la température affecte la mémoire des individus, et donc leur comportement de recherche des ressources (Abram et al., 2015).

Nous avons émis au chapitre 5 plusieurs hypothèses permettant d'expliquer pourquoi, à haute température, les femelles rejetaient les hôtes parasités après insertion de l'ovipositeur plutôt que par contact antennaire. Ce changement de comportement peut ainsi s'expliquer par : (1) l'altération du marquage par la femelle directement après la ponte; (2) des modifications de la quantité et qualité de phéromones de marquage à différentes températures; (3) des changements dans la capacité de la femelle à reconnaître les kairomones, ou (4) une combinaison de toutes ces possibilités. Il serait par conséquent intéressant de tester ces différentes hypothèses, par exemple en utilisant la chromatographie en phase gazeuse couplée à la spectrométrie de masse (*Gas chromatography-mass spectrometry* - GC-MS), permettant de séparer et identifier les composés chimiques volatiles, combinée à des études comportementales (Conrad et al., 2017).

Il existe des exemples d'ajustement des préférences du signal en fonction de la température. Ainsi, chez *D. melanogaster*, Riveron et al. (2009) ont montré que les changements de sensibilité olfactives pour deux composés chimiques compensaient les changements thermiques subis. Ainsi à températures élevées, pour lesquelles les concentrations de substances volatiles sont plus élevées, la sensibilité des mouches à ces substances volatiles diminuait, et inversement à basse température. D'après l'hypothèse de couplage de la température (*Temperature Coupling Hypothesis* - TCH) (Ritchie et al., 2001), les individus ajustent leurs préférences pour le signal selon la température ressentie. Cet effet, permettant le maintien de la communication pour des conditions thermiques variées, a été démontré chez certaines espèces lorsque le signal est de nature acoustique ou vibrationnelle (Ritchie et al., 2001; Greenfield et Medlock, 2007; Conrad et al., 2017; Jocson et al., 2019). Cet effet pourrait se retrouver également pour les signaux chimiques (Conrad et al., 2017), mais peu d'études ont été réalisées à ce sujet.

Il serait ainsi intéressant de tester la TCH chez des parasitoïdes dans un contexte d'accouplement, également en combinant des expériences comportementales avec une chromatographie en phase gazeuse couplée à la spectrométrie de masse. Une femelle vierge placée à différentes températures pourrait être lavée avec un solvant organique permettant de récupérer ses hydrocarbones cuticulaires (Steiner et al., 2006; Ruther et al., 2011). Ces composés chimiques seraient ensuite testés sur un mâle, à différentes températures. On pourrait ainsi observer s'il réagit différent aux composés en fonction de la température à laquelle était exposée la femelle lors de leur émission, et la température du mâle lors de leur réception. On s'attendrait alors à ce que le mâle préfère (réagisse plus fortement ou plus rapidement) aux composés émis à la même température à laquelle il est exposé lors du test (Ritchie et al., 2001). De manière complémentaire, on pourrait récupérer les substances volatiles émises par le mâle lors de sa cour à différentes températures, y exposer la femelle également à différentes températures, et observer si elle accepte de s'accoupler.

8.4.2 / Le système nerveux

Une partie importante de cette thèse consiste en la distinction entre les réponses kinétiques à la température et les réponses intégrées. La principale différence entre les deux repose sur le rôle du système nerveux central dans la réponse observée. Par conséquent, l'une des perspectives intéressantes de recherche consisterait à étudier plus en détail l'impact de la température sur le système nerveux des ectothermes, et surtout les conséquences sur leur comportement. Kerkut et Taylor (1958) ont montré que l'activité des ganglions isolés de cafards variait avec la température. Les potentiels de synapse maximum se produisent à température intermédiaire (Prosser et Nelson, 1981). A températures extrêmes, les circuits neuronaux défaillent à cause d'une perte (réversible) de l'homéostasie ionique (Roberston et Money, 2012). Ainsi, les limites thermiques à la viabilité des organismes ne seraient pas liées à la mort cellulaire ou la dénaturation des protéines, mais bien aux mécanismes de contrôles homéostasiques (Robertson et Money, 2012). La température affecte le système nerveux des insectes selon différents mécanismes : en modifiant le taux des réponses (Walker, 1975) (ce qui correspondrait aux effets kinétiques), des effets de compensation, d'ajustement (*tuning*), d'acclimatation (Prosser et Nelson, 1981) et de thermotolérance grâce aux *Heat Shock Proteins* (Robertson, 2004a; Robertson, 2004b; Roberston et Money, 2012). Le système nerveux peut également être protégé des températures extrêmes par les hormones telles que l'amine octopamine (Armstrong et Robertson, 2006). Notre compréhension de l'effet de la température sur le système nerveux reste malgré tout limitée (Roberston et Money, 2012), bien qu'elle s'avère critique lorsqu'on s'intéresse à la détection des signaux environnementaux, par exemple pour les études d'électro-antennographie (Olsson et Hanson, 2013; Schott et al.,

2013) ou de thermorégulation (Nurme et al., 2019; Gonzalez-Tokman et al, 2020).

On peut s'intéresser de deux manières à la façon dont la température affecte le système nerveux des insectes : (1) au niveau de la réception de l'information et (2) au niveau du traitement de l'information. La première manière d'étudier la problématique est à ce jour plus aisée que la seconde, pour laquelle les connaissances manquent encore. Dans le cadre du présent projet, on pourrait s'intéresser plus en détails à la manière dont la perception de l'information thermique affecte le comportement de l'insecte. La méthode préférentielle permettant d'étudier cet effet reste l'utilisation de mutants thermo-insensibles, tels qu'utilisés par Soto-Padilla et al. (2018) chez *Drosophila melanogaster*. Les mutants n'étant plus capables de détecter la température ambiante, leurs comportements seront seulement kinétiques, et non pas intégrés. Nous pouvons alors comparer leur réponse à celles des individus non-mutants pour déterminer si la réponse à la température de l'espèce est de nature kinétique ou intégrée (Abram et al., 2017).

Pour les espèces dont l'obtention de mutants thermo-insensibles est plus complexe, il demeure possible de bloquer les récepteurs hygro-thermiques présents sur les antennes des individus, par exemple en utilisant de la peinture, ou encore en retirant une ou les deux antennes (Flores and Lazzari, 1996). La majorité des thermo-recepteurs étant présents sur les antennes des insectes (Flores and Lazzari, 1996; Gonzalez-Tokman et al., 2020), il serait encore une fois possible de comparer le comportement en conditions de thermo-sensibilité standard (individus témoins) et thermo-sensibilité diminuée (individus dont on a bloqué les thermo-recepteurs) afin de déterminer la nature kinétique ou intégrée des réponses comportementales observées.

8.4.3 / L'importance de la variabilité inter-individuelle

L'une des questions soulevées par l'utilisation d'Individual-Based-Model est la variation inter-individuelle. « *Les écologistes ont longtemps décrit l'écologie d'une espèce comme un tout, et traité les individus conspécifiques comme écologiquement équivalents. Par exemple la majorité des modèles de compétition intraspécifiques, de dynamiques prédateurs-proie, ainsi que les structures de réseaux trophiques supposent que tous les individus conspécifiques sont identiques* » (Bolnick et al., 2003). On observe cependant un changement de ce raisonnement. Ainsi plusieurs modèles commencent à tenir compte de la variation inter-individuelle, par exemple dans le comportement de recherche des ressources (Goss-Custard et al., 1995; Vet et al., 2001), la dispersion (Hawkes et al., 2009), le développement (Struelens et al., 2018), ou encore le risque d'extinction (Jager, 2001). Les études d'histoires de vie devraient également considérer l'hétérogénéité entre la qualité et la performance des individus (Hamel et al., 2009). En effet, cette variation inter-individuelle peut être grande au niveau de la physiologie (Chown, 2001) et du comportement (Jeanson and Weidenmuller, 2014), et avoir des conséquences importantes sur les communautés (Bolnick et al., 2011). Ses bases peuvent être génétiques, épigénétiques (Herrera et Bazaga, 2011), physiologiques, résulter d'expériences précédentes, ou une combinaison de tous ces facteurs (Jeanson et Weidenmuller, 2014). Minkenberg et al., (1992) ont par exemple rapporté que la recherche de ressources et la ponte chez les insectes étaient fortement liées à la charge d'œufs des femelles. La performance de vol des individus *Megarhyssa nortoni* varie selon le sexe, la morphologie et l'histoire de vie des individus (Fischbein et al., 2018). S'il est important de tenir compte de la variation existante, il est également intéressant de la mesurer (Dingemanse et Dochtermann, 2017). L'existence de variations entre les individus au sein d'une population est à la base de la sélection naturelle et sexuelle (Widemo et Saether, 1999), et constitue donc un intérêt particulier pour les possibilités d'adaptation aux changements environnementaux (Alonzo, 2015). Elle peut ainsi être considérée lors du développement de stratégies de conservation pour contrer les impacts des changements climatiques (Macdonald et al., 2017). L'existence de génotypes adaptés aux nouvelles conditions constitue d'ailleurs l'une des limites potentielles d'adaptation par évolution aux changements climatiques (Hoffmann et Sgrò, 2011; Reed et al., 2011).

Dans le contexte des changements climatiques et d'organismes à courte vie, il serait intéressant de mesurer l'effet des températures expérimentées précédemment sur le comportement à une température donnée. Les femelles pourraient ainsi agir différemment en fonction des microclimats auxquelles elles ont été exposées au cours de leur vie. Les individus savent-ils qu'ils sont dans des conditions non-optimales et attendent-ils effectivement le retour des conditions plus adaptées, tel que parfois suggéré pour l'accouplement (McNeil and Brodeur, 1995)? Une femelle placée à une température élevée au début de sa vie va-t-elle ajuster son comportement de ponte et de recherche d'hôte pour augmenter sa valeur adaptative? On peut par exemple observer un comportement de ce type chez les femelles vierges, qui adaptent leur comportement en se basant sur de futures opportunités d'accouplement (Fauvergue et al., 2008).

8.4.4 / La lutte biologique

Finalement, les résultats de cette thèse sont d'intérêt pour la lutte biologique, par la compréhension du comportement des ennemis naturels dans le contexte des changements climatiques. Les connaissances actuelles ne permettent pas encore de prédire efficacement l'effet des changements climatiques sur les insectes ravageurs (Bale et al., 2002) et leurs ennemis naturels. En effet, il reste difficile de généraliser les prédictions des effets des changements climatiques sur les insectes (Harrington et al., 2001; Romo et Tylianakis, 2013; Lemoine et al., 2014). Les études portant sur les problématiques agricoles prédisent plutôt une augmentation des problèmes liés aux ravageurs, de par l'augmentation des populations de ravageurs (Deutsch et al., 2018) et la diminution du contrôle par les ennemis naturels (Hance et al., 2007; Furlong et Zalucki, 2017), alors que les études portant sur les problématiques de conservation prédisent une diminution des populations (Harrington et al., 2001), qui semble se confirmer (Hallmann et al., 2017; Carnicer et al., 2019; Sánchez-Bayo et Wyckhuys, 2019; Wepprich et al., 2019). Il semble ainsi que les efforts de recherche et de mitigation doivent se concentrer sur les espèces individuelles, selon leur contexte écologique et évolutif (Lehmann et al., 2018). Ces connaissances sont nécessaires pour s'adapter aux changements, en particulier dans le secteur agricole (Ladányi et Horváth, 2010), et dans le cadre de la lutte biologique (Thomson et al., 2010).

Dans ce contexte, des projets de recherche devraient inclure des tests des relations ravageurs-ennemis naturels en conditions de changements climatiques, telles que celles réalisées par Barton et al., (2009). Plutôt que de seulement modéliser les populations selon des températures représentatives des changements climatiques, il faudrait tester expérimentalement l'effet de ces conditions thermiques sur les ravageurs, leurs ennemis naturels, et les relations entre les deux, par exemple en augmentant la température de manière artificielle (Barton et al., 2009), ou en créant des conditions plus variables et extrêmes. La température n'est d'ailleurs pas le seul facteur d'importance pour les organismes, et les autres facteurs climatiques affectés par les changements globaux doivent également être testés (Barton, 2017), par exemple les précipitations et le vent qui peuvent être simulés expérimentalement (Fink and Volk, 1995) d'après les conditions prévues par les changements climatiques. La stabilité des systèmes ravageurs/ennemis naturels pourra ainsi être étudiée selon les axes de synchronisme et de maintien du contrôle du ravageur par l'ennemi naturel, pour les conditions climatiques futures.

La modélisation reste un outil important, permettant entre autres de prédire les répartitions futures des espèces, ce qui pourrait permettre d'identifier les espèces invasives susceptibles de s'établir dans certaines régions. Sachant que les CT_{min} et CT_{max}, fréquemment utilisées pour déterminer la future répartition géographique des espèces, ne sont pas forcément adaptées (Kellermann et van Heerwaarden, 2019), il serait possible de comparer différentes mesures de performance thermique (gamme possible et optimale pour différent comportements, développement, etc.) afin de déterminer un prédicteur plus fiable des répartitions des espèces pour les conditions climatiques futures.

8.5 / Conclusion

La température modifie le comportement de la guêpe parasitoïde des œufs *Anaphes listronoti*. Certaines réponses comportementales s'avèrent de nature kinétique; d'autres sont intégrées. La distinction entre les deux types de réponses reste complexe, d'autant qu'elles ne sont pas forcément exclusives pour un comportement donné. De même, certaines réponses sont adaptatives et d'autres résultent de contraintes selon des mécanismes physiques ou chimiques, incluant la kinétique, la détection des messages chimiques et autres. La plupart des contraintes observées semblent liées à la communication chimique et à la perte de temps provoquée par la diminution de l'activité : des individus inactifs ne recherchent pas leurs hôtes ou leurs partenaires sexuels.

Plusieurs mécanismes d'adaptation aux conditions thermiques sous-optimales existent à l'échelle individuelle (physiologique, comportementale, circadienne, phénologique, etc.), et ont des effets qui se répercutent à l'échelle de la population. Ces mécanismes permettent à la population de se maintenir dans un environnement, même lorsque la plupart de ses composantes subissent des contraintes à leur développement et reproduction. Ainsi, pour les conditions climatiques actuelles, des comportements individuels, tel que ceux mesurés au laboratoire chez *A. listronoti*, permettent le maintien d'une population tout au long de la saison. Cependant, lorsque les conditions deviennent plus variables et extrêmes, certains comportements sont perturbés (accouplement, ponte, déplacement, etc.), leur optimum thermique étant inférieur à 30°C. Quel sera le devenir de ces populations? L'espèce aura-t-elle développé de nouvelles adaptations aux conditions futures?

Malgré le fait que la température soit considérée comme le facteur abiotique le plus important du cycle de vie des insectes, de nombreux éléments manquent encore pour dresser une image complète de l'effet des changements climatiques sur leurs populations. D'autres facteurs abiotiques, moins bien étudiés, ont également une importance non négligeable dans le cycle de vie et l'abondance d'un insecte, notamment les précipitations, la radiation solaire et le vent. Les capacités d'adaptation des espèces s'avèrent cependant grandes chez ces organismes à courte génération. Ainsi, les conséquences écologiques négatives ne se révèleront sans doute pas aussi considérables que précédemment envisagées.

8.6 / Références

Ablard, K. M. (2012). Local mate competition, and mechanisms, functions and fitness consequences of courtship and mating behaviour in the parasitoid wasp *Ooencyrtus kuvanae* (Hymenoptera: Encyrtidae) [PhD Thesis]. Science: Biological Sciences Department.

Abram, P. K., Boivin, G., Moiroux, J., et Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: Unifying thermal physiology and behavioural plasticity. *Biological Reviews*, *92*(4), 1859–1876. https://doi.org/10.1111/brv.12312

Abram, P. K., Cusumano, A., Peri, E., Brodeur, J., Boivin, G., et Colazza, S. (2015). Thermal stress affects patch time allocation by preventing forgetting in a parasitoid wasp. *Behavioral Ecology*, *26*(5), 1326–1334. https://doi.org/10.1093/beheco/arv084

Addo-Bediako, A., Chown, S. L., et Gaston, K. J. (2001). Revisiting water loss in insects: A large scale view. *Journal of Insect Physiology*, *47*(12), 1377–1388. https://doi.org/10.1016/S0022-1910(01)00128-7

Agrell, J., McDonald, E. P., et Lindroth, R. L. (2000). Effects of CO2 and light on tree phytochemistry and insect performance. *Oikos*, *88*(2), 259–272. https://doi.org/10.1034/j.1600-0706.2000.880204.x

Alonzo, S. H. (2015). Integrating the how and why of within-individual and among-individual variation and plasticity in behavior. *Current opinion in behavioral sciences*, *6*, 69-75.

Andrew, N. R., Hill, S. J., Binns, M., Bahar, M. H., Ridley, E. V., Jung, M.-P., Fyfe, C., Yates, M., et Khusro, M. (2013). Assessing insect responses to climate change: What are we testing for? Where should we be heading? *PeerJ*, *1*, e11. https://doi.org/10.7717/peerj.11

Armstrong, G. A., et Robertson, R. M. (2006). A role for octopamine in coordinating thermoprotection of an insect nervous system. *Journal of Thermal Biology*, *31*(1-2), 149-158.

Bale, J. S., et Hayward, S. A. L. (2010). Insect overwintering in a changing climate. *Journal of Experimental Biology*, *213*(6), 980–994. https://doi.org/10.1242/jeb.037911

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D., et Whittaker, J. B. (2002). Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. *Global Change Biology*, *8*(1), 1–16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B., et Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57. https://doi.org/10.1038/nature09678

Barton, B. T. (2017). Beyond global warming: Putting the "climate" back into "climate change ecology". *Food webs*, *13*, 51-52.

Barton, B. T., Beckerman, A. P., et Schmitz, O. J. (2009). Climate warming strengthens indirect interactions in an old-field food web. *Ecology*, *90*(9), 2346-2351.

Bazinet, A. L., Marshall, K. E., MacMillan, H. A., Williams, C. M., et Sinclair, B. J. (2010). Rapid changes in desiccation resistance in *Drosophila melanogaster* are facilitated by changes in cuticular permeability. *Journal of Insect Physiology*, *56*(12), 2006–2012. https://doi.org/10.1016/j.jinsphys.2010.09.002

Bellamy, D. E., et Byrne, D. N. (2001). Effects of gender and mating status on self-directed dispersal by the whitefly parasitoid *Eretmocerus eremicus*. *Ecological Entomology*, *26*(6), 571–577. https://doi.org/10.1046/j.1365-2311.2001.00370.x

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., et Courchamp, F. (2012). Impacts of climate change on the future of biodiversity: Biodiversity and climate change. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Beltrà, A., Pekas, A., Soto, A., et Tena, A. (2014). Employing evolutionary theory to improve biological pest control: Causes of non-adaptive sex allocation behavior in parasitoid wasps and implications. *Basic and Applied Ecology*, *15*(7), 625–632. https://doi.org/10.1016/j.baae.2014.09.002

Beyaert, I., et Hilker, M. (2014). Plant odour plumes as mediators of plant–insect interactions. *Biological Reviews*, *89*(1), 68-81.

Boivin, G., et Martel, V. (2012). Size-induced reproductive constraints in an egg parasitoid. *Journal of Insect Physiology*, *58*(12), 1694–1700. https://doi.org/10.1016/j.jinsphys.2012.10.014

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., et Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1-28.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., ... et Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution*, *26*(4), 183-192.

Bonebrake, T. C., et Deutsch, C. A. (2012). Climate heterogeneity modulates impact of warming on tropical insects. *Ecology*, *93*(3), 449–455. https://doi.org/10.1890/11-1187.1

Bonebrake, T. C., et Mastrandrea, M. D. (2010). Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proceedings of the National Academy of Sciences*, *107*(28), 12581–12586. https://doi.org/10.1073/pnas.0911841107

Boullis, A., Francis, F., et Verheggen, F. J. (2015). Climate change and tritrophic interactions: Will modifications to greenhouse gas emissions increase the vulnerability of herbivorous insects to natural enemies? *Environmental Entomology*, *44*(2), 277–286. https://doi.org/10.1093/ee/nvu019

Boullis, A., Detrain, C., Francis, F., et Verheggen, F. J. (2016). Will climate change affect insect pheromonal communication? *Current Opinion in Insect Science*, *17*, 87–91. https://doi.org/10.1016/j.cois.2016.08.006

Boullis, A., Fassotte, B., Sarles, L., Lognay, G., Heuskin, S., Vanderplanck, M., Bartram, S., Haubruge, E., Francis, F., et Verheggen, F. J. (2017). Elevated carbon dioxide concentration reduces alarm signaling in aphids. *Journal of Chemical Ecology*, *43*(2), 164–171. https://doi.org/10.1007/s10886-017-0818-z

Bourdais, D., Vernon, P., Krespi, L., Le Lannic, J., et Van Baaren, J. (2006). Antennal structure of male and female *Aphidius rhopalosiphi* DeStefani-Peres (Hymenoptera: Braconidae): Description and morphological alterations after cold storage or heat exposure. *Microscopy Research and*

Technique, *69*(12), 1005-1013.

Bourdais, D., Vernon, P., Krespi, L., et van Baaren, J. (2012). Behavioural consequences of cold exposure on males and females of *Aphidius rhopalosiphi* De Stephani Perez (Hymenoptera: Braconidae). *BioControl*, *57*(3), 349–360. https://doi.org/10.1007/s10526-011-9396-0

Bouwer, M. C., Slippers, B., Wingfield, M. J., Allison, J. D., et Rohwer, E. R. (2017). Optimization of pheromone traps for *Coryphodema tristis* (Lepidoptera: Cossidae). *Journal of Economic Entomology*, *110*(4), 1603–1610. https://doi.org/10.1093/jee/tox171

Buckley, L. B., Ehrenberger, J. C., et Angilletta, M. J. (2015). Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Functional Ecology*, *29*(8), 1038–1047. https://doi.org/10.1111/1365-2435.12406

Candolin, U., et Wong, B. B. M. (2012). *Behavioural responses to a changing world: Mechanisms and consequences*. Oxford University Press.

Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Ari Noriega, J., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., … Samways, M. J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, *242*, 108426. https://doi.org/10.1016/j.biocon.2020.108426

Carnicer, J., Stefanescu, C., Vives-Ingla, M., López, C., Cortizas, S., Wheat, C., Vila, R., Llusià, J., et Peñuelas, J. (2019). Phenotypic biomarkers of climatic impacts on declining insect populations: A key role for decadal drought, thermal buffering and amplification effects and host plant dynamics. *Journal of Animal Ecology*, *88*(3), 376–391. https://doi.org/10.1111/1365-2656.12933

Caulfield, F., et Bunce, J. A. (1994). Elevated atmospheric carbon dioxide concentration affects interactions between *Spodoptera exigua* (Lepidoptera: Noctuidae) larvae and two host plant species outdoors. *Environmental Entomology*, *23*(4), 999–1005. https://doi.org/10.1093/ee/23.4.999

Chown, S. L. (2001). Physiological variation in insects: Hierarchical levels and implications. *Journal of Insect Physiology*, *47*(7), 649–660. https://doi.org/10.1016/S0022-1910(00)00163-3

Chown, S. L., Sørensen, J. G., et Terblanche, J. S. (2011). Water loss in insects: An environmental change perspective. *Journal of Insect Physiology*, *57*(8), 1070–1084. https://doi.org/10.1016/j.jinsphys.2011.05.004

Clusella-Trullas, S., Blackburn, T. M., et Chown, S. L. (2011). Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *The American Naturalist*, *177*(6), 738–751. https://doi.org/10.1086/660021

Colinet, H., et Boivin, G. (2011). Insect parasitoids cold storage: A comprehensive review of factors of variability and consequences. *Biological Control*, *58*(2), 83–95. https://doi.org/10.1016/j.biocontrol.2011.04.014

Collins, R. D., et Grafius, E. (1986). Biology and life cycle of *Anaphes sordidatus* (Hymenoptera: Mymaridae), an egg parasitoid of the carrot weevil (Coleoptera: Curculionidae). *Environmental Entomology*, *15*(1), 100–105.

Conrad, T., Stöcker, C., et Ayasse, M. (2017). The effect of temperature on male mating signals and female choice in the red mason bee, *Osmia bicornis* (L.). *Ecology and Evolution*, *7*(21), 8966–8975. https://doi.org/10.1002/ece3.3331

Coope, G. R. (1970). Interpretations of Quaternary insect fossils. *Annual Review of Entomology*, *15*(1), 97–121. https://doi.org/10.1146/annurev.en.15.010170.000525

Cormier, D., Royer, L., Vigneault, C., Panneton, B., et Boivin, G. (1998). Effect of female age on daily cycle of sexual pheromone emission in gregarious egg parasitoid *Anaphes listronoti*. *Journal of Chemical Ecology*, *24*(10), 1595–1610.

Davis, M. B., et Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, *292*(5517), 673–679. https://doi.org/10.1126/science.292.5517.673

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., et Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Deutsch, Curtis A., Tewksbury, J. J., Tigchelaar, M., Battisti, D. S., Merrill, S. C., Huey, R. B., et Naylor, R. L. (2018). Increase in crop losses to insect pests in a warming climate. *Science*, *361*(6405), 916–919. https://doi.org/10.1126/science.aat3466

Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Toro, I. D., Hirsch, C., Oberg, E., et Dunn, R. R. (2012). Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*, *18*(2), 448–456. https://doi.org/10.1111/j.1365-2486.2011.02542.x

Dingemanse, N. J., et Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39-54.

Drake, J. M. (2005). Population effects of increased climate variation. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1574), 1823–1827. https://doi.org/10.1098/rspb.2005.3148

Estay, S. A., Lima, M., et Bozinovic, F. (2014). The role of temperature variability on insect performance and population dynamics in a warming world. *Oikos*, *123*(2), 131–140. https://doi.org/10.1111/j.1600-0706.2013.00607.x

Etterson, J. R., et Shaw, R. G. (2001). Constraint to adaptive evolution in response to global warming. *Science*, *294*(5540), 151–154.

Faldyn, M. J., Hunter, M. D., et Elderd, B. D. (2018). Climate change and an invasive, tropical milkweed: An ecological trap for monarch butterflies. *Ecology*, *99*(5), 1031–1038. https://doi.org/10.1002/ecy.2198

Fatouros, N. E., Dicke, M., Mumm, R., Meiners, T., et Hilker, M. (2008). Foraging behavior of egg parasitoids exploiting chemical information. *Behavioral Ecology*, *19*(3), 677–689. https://doi.org/10.1093/beheco/arn011

Fauvergue, X., Lo Genco, A., et Lo Pinto, M. (2008). Virgins in the wild: Mating status affects the behavior of a parasitoid foraging in the field. *Oecologia*, *156*(4), 913–920. https://doi.org/10.1007/s00442-008-1037-7

Fink, U., et Völkl, W. (1995). The effect of abiotic factors on foraging and oviposition success of the aphid parasitoid, Aphidius rosae. *Oecologia*, *103*(3), 371–378.

Fischbein, D., Villacide, J. M., De La Vega, G., et Corley, J. C. (2018). Sex, life history and morphology drive individual variation in flight performance of an insect parasitoid: Variation in flight performance of a parasitoid wasp. *Ecological Entomology*, *43*(1), 60–68. https://doi.org/10.1111/een.12469

Flores, G. B., et Lazzari, C. R. (1996). The role of the antennae in *Triatoma infestans*: orientation towards thermal sources. *Journal of insect physiology*, *42*(5), 433-440.

Folguera, G., Bastías, D. A., Caers, J., Rojas, J. M., Piulachs, M.-D., Bellés, X., et Bozinovic, F. (2011). An experimental test of the role of environmental temperature variability on ectotherm molecular, physiological and life-history traits: Implications for global warming. *Comparative Biochemistry and Physiology Part A: Molecular et Integrative Physiology*, *159*(3), 242–246. https://doi.org/10.1016/j.cbpa.2011.03.002

Fournier, F., et Boivin, G. (2000). Comparative dispersal of *Trichogramma evanescens* and Trichogramma pretiosum (Hymenoptera: Trichogrammatidae) in relation to environmental conditions. *Environmental Entomology*, *29*(1), 55–63.

Furlong, M. J., et Zalucki, M. P. (2017). Climate change and biological control: The consequences of increasing temperatures on host–parasitoid interactions. *Current Opinion in Insect Science*, *20*, 39–44. https://doi.org/10.1016/j.cois.2017.03.006

Gibbs, A. G. (2002). Lipid melting and cuticular permeability: New insights into an old problem. *Journal of Insect Physiology*, *48*(4), 391–400. https://doi.org/10.1016/S0022-1910(02)00059-8

Gibbs, A. G., Louie, A. K., et Ayala, J. A. (1998). Effects of temperature on cuticular lipids and water balance in desert drosophila: Is thermal acclimation beneficial ? *Journal of Experimental Biology*, *201*(1), 71–80.

Goldansaz, S. H., et McNeil, J. N. (2006). Effect of wind speed on the pheromone-mediated behavior of sexual morphs of the potato aphid, *Macrosiphum euphorbiae* (Thomas) under laboratory and field conditions. *Journal of Chemical Ecology*, *32*(8), 1719–1729. https://doi.org/10.1007/s10886-006-9104-1

González-Tokman, D., Córdoba-Aguilar, A., Dáttilo, W., Lira-Noriega, A., Sánchez-Guillén, R. A., et Villalobos, F. (2020). Insect responses to heat: physiological mechanisms, evolution and ecological implications in a warming world. *Biological Reviews*, *95*(3), 802-821.

Goss-Custard, J. D., Caldow, R. W. G., Clarke, R. T., et West, A. D. (1995). Deriving population parameters from individual variations in foraging behaviour. II. Model tests and population parameters. *Journal of Animal Ecology*, 277-289.

Graham, R. W., et Grimm, E. C. (1990). Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology et Evolution*, *5*(9), 289–292.

Greenfield, M. D., et Medlock, C. (2007). Temperature coupling as an emergent property: Parallel thermal effects on male song and female response do not contribute to species recognition in an acoustic moth. *Evolution*, *61*(7), 1590–1599. https://doi.org/10.1111/j.1558-5646.2007.00140.x

Grimm-Seyfarth, A., Mihoub, J.-B., Gruber, B., et Henle, K. (2018). Some like it hot: From individual to population responses of an arboreal arid-zone gecko to local and distant climate. *Ecological*

Monographs, *88*(3), 336–352. https://doi.org/10.1002/ecm.1301

Gu, H., et Dorn, S. (2000). Genetic variation in behavioral response to herbivore-infested plants in the parasitic wasp, *Cotesia glomerata* (L.) (Hymenoptera: Braconidae). *Journal of Insect Behavior*, *13*(1), 141–156.

Hallman, G. J., et Denlinger, D. L. (1998). *Temperature sensitivity in insects and application in integrated pest management*.

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D., et de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE*, *12*(10), e0185809. https://doi.org/10.1371/journal.pone.0185809

Hamel, S., Côté, S. D., Gaillard, J. M., et Festa-Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: High-quality females always do better. *Journal of Animal Ecology*, *78*(1), 143-151.

Hance, T., van Baaren, J., Vernon, P., et Boivin, G. (2007). Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology*, *52*(1), 107–126. https://doi.org/10.1146/annurev.ento.52.110405.091333

Harmon, J. P., et Barton, B. T. (2013). On their best behavior: How animal behavior can help determine the combined effects of species interactions and climate change. *Annals of the New York Academy of Sciences*, *1297*(1), 139–147. https://doi.org/10.1111/nyas.12192

Harrington, R., Fleming, R. A., et Woiwod, I. P. (2001). Climate change impacts on insect management and conservation in temperate regions: Can they be predicted? *Agricultural and Forest Entomology*, *3*(4), 233–240. https://doi.org/10.1046/j.1461-9555.2001.00120.x

Harvey, J. A., Poelman, E. H., et Tanaka, T. (2013). Intrinsic inter- and intraspecific competition in parasitoid wasps. *Annual Review of Entomology*, *58*(1), 333–351. https://doi.org/10.1146/annurev-ento-120811-153622

Hawkes, C. (2009). Linking movement behaviour, dispersal and population processes: is individual variation a key?. *Journal of Animal Ecology*, *78*(5), 894-906.

Heimpel, G. E. (2019). Linking parasitoid nectar feeding and dispersal in conservation biological control. *Biological Control*, *132*, 36–41. https://doi.org/10.1016/j.biocontrol.2019.01.012

Herrera, C. M., et Bazaga, P. (2011). Untangling individual variation in natural populations: ecological, genetic and epigenetic correlates of long-term inequality in herbivory. *Molecular ecology*, *20*(8), 1675-1688. https://doi.org/10.1111/j.1365-2435.2012.02036.x

Hoffmann, A. A., Chown, S. L., et Clusella-Trullas, S. (2013). Upper thermal limits in terrestrial ectotherms: How constrained are they? *Functional Ecology*, *27*(4), 934–949.

Hoffmann, A. A., et Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, *470*(7335), 479–485. https://doi.org/10.1038/nature09670

Holway, D. A., et Suarez, A. V. (1999). Animal behavior: An essential component of invasion biology. *Trends in Ecology et Evolution*, *14*(8), 328–330. https://doi.org/10.1016/S0169-5347(99)01636-5

Howard, R. W., et Blomquist, G. J. (2005). Ecological, behavioral, and biochemical aspects of insect hydrocarbons. *Annual Review of Entomology*, *50*(1), 371–393. https://doi.org/10.1146/annurev.ento.50.071803.130359

Huey, R. B., et Tewksbury, J. J. (2009). Can behavior douse the fire of climate warming? *Proceedings of the National Academy of Sciences*, *106*(10), 3647–3648. https://doi.org/10.1073/pnas.0900934106

Huey, Raymond B., Deutsch, C. A., Tewksbury, J. J., Vitt, L. J., Hertz, P. E., Álvarez Pérez, H. J., et Garland, T. (2009). Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1664), 1939–1948. https://doi.org/10.1098/rspb.2008.1957

Iltis, C., Louâpre, P., Pecharová, K., Thiéry, D., Zito, S., Bois, B., et Moreau, J. (2019). Are life-history traits equally affected by global warming? A case study combining a multi-trait approach with fine-grain climate modeling. *Journal of Insect Physiology*, *117*, 103916. https://doi.org/10.1016/j.jinsphys.2019.103916

Ives, A. R. (1995). Spatial heterogeneity and host-parasitoid population dynamics: Do we need to study behavior? *Oikos*, *74*(3), 366–376. https://doi.org/10.2307/3545981

Jager, H. I. (2001). Individual variation in life history characteristics can influence extinction risk. *Ecological modelling*, *144*(1), 61-76.

Jeanson, R., et Weidenmüller, A. (2014). Interindividual variability in social insects–proximate causes and ultimate consequences. *Biological Reviews*, *89*(3), 671-687.

Jocson, D. M. I., Smeester, M. E., Leith, N. T., Macchiano, A., et Fowler-Finn, K. D. (2019). Temperature coupling of mate attraction signals and female mate preferences in four populations of *Enchenopa treehopper* (Hemiptera: Membracidae). *Journal of evolutionary biology*, *32*(10), 1046-1056.

Johansson, B. G., et Jones, T. M. (2007). The role of chemical communication in mate choice. *Biological Reviews*, *82*(2), 265–289. https://doi.org/10.1111/j.1469-185X.2007.00009.x

Johnson, J. A., Valero, K. A., Wang, S., et Tang, J. (2004). Thermal death kinetics of red flour beetle (Coleoptera: Tenebrionidae). *Journal of Economic Entomology*, *97*(6), 1868–1873.

Johnson, S. N., et Züst, T. (2018). Climate change and insect pests: Resistance is not futile? *Trends in Plant Science*, *23*(5), 367–369. https://doi.org/10.1016/j.tplants.2018.03.001

Jones, T. H. (1998). Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science*, *280*(5362), 441–443. https://doi.org/10.1126/science.280.5362.441

Kellermann, V., Hoffmann, A. A., Overgaard, J., Loeschcke, V., et Sgrò, C. M. (2018). Plasticity for desiccation tolerance across *Drosophila* species is affected by phylogeny and climate in complex ways. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1874), 20180048. https://doi.org/10.1098/rspb.2018.0048

Kellermann, V., et Sgrò, C. M. (2018). Evidence for lower plasticity in CT $_{\text{MAX}}$ at warmer developmental temperatures. *Journal of Evolutionary Biology*, *31*(9), 1300–1312. https://doi.org/10.1111/jeb.13303

Kellermann, V., et van Heerwaarden, B. (2019). Terrestrial insects and climate change: Adaptive responses in key traits. *Physiological Entomology*, *44*(2), 99–115. https://doi.org/10.1111/phen.12282

Kerkut, G. A., et Taylor, B. J. R. (1958). The effect of temperature changes on the activity of poikilotherms. *Behaviour*, *13*(3), 259–279.

Kingsolver, J. G. (2009). The well-temperatured biologist: (American Society of Naturalists Presidential Address). *The American Naturalist*, *174*(6), 755–768. https://doi.org/10.1086/648310

Koltz, A. M., Schmidt, N. M., et Høye, T. T. (2018). Differential arthropod responses to warming are altering the structure of Arctic communities. *Royal Society Open Science*, *5*(4), 171503.

Kruidhof, H. M., Kostenko, O., Smid, H. M., et Vet, L. E. M. (2019). Integrating parasitoid olfactory conditioning in augmentative biological control: Potential impact, possibilities, and challenges. *Frontiers in Ecology and Evolution*, *7*(84). https://doi.org/10.3389/fevo.2019.00084

Ladányi, M., et Horváth, L. (2010). A review of the potential climate change impact on insect populations—General and agricultural aspects. *Applied Ecology and Environmental Research*, *8*(2), 143–151. https://doi.org/10.15666/aeer/0802_143151

Laws, A. N. (2017). Climate change effects on predator–prey interactions. *Current opinion in insect science*, *23*, 28-34.

Lehmann, P., Ammunét, T., Barton, M., Battisti, A., Eigenbrode, S. D., Jepsen, J. U., Kalinkat, G., Neuvonen, S., Niemelä, P., Økland, B., Terblanche, J. S., et Björkman, C. (2018). *Complex responses of global insect pests to climate change* [Preprint]. Ecology. https://doi.org/10.1101/425488

Lemoine, N. P., Burkepile, D. E., et Parker, J. D. (2014). Variable effects of temperature on insect herbivory. *PeerJ*, *2*, e376. https://doi.org/10.7717/peerj.376

Levin, P. S. (2000). Integrating individual behavior and population ecology: The potential for habitat-dependent population regulation in a reef fish. *Behavioral Ecology*, *11*(5), 565–571. https://doi.org/10.1093/beheco/11.5.565

Macdonald, S. L., Llewelyn, J., Moritz, C., et Phillips, B. L. (2017). Peripheral isolates as sources of adaptive diversity under climate change. *Frontiers in Ecology and Evolution*, *5*. https://doi.org/10.3389/fevo.2017.00088

Macfadyen, S., McDonald, G., et Hill, M. P. (2018). From species distributions to climate change adaptation: knowledge gaps in managing invertebrate pests in broad-acre grain crops. *Agriculture, ecosystems & environment*, *253*, 208-219.

Marchand, D., et McNeil, J. N. (2000). Effects of wind speed and atmospheric pressure on mate searching behavior in the aphid parasitoid Aphidius nigripes (Hymenoptera: Aphidiidae). *Journal of Insect Behavior*, *13*(2), 187–199.

Matthews, R. W., et Matthews, J. R. (2009). The history and scope of insect behavior. In *Insect Behavior* (pp. 1-44). Springer, Dordrecht.

McClure, M., Whistlecraft, J., et McNeil, J. N. (2007). Courtship behavior in relation to the female sex pheromone in the parasitoid, *Aphidius ervi* (Hymenoptera: Braconidae). *Journal of Chemical Ecology*, *33*(10), 1946–1959. https://doi.org/10.1007/s10886-007-9355-5

McDonough, L. M., Brown, D. F., et Aller, W. C. (1989). Insect sex pheromones. *Journal of chemical ecology*, *15*(3), 779-790.

McNeil, J N. (1991). Behavioral ecology of pheromone-mediated communication in moths and its importance in the use of pheromone traps. *Annual Review of Entomology*, *36*(1), 407–430.

McNeil, J. N., et Brodeur, J. (1995). Pheromone-mediated mating in the aphid parasitoid, *Aphidius nigripes* (Hymenoptera: Aphididae). *Journal of Chemical Ecology*, *21*(7), 959–972.

Metzger, M. (2008). *Rôle de l'information dans l'acquisition des partenaires sexuels et le choix du sexe de la descendance chez les hyménoptères parasitoïdes–Exemple de Venturia Canescens Gravenhorst (Hymenoptera: Ichneumonidae)* [PhD Thesis]. Université Claude Bernard-Lyon I.

Mills, N. J., et Heimpel, G. E. (2018). Could increased understanding of foraging behavior help to predict the success of biological control? Current Opinion in Insect Science, 27, 26–31. https://doi.org/10.1016/j.cois.2018.02.013

Minkenberg, O. P. J. M., Tatar, M., et Rosenheim, J. A. (1992). Egg load as a major source of variability in insect foraging and oviposition behavior. *Oikos*, *65*(1), 134–142. https://doi.org/10.2307/3544896

Molina-Montenegro, M.A., Briones, R., et Cavieres, L.A. (2009). Does global warming induce segregation among alien and native beetle species in a mountain-top*? Ecological Research*, 24(1), 31-36.

Nolan, C., Overpeck, J. T., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., Dodson, J., Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Huntley, B., Ivory, S. J., Kershaw, A. P., … Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Science*, 361(6405), 920–923. https://doi.org/10.1126/science.aan5360

Nurme, K., Must, A., et Merivee, E. (2019). Link between elevated locomotor activity and the spike bursting of antennal thermosensitive neurons in the carabid beetle *Pterostichus oblongopunctatus*. *Acta Zoologica Academiae Scientiarum Hungaricae*, *65*(Suppl), 21–31. https://doi.org/10.17109/AZH.65.Suppl.21.2019

Olsson, S. B., et Hansson, B. S. (2013). Electroantennogram and single sensillum recording in insect antennae. In *Pheromone Signaling* (pp. 157-177). Humana Press, Totowa, NJ.

Ouranos. (2010). *Savoir s'adapter aux changements climatiques*. Ouranos. http://collections.banq.qc.ca/ark:/52327/2052216

Ouranos (2015). Vers l'adaptation. Synthèse des connaissances sur les changements climatiques au Québec. Partie 1 : Évolution climatique au Québec. Édition 2015. Montréal, Québec : Ouranos, 114 p.

Paaijmans, K. P., Heinig, R. L., Seliga, R. A., Blanford, J. I., Blanford, S., Murdock, C. C., et Thomas, M. B. (2013). Temperature variation makes ectotherms more sensitive to climate change. *Global Change Biology*, *19*(8), 2373–2380. https://doi.org/10.1111/gcb.12240

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *3*, 637–669.

Parmesan, C., Root, T. L., et Willig, M. R. (2000). Impacts of extreme weather and climate on terrestrial biota *. *Bulletin of the American Meteorological Society*, *81*(3), 443–450. https://doi.org/10.1175/1520-0477(2000)081

Prosser, C. L., et Nelson, D. O. (1981). The role of nervous systems in temperature adaptation of poikilotherms. *Annual Review of Physiology*, *43*(1), 281–300. https://doi.org/10.1146/annurev.ph.43.030181.001433

Quintero, I., et Wiens, J. J. (2013). Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. *Ecology Letters*, *16*(8), 1095–1103. https://doi.org/10.1111/ele.12144

Ramirez-Romero, R., Sivinski, J., Copeland, C. S., et Aluja, M. (2012). Are individuals from thelytokous and arrhenotokous populations equally adept as biocontrol agents? Orientation and host searching behavior of a fruit fly parasitoid. *BioControl*, *57*(3), 427–440. https://doi.org/10.1007/s10526-011-9413-3

Reddy, G. V. P., Holopainen, J. K., et Guerrero, A. (2002). Olfactory responses of *Plutella xylostella* natural enemis to host pheromone, larval frass, and green leaf cabbage volatiles. *Journal of Chemical Ecology*, *28*(1), 131–143.

Reed, T. E., Schindler, D. E., et Waples, R. S. (2011). Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate: Evolution, plasticity, and climate change. *Conservation Biology*, *25*(1), 56–63. https://doi.org/10.1111/j.1523-1739.2010.01552.x

Ritchie, M. G., Saarikettu, M., Livingstone, S., et Hoikkala, A. (2001). Characterization of female preference functions for *Drosophila montana* courtship song and a test of the temperature coupling hypothesis. *Evolution*, *55*(4), 721–727.

Riveron, J., Boto, T., et Alcorta, E. (2009). The effect of environmental temperature on olfactory perception in Drosophila melanogaster. *Journal of Insect Physiology*, *55*(10), 943–951. https://doi.org/10.1016/j.jinsphys.2009.06.009

Roberts, L. (1988). Is there life after climate change? *Science*, *242*(4881), 1010–1012. https://doi.org/10.1126/science.242.4881.1010

Robertson, R. M. (2004a). Thermal stress and neural function: Adaptive mechanisms in insect model systems. *Journal of Thermal Biology*, *29*(7–8), 351–358. https://doi.org/10.1016/j.jtherbio.2004.08.073

Robertson, R. M. (2004b). Modulation of neural circuit operation by prior environmental stress. *Integrative and Comparative Biology*, *44*(1), 21-27.

Robertson, R. M., et Money, T. G. (2012). Temperature and neuronal circuit function: compensation, tuning and tolerance. *Current opinion in neurobiology*, *22*(4), 724-734.

Rohr, J. R., et Palmer, B. D. (2013). Climate change, multiple stressors, and the decline of ectotherms. *Conservation Biology*, *27*(4), 741-751.

Romo, C. M., et Tylianakis, J. M. (2013). Elevated temperature and drought interact to reduce parasitoid effectiveness in suppressing hosts. *PLoS ONE*, *8*(3), e58136. https://doi.org/10.1371/journal.pone.0058136

Rosenheim, J. A., et Rosen, D. (1991). Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: Distinguishing the influences of egg load and experience. *The Journal of Animal Ecology*, *60*(3), 873. https://doi.org/10.2307/5419

Roth, S. K., et Lindroth, R. L. (1995). Elevated atmospheric CO2: Effects on phytochemistry, insect performance and insect-parasitoid interactions. *Global Change Biology*, *1*(3), 173–182. https://doi.org/10.1111/j.1365-2486.1995.tb00019.x

Ruther, J., Döring, M., et Steiner, S. (2011). Cuticular hydrocarbons as contact sex pheromone in the parasitoid

Dibrachys cavus. *Entomologia Experimentalis et Applicata*, *140*(1), 59–68. https://doi.org/10.1111/j.1570-7458.2011.01129.x

Samways, M. J., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kaila, L., Kwak, M. L., Maes, D., Mammola, S., Noriega, J. A., Orfinger, A. B., Pedraza, F., … Cardoso, P. (2020). Solutions for humanity on how to conserve insects. *Biological Conservation*, *242*, 108427. https://doi.org/10.1016/j.biocon.2020.108427

Sánchez-Bayo, F., et Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, *232*, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Schott, M., Wehrenfennig, C., Gasch, T., et Vilcinskas, A. (2013). Insect antenna-based biosensors for in situ detection of volatiles. In *Yellow Biotechnology II* (pp. 101-122). Springer, Berlin, Heidelberg.

Sentis, A., Ramon-Portugal, F., Brodeur, J., et Hemptinne, J.-L. (2015). The smell of change: Warming affects species interactions mediated by chemical information. *Global Change Biology*, *21*(10), 3586–3594. https://doi.org/10.1111/gcb.12932

Sergio, F., Blas, J., et Hiraldo, F. (2018). Animal responses to natural disturbance and climate extremes: A review. *Global and Planetary Change*, *161*, 28–40. https://doi.org/10.1016/j.gloplacha.2017.10.009

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, *85*(5), 1077–1088. https://doi.org/10.1016/j.anbehav.2013.02.017

Sih, A., Ferrari, M. C. O., et Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change: Behaviour and evolution. *Evolutionary Applications*, *4*(2), 367–387. https://doi.org/10.1111/j.1752-4571.2010.00166.x

Sih, A., Trimmer, P. C., et Ehlman, S. M. (2016). A conceptual framework for understanding behavioral responses to HIREC. *Current Opinion in Behavioral Sciences*, *12*, 109–114. https://doi.org/10.1016/j.cobeha.2016.09.014

Singer, T. L. (1998). Roles of hydrocarbons in the recognition systems of insects. *American Zoologist*, *38*(2), 394–405.

Soto-Padilla, A., Ruijsink, R., Sibon, O. C. M., van Rijn, H., et Billeter, J.-C. (2018). Thermosensory perception regulates speed of movement in response to temperature changes in *Drosophila melanogaster*. *The Journal of Experimental Biology*, *221*(10), jeb174151. https://doi.org/10.1242/jeb.174151

Stange, G. (1997). Effects of changes in atmospheric carbon dioxide on the location of hosts by the moth, Cactoblastis cactorum. *Oecologia*, *110*(4), 539–545. https://doi.org/10.1007/s004420050192

Steiner, S., Hermann, N., & Ruther, J. (2006). Characterization of a female-produced courtship pheromone in the parasitoid *Nasonia vitripennis*. *Journal of chemical ecology*, *32*(8), 1687-1702.

Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M. M. B., Allen, S. K., Boschung, J., Naeuls, A., Xia, Y., Bex, V., et Midgley, P. M. (2013). *Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*.

Struelens, Q., Rebaudo, F., Quispe, R., et Dangles, O. (2018). Thermal pace-of-life strategies improve phenological predictions in ectotherms. *Scientific reports*, *8*(1), 1-9.

Svenning, J.-C. (2003). Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora: Deterministic Plio-Pleistocene extinctions. *Ecology Letters*, *6*(7), 646–653. https://doi.org/10.1046/j.1461-0248.2003.00477.x

Tenhumberg, B. (2004). *Predicting predation efficiency of biocontrol agents: Linking behavior of individuals and population dynamics*. 2nd international congress on environmental modelling and software, Osnabrück, Germany.

Thacker, J. I., Thieme, T., et Dixon, A. F. G. (1997). Forecasting of periodic fluctuations in annual abundance of the bean aphid: The role of density dependence and weather. *Journal of Applied Entomology*, *121*(1–5), 137–145. https://doi.org/10.1111/j.1439-0418.1997.tb01383.x

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Peterson, A. T., Phillips, O. L., et Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145–148.

Thomson, L. J., Macfadyen, S., et Hoffmann, A. A. (2010). Predicting the effects of climate change on natural enemies of agricultural pests. *Biological Control*, *52*(3), 296–306. https://doi.org/10.1016/j.biocontrol.2009.01.022

Tougeron, K., Brodeur, J., Le Lann, C., et van Baaren, J. (2019). How climate change affects the seasonal ecology of insect parasitoids. *Ecological Entomology*. https://doi.org/10.1111/een.12792

Tuomainen, U., et Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, *86*(3), 640–657. https://doi.org/10.1111/j.1469-185X.2010.00164.x

van Baaren, J., Boivin, G., et Outreman, Y. (2005a). Patch exploitation strategy by an egg parasitoid in constant or variable environment. *Ecological Entomology*, *30*(5), 502–509. https://doi.org/10.1111/j.0307-6946.2005.00718.x

van Baaren, J., Outreman, Y., et Boivin, G. (2005b). Effect of low temperature exposure on oviposition behaviour and patch exploitation strategy in parasitic wasps. *Animal Behaviour*, *70*(1), 153–163. https://doi.org/10.1016/j.anbehav.2004.10.016

van Baaren, J., Boivin, G., et Outreman, Y. (2006). Deleterious effects of low temperature exposure on learning expression in a parasitoid. *International Journal of Comparative Psychology*, *19*(3). https://escholarship.org/uc/item/1nz635w3.pdf

Van Dyck, H., Bonte, D., Puls, R., Gotthard, K., et Maes, D. (2015). The lost generation hypothesis: Could climate change drive ectotherms into a developmental trap? *Oikos*, *124*(1), 54–61. https://doi.org/10.1111/oik.02066

Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., Savage, V., Tunney, T. D., et O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20132612. https://doi.org/10.1098/rspb.2013.2612

Vet, L. E. (2001). Parasitoid searching efficiency links behaviour to population processes. *Applied Entomology and Zoology*, *36*(4), 399-408.

Vinson, S. B. (1976). Host selection by insect parasitoids. *Annual Review of Entomology*, *21*(1), 109–133.

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1635), 649–659. https://doi.org/10.1098/rspb.2007.0997

Wajnberg, É. (2006). Time allocation strategies in insect parasitoids: From ultimate predictions to proximate behavioral mechanisms. *Behavioral Ecology and Sociobiology*, *60*(5), 589–611. https://doi.org/10.1007/s00265-006-0198-9

Wajnberg, E., Rosi, M. C., et Colazza, S. (1999). Genetic variation in patch time allocation in a parasitic wasp. *Journal of Animal Ecology*, *68*(1), 121–133.

Walker, T. J. (1975). Effects of temperature on rates in poikilotherm nervous systems: evidence from the calling songs of meadow katydids (Orthoptera: Tettigoniidae: Orchelimum) and reanalysis of published data. *Journal of Comparative Physiology*, *101*(1), 57-69.

Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., et Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PloS One*, *14*.

Widemo, F., et Sæther, S. A. (1999). Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends in Ecology & Evolution*, *14*(1), 26-31.

Wilf, P., et Labandeira, C. C. (1999). Response of plant-insect associations to Paleocene-Eocene warming. *Science*, *284*(5423), 2153–2156.

Wong, B. B. M., et Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, *26*(3), 665–673. https://doi.org/10.1093/beheco/aru183

Woods, H. A., Dillon, M. E., et Pincebourde, S. (2015). The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *Journal of Thermal Biology*, *54*, 86–97. https://doi.org/10.1016/j.jtherbio.2014.10.002

Yuan, J. S., Himanen, S. J., Holopainen, J. K., Chen, F., et Stewart, C. N. (2009). Smelling global climate change: Mitigation of function for plant volatile organic compounds. *Trends in Ecology et Evolution*, *24*(6), 323–331. https://doi.org/10.1016/j.tree.2009.01.012

Zhu, H., Thistle, H. W., Ranger, C. M., Zhou, H., et Strom, B. L. (2015). Measurement of semiochemical release rates with a dedicated environmental control system. *Biosystems Engineering*, *129*, 277–287. https://doi.org/10.1016/j.biosystemseng.2014.11.003

Zhu, L., Wang, L., et Ma, C.-S. (2019). Sporadic short temperature events cannot be neglected in predicting impacts of climate change on small insects. *Journal of Insect Physiology*, *112*, 48–56. https://doi.org/10.1016/j.jinsphys.2018.12.003