

Université de Montréal

La vigilance chez le moineau domestique : l'avertissement mutuel et la variation individuelle

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Résumé

Ce mémoire se concentre sur les avantages de la vie en groupe au niveau de la diminution du risque de prédation. L'introduction aborde les différents mécanismes d'anti-prédation tels que l'effet de dilution, l'effet de confusion et l'avertissement mutuel. Par la suite, la vigilance et les différents facteurs qui l'influencent sont expliqués. Une attention particulière est portée à l'effet de la taille du groupe et une des raisons pour laquelle celui-ci pourrait varier : la personnalité. Finalement, une brève description de l'espèce à l'étude, le moineau domestique, *Passer domesticus*, est présentée.

Le deuxième chapitre évalue l'efficacité de l'avertissement mutuel chez les espèces sans cri d'alarme à l'aide des temps de réaction (intervalle de temps entre les vols successifs causés par des alarmes). Trois facteurs semblent les influencer : la taille du groupe, l'étalement du groupe et le risque de prédation. Nos résultats montrent des temps de réaction plus courts chez les grands groupes. De plus, durant des périodes de haut risque, les moineaux sont plus proches les uns des autres et ont des temps de réaction raccourcis, ce qui suggère une adaptation permettant de diminuer le risque de prédation.

Le troisième chapitre évalue la présence de profils individuels de vigilance ainsi que la capacité d'adaptation (plasticité) des individus lorsque la taille du groupe varie. Nos résultats montrent une capacité d'adaptation et des profils de vigilance différents pour les 14 individus bagués, ce qui suggère que la vigilance et sa plasticité sont un possible trait de personnalité. L'établissement et le maintien de ce trait sont probablement causés par l'état de l'individu (âge). Ainsi, les individus plus âgés passent moins de temps vigilants.

La discussion générale aborde les découvertes faites par les deux projets ainsi que, brièvement, l'importance de l'éthologie en médecine vétérinaire. La conclusion résume les points saillants de ce mémoire.

Mots clés : avertissement mutuel, moineau domestique, plasticité, taille des groupes, trait de personnalité, vigilance

Abstract

This thesis elaborates on the advantages of group living especially with respect to its effect on predation risk. The introduction summarizes anti-predator mechanisms such as the dilution effect, confusion effect and collective detection. The drivers of vigilance are presented with the emphasis on the effect of group size. Animal personality and plasticity are also reviewed as they might explain why the relationship between vigilance and group size appears so heterogeneous. A brief description of the house sparrow (*Passer domesticus*) is provided because all our predictions were tested with this species.

The second chapter examines the occurrence of collective detection in animals without alarm calls by using reaction times (the time it takes to react to the alarm of a companion). Three factors influenced the spread of alarm in flocks of house sparrows: group size, inter-individual distances and predation risk. Our results showed faster reaction times in larger groups. Furthermore, in high-risk situations, sparrows remained in close proximity and adopted shorter reaction times.

The third chapter evaluates individual profiles of vigilance and plasticity when group size varies. Our results showed evidence for individual vigilance profiles and for plasticity in response to variation in flock size in the 14 banded individuals. Adjustments in vigilance brought by variation in the state of an individual (e.g. age) might explain the presence of individuality in sparrows' vigilance.

The general discussion summarizes our findings and emphasizes the importance of ethology in veterinary medicine.

Key words: animal personality, collective detection, group size, house sparrow, plasticity, vigilance

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Liste des sigles et des abréviations

HB-M : Hakima Boujja Miljour

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Chapitre 1 : Revue de littérature

Introduction

L'éthologie désigne l'ensemble des recherches sur le comportement animal (Giraldeau & Dubois 2009). Tinbergen, un des biologistes ayant marqué l'histoire de l'éthologie, propose quatre questions permettant de mieux comprendre le comportement animal : la cause proximale, l'ontogenèse, la phylogenèse et la cause fonctionnelle liée à la survie (Giraldeau & Dubois 2009; Bateson & Laland 2013). Ces questions permettent d'avoir une vision complète des facteurs importants déclenchant un comportement, de son développement chez l'individu, de son développement chez l'espèce et de l'importance de celui-ci pour la survie de l'individu. Encore de nos jours, les quatre questions de Tinbergen guident les biologistes dans leur recherche.

Un des sujets grandement étudiés en éthologie est la vie en groupe. Dans la nature, il est possible d'observer des espèces qui vivent en très grands groupes pendant toute l'année comme la bernache du Canada (*Branta canadensis*) mais aussi des espèces beaucoup plus solitaires comme le faucon pèlerin (*Falco peregrinus*) qui ne sont en groupes que pendant la saison de reproduction. Mais alors, pourquoi retrouve-t-on des espèces grégaires et d'autres plus solitaires? Quels sont les avantages présentés par la vie en groupe ? Plusieurs études ont démontré que la vie en groupe apporte des bénéfices en lien à l'exploitation des ressources (ex. meilleure détection et défense des ressources) (Beauchamp 2014), mais aussi au risque de prédation. Ce mémoire cible les mécanismes permettant la diminution

du taux de prédation au sein d'un groupe, particulièrement chez le moineau domestique (*Passer domesticus*), l'espèce à l'étude.

Les mécanismes d'anti-prédation

Il y a plusieurs éléments qui contribuent à la diminution du taux de prédation d'un individu dans un groupe, dont l'effet de confusion, l'effet de dilution, l'effet de détection et l'avertissement mutuel.

Lorsqu'un prédateur attaque plusieurs individus en même temps, ayant chacun différentes vitesses et trajectoires, il devient plus difficile de cibler une proie en particulier (Giraldeau & Dubois 2009). C'est ce que l'on définit par l'effet de confusion. Il suffit d'essayer d'attraper une mouche seule volant dans les airs par rapport à une mouche dans un nuage d'individus pour l'expérimenter : la tâche devient beaucoup plus difficile lorsque la mouche est dans un groupe. Le système neuronal pourrait avoir de la difficulté à analyser la répartition spatiale de plusieurs proies à la fois expliquant cet effet (Krakauer 1995; Loannou et coll. 2007). L'effet de confusion a été observé entre autres chez les oiseaux, les reptiles et les mammifères (Cresswell 1994; Schradin 2000).

L'effet de dilution représente la diminution de la probabilité d'être attaqué lorsque la taille du groupe augmente (Bertram 1978). De façon simplifiée, plus la taille du groupe augmente, plus les chances qu'un individu en particulier soit ciblé par un prédateur sont moindres. Cependant, cela sous-entend que le prédateur ne peut capturer qu'une seule proie à la fois et que tous les individus ont la même chance d'être ciblés (Treves 2000). Évidemment, cela n'est pas toujours le cas, car il y a différentes composantes qui peuvent

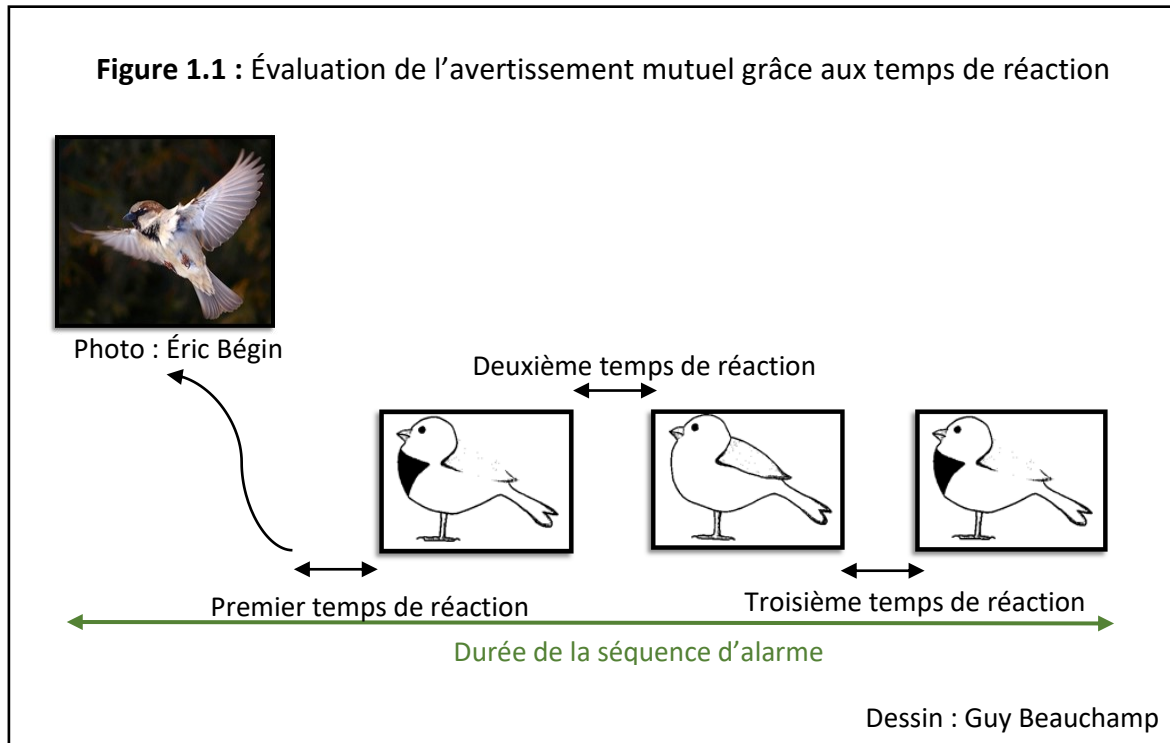
augmenter le risque de prédation pour un individu. Cela sera approfondi dans la section vigilance de cette introduction. Néanmoins, plusieurs études ont démontré l'importance de l'effet de dilution dans le règne animal (Cresswell 1994; Hebblewhite & Pletscher 2002).

Lorsque la taille du groupe augmente, il y a plus de yeux et d'oreilles disponibles pour la détection d'un prédateur. Ainsi, il y a plus de chance qu'un prédateur soit détecté rapidement (Caraco et coll. 1980a). Cela devient d'autant plus avantageux pour le reste du groupe lorsque l'individu ayant détecté le prédateur prévient les autres congénères du danger (Lima 1996). Cela est défini respectivement par la détection hâtive et l'avertissement mutuel.

Ce transfert d'information à travers le groupe peut se faire de différentes façons. Chez les suricates (*Suricata suricatta*), par exemple, un système élaboré de différents cris d'alarme permet d'avertir les autres membres du groupe d'un danger imminent (Manser et coll. 2001). Le message de menace peut également se faire de façon beaucoup plus subtile. Par exemple, chez le kangourou géant (*Macropus giganteus*), un changement de posture chez l'individu ayant détecté le prédateur permet d'informer les autres membres du groupe (Pays et coll. 2013). Cependant, chez beaucoup d'espèces d'oiseaux, il ne semble pas y avoir de signaux clairs comme un cri d'alarme permettant le transfert d'information dans le groupe. À vrai dire, le seul élément permettant d'avertir les autres membres du groupe est le départ hâtif de l'individu qui vient de détecter un danger. Alors, comment les oiseaux font-ils pour différencier entre un départ causé par un danger imminent et un départ causé

par d'autres raisons comme la satiété ? Est-ce que l'avertissement mutuel peut réellement être efficace dans de telles situations?

Afin de vérifier l'efficacité de l'avertissement mutuel chez ces espèces, les séquences d'alarme peuvent être mesurées. Une séquence d'alarme comporte une série d'envols successifs dans tout le groupe suite à la détection du danger par un individu (**Figure 1.1**). Par la suite, il est possible de mesurer les temps de réaction, c'est-à-dire le temps écoulé entre l'envol de chaque individu (**Figure 1.1**).



Cet ajout permet de constater les différentes tendances dans le transfert d'information entre les premiers envols et les derniers du groupe. Ainsi, on devrait s'attendre à observer des temps de réaction courts lorsque l'avertissement mutuel est efficace et donc obtenir des bénéfices reliés à la diminution du risque de prédation. Comme

la prédation ne s'observe pas très souvent, il est quand même possible d'étudier les temps de réaction mais dans des situations de fausses alarmes qui sont beaucoup plus fréquentes. Le terme fausse alarme est utilisé lorsqu'il nous est impossible de détecter le danger ayant provoqué l'alarme dans le groupe. L'efficacité de l'avertissement mutuel chez les espèces sans signaux d'alarme sera abordée plus en détails dans le deuxième chapitre de ce mémoire : « Spread of Alarm in Foraging Flocks of House Sparrows ».

La vigilance

La vigilance est définie comme l'action ou l'état de surveillance attentive, sans défaillance, pour un danger potentiel (Beauchamp 2015). Dans le contexte du comportement animal, la vigilance est le temps qu'un individu va être aux aguets pour un danger potentiel. Chez les oiseaux, le pourcentage de temps vigilant est souvent mesuré en fonction de la position du bec (Robinette & Ha 2001). Lorsque le bec est parallèle au sol, l'animal est considéré vigilant et cette séquence s'arrête lorsque le bec s'abaisse plus bas que l'horizontal (**Figure 1.2**) (Lima et coll. 1999). La vigilance est aussi mesurée en fonction de la position de la tête étant donné que beaucoup d'animaux doivent baisser leur tête pour s'approvisionner en nourriture (Tête haute : vigilant / tête baissée : quête de nourriture, Jones 1998; Treves 2000). Ces deux techniques supposent que l'alimentation et la vigilance sont des comportements mutuellement exclusifs (McVean & Haddlesey 1980). Par contre, cela n'est pas toujours le cas. À vrai dire, un animal pourrait être vigilant lorsqu'il se nourrit dépendant du type d'environnement où il s'alimente et du champ visuel propre à l'espèce

(Guillemain et coll. 2001; Fernández-Juricic et coll. 2008). À défaut d'autres techniques, cela reste néanmoins une des méthodes les plus utilisées en comportement animal.

Figure 1.2 : Position du bec lors de l'évaluation du temps vigilant



Individu vigilant, bec en position horizontale

(Photo : Jessica)



Individus non vigilant, bec vers le bas

(Photo : Melvin Yap)

Figure 1.2 : La vigilance est mesurée de différentes façons. Premièrement, il est possible de mesurer le pourcentage de temps alloué à la vigilance. Cela correspond à la durée du temps vigilant de l'animal divisé par le temps où celui-ci a été observé. Ainsi, lorsque l'oiseau a la tête vers le bas et se nourrit, il n'est pas considéré vigilant. La période de temps vigilant commence lorsque l'animal a le bec parallèle au sol (gauche) et se termine lorsque l'animal descend la tête (droite).

La vigilance peut être séparée en deux types : sociale et anti-prédateur (Favreau et coll. 2010). La vigilance anti-prédateur se définit comme le temps qu'un individu reste aux aguets afin de détecter des prédateurs ou dangers potentiels contrairement à la vigilance sociale où l'individu surveille ses congénères. De plus, il y a différents facteurs pouvant faire varier la vigilance anti-prédateur chez un individu (**Tableau 1.1**).

Tableau 1.1 : Facteurs influençant la vigilance individuelle

Facteur	Prédiction	Explication	Références
1. Position dans le groupe	Les individus en périphérie devraient être plus vigilants	Risque de prédation plus élevé	(Fitzgibbon 1990; Keddar et coll. 2009)
2. Taille du groupe	La vigilance diminue lorsque la taille du groupe augmente	Diminution du risque de prédation, compétition pour les ressources	(Beauchamp 2003)
3. Distance entre les individus	Augmentation de la vigilance avec la distance interindividuelle	Lorsque la distance augmente, l'individu ne profite pas autant des mécanismes d'anti-prédation	(Pöysä 1994)
4. Distance jusqu'à l'abri protecteur	La vigilance diminue avec la distance jusqu'à l'abri	Lorsque l'abri est plus loin, une détection plus hâtive est nécessaire afin de fuir le prédateur	(Caraco et coll. 1980b)
5. Visibilité dans l'habitat	Lorsque la visibilité diminue, il y a une augmentation de la vigilance	Une augmentation de la vigilance permet de détecter le prédateur plus rapidement, malgré l'obstruction visuelle	(Burger et coll. 2000)
6. Risque de prédation	Plus vigilant lorsque le risque augmente	Diminuer le risque d'être capturé par le prédateur	(Sharpe & Van Horne 1998)
7. Sexe¹ (varie selon l'espèce et le statut reproducteur)	1. Sexe le plus petit est plus vigilant 2. Mâle plus vigilant	1. Sexe plus imposant doit acquérir plus de ressources 2. Risque de prédation plus élevé, surveille et agresse la femelle	(Mayhew 1987; Gauthier-Clerc et coll. 1998; Pays & Jarman 2008)
8. Température	Température plus élevée, individu moins vigilant	Lorsque la température est basse, l'individu doit s'alimenter davantage afin de maintenir un métabolisme élevé	(Pravosudov & Grubb 1998)
9. Présence de juvéniles	Vigilance plus élevée chez l'individu s'occupant de la progéniture	Progéniture plus vulnérable, surveiller la distance entre le parent et la progéniture	(Childress & Lung 2003)

*Ce tableau est une énumération non exhaustive des facteurs influençant la vigilance. Ceux-ci comprennent les principaux éléments ayant influencé la vigilance dans les chapitres 2 et 3 de ce mémoire. Les variables 1 à 3 peuvent être classées dans la catégorie dynamique de groupe, 4 à 6 environnement et, 7 à 9 caractéristiques individuelles (Favreau et coll. 2010), ¹ l'effet du sexe sur la vigilance dépend de l'espèce (dimorphisme sexuel : Femelle plus vigilante chez le kangourou géant (*Macropus giganteus*) / Mâle plus vigilant chez le canard siffleur (*Anas penelope*))*

L'effet de la taille du groupe est fréquemment cité dans la littérature comme étant une diminution de la vigilance individuelle lorsque la taille du groupe augmente. Les plus grands groupes auraient un risque moins élevé de prédation expliquant la diminution de la vigilance. La détection hâtive est souvent citée afin d'expliquer la relation entre la vigilance et la taille du groupe, mais l'effet de dilution pourrait aussi participer à cette relation (Beauchamp & Ruxton 2007). En effet, les deux donnent des prédictions similaires concernant la diminution du risque de prédation, les rendant difficiles à différencier (Beauchamp & Ruxton 2008). De plus, Fairbanks et Dobson (2007) montrent que l'importance de ces deux mécanismes n'est pas nécessairement la même chez toutes les espèces. Il est aussi important de prendre en compte que dans certaines situations les plus grands groupes sont plus facilement détectables par les prédateurs (l'effet d'attraction). Malgré cela, de nombreuses études montrent que l'effet de dilution contrecarre souvent cette tendance (Beauchamp 2014; Krebs et coll. 2014). Ce n'est cependant pas toujours le cas. Ale et Brown (2007) ont élaboré un modèle permettant de prédire les situations où l'effet groupe peut être observé lorsque l'on fait varier l'impact de la détection hâtive, l'effet de dilution et d'attraction des prédateurs.

Une autre hypothèse expliquant la relation inversement proportionnelle entre la vigilance et la taille du groupe est l'hypothèse de la compétition. Les membres du groupe ne diminueraient pas leur vigilance à cause d'une baisse du risque de prédation, mais plutôt en raison de l'augmentation de la compétition pour les ressources limitées lorsque la taille

du groupe augmente (Grand & Dill 1999). Cette hypothèse ne s'applique qu'aux situations où il est impossible d'obtenir des ressources et d'être vigilant en même temps.

À l'opposé, il y a plusieurs travaux qui ne montrent aucun effet de la taille du groupe sur la vigilance, particulièrement chez les primates (Treves 2000). Cela pourrait être causé par un manque de puissance statistique (Beauchamp 2015), du chapardage des ressources par les congénères ou encore par une différence individuelle au niveau du taux de prédation (Robinette & Ha 2001). Ces différences peuvent être causées entre autres par le sexe de l'individu, ses réserves énergétiques ou un trait de personnalité (Elgar 1989; Edwards et coll. 2013). Ce dernier aspect est très peu étudié dans la littérature, particulièrement son importance dans les mécanismes d'anti-prédation. La prochaine section de cette introduction et le troisième chapitre du mémoire (« Individual Vigilance Profiles in Flocks of House Sparrows») explorent le lien entre la personnalité animale et la vigilance.

Les traits de personnalité

En éthologie, un trait de personnalité se définit par des différences interindividuelles stables dans la population à travers le temps ou dans différents contextes (Bergmüller & Taborsky 2010). La constance du trait est au niveau de la population, cela implique qu'il doit toujours y avoir des différences entre les individus. L'individu peut quand même changer selon son âge ou l'environnement (Reale et coll. 2007). Ainsi, si la vigilance est un trait de personnalité, nous devrions observer dans la population des individus ayant différents niveaux de vigilance et observer ces particularités dans différents contextes pendant une certaine période de temps. De plus, un trait de personnalité doit démontrer

une variation phénotypique, de la répétabilité et de l'héritabilité dans la population (Reale et coll. 2007).

Dans la littérature, il est souvent question du « shy-boldness continuum » afin de décrire la personnalité animale. Ce continuum est constitué de deux personnalités opposées : timide et téméraire. Afin d'évaluer la témérité d'un individu, la présentation d'un nouvel objet est souvent utilisée (Kurvers et coll. 2009). Dès lors, la distance et le temps pris pour approcher l'objet servent de mesure pour évaluer l'animal. La notion de syndrome comportemental est un autre concept fréquemment mentionné dans les études sur la personnalité animale. Ceci est décrit comme étant une corrélation entre la présence de deux ou plusieurs traits de personnalité (Wolf & Weissing 2012) . Chez le diamant mandarin (*Taenopygia guttata*), par exemple, il y a une relation entre l'activité, la néophobie, les tendances exploratrices et la témérité d'un individu (David et coll. 2011). Cela démontre que plusieurs traits doivent être identifiés afin de décrire entièrement la personnalité animale et mieux prédire les impacts que cela peut avoir sur le succès individuel.

L'individu pourrait aussi démontrer de la plasticité. Autrement dit, celui-ci pourrait adapter son comportement aux différents stimuli rencontrés dans l'environnement (Wolf et coll. 2008). Cela pourrait autant être vu de façon globale et uniforme dans la population ou, au contraire, avoir une capacité d'adaptation propre à l'individu (Trait de personnalité). Par exemple, l'effet de la taille du groupe sur la vigilance pourrait être plus ou moins marqué chez différents individus.

Dingemanse et coll. (2010) ont élaboré un modèle de régression aléatoire permettant d'étudier un trait de personnalité et sa plasticité. Ce modèle a été utilisé dans l'article du chapitre III afin d'analyser la relation entre la vigilance et la taille du groupe. Dans ce modèle, l'ordonnée à l'origine correspond au comportement généralement observé chez l'individu tandis que la pente représente la capacité d'adaptation de l'individu lorsqu'il y a une variation dans le contexte choisi. La **figure 1.3** illustre les différentes possibilités qu'on pourrait observer sur la vigilance en fonction de la taille du groupe.

Figure 1.3 : Évaluation de la présence d'un trait de personnalité et sa plasticité

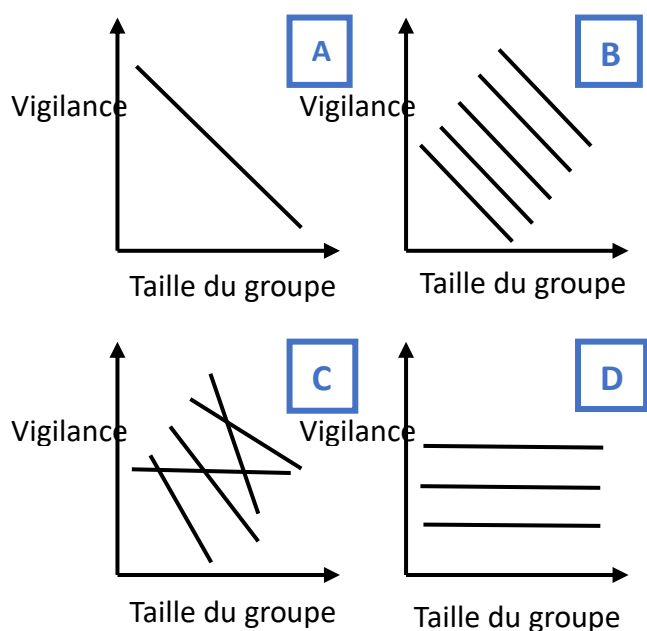


Figure 1.3: Ces différents modèles sont des régressions linéaires multiples fictives sur la relation entre la vigilance et la taille du groupe. Les lignes représentent différents individus. L'ordonnée à l'origine nous informe sur la réponse observée généralement chez l'individu et la pente nous informe sur la plasticité du comportement. La **figure A** ne présente aucune variation individuelle tant au niveau de la vigilance que de sa plasticité. La **figure B** montre des interceptes différents trahissant des profils de vigilance différents d'un individu à l'autre, mais une plasticité similaire pour tous les individus. Ainsi, dans la figure B, seulement le niveau moyen de vigilance pourrait être un trait de personnalité. La **figure C** montre des différences individuelles autant pour la vigilance que la plasticité. Finalement, la **figure D** montre différents interceptes, mais aucune plasticité dans le groupe. Conséquemment, les individus ne s'adaptent pas au changement de la taille du groupe. Adapté de (Dingemanse et coll. 2010)

Une fois la présence d'un trait de personnalité établi chez l'individu, il serait intéressant de découvrir ce qui le maintient dans la population. À ce jour, deux courants de pensée permettent d'expliquer l'apparition et le maintien d'un trait de personnalité dans la population. Un trait pourrait surgir de l'état de l'individu (e.g. réserve énergétique, sexe) ou d'une sélection fréquence-dépendante négative (Mathot et coll. 2011). Les deux mécanismes seront élaborés plus en détail dans le chapitre III du mémoire.

Le moineau domestique

Le moineau domestique, *Passer domesticus*, est un petit passériforme introduit en Amérique du nord en 1850 (Barrows 1889). Ce petit oiseau s'est particulièrement bien adapté à notre environnement étant donné sa préférence pour les milieux modifiés par les humains (Saetre et coll. 2012). Son abondance et plusieurs de ses particularités (dimorphisme sexuel important et grégarité) le rendent attrayant comme sujet d'étude pour plusieurs scientifiques (Lowther & Cink 2006). Conséquemment, plusieurs éléments sont maintenant connus sur le comportement du moineau.

Figure 1.4 : Moineau domestique mâle



Photo par Kurt

Figure 1.5 : Moineau domestique femelle



Photo par Jacob Spinks

Concernant la vigilance, l'effet de la taille du groupe a été démontré par plusieurs chercheurs chez le moineau (Studd et coll. 1983; Harkin et coll. 2000). Selon Studd et coll., la diminution du temps vigilant se fait en écourtant la durée des périodes de vigilance, mais en gardant la même fréquence de vigilance à travers le temps. Par contre, plusieurs éléments peuvent affecter la vigilance chez le moineau comme discuté dans la section vigilance. Par exemple, l'obstruction visuelle semble augmenter le temps alloué à la vigilance par une élévation de la perception du risque de prédation ou une sous-estimation de la taille du groupe. De plus, les grands groupes semblent profiter de la détection hâtive, car ils détectent les prédateurs plus rapidement que les petits groupes (Harkin et coll. 2000). Cependant, les moineaux ne possèdent aucun signal évident, comme un cri d'alarme, permettant d'avertir leurs congénères d'un danger imminent. La compétition pour les ressources, la distance jusqu'à l'abri et le risque de prédation sont d'autres exemples d'influents de la vigilance ayant déjà été étudié chez le moineau (Barnard 1980; Johnson et coll. 2004).

Les niveaux sériques de corticostérone et probablement aussi de testostérone pourraient être responsables de la génération et du maintien d'un trait de personnalité (Kralj-Fišer et coll. 2007). Chez le moineau, la bavette et le bec noir du mâle sont des caractéristiques sexuelles secondaires liées au niveau sérique de testostérone (Laucht et coll. 2010). De plus, la taille de la bavette semble être associée à l'âge, à la condition physique et au statut hiérarchique et reproducteur du moineau (Veiga 1993; Nakagawa et coll. 2007). Ces variations phénotypiques peuvent donc nous aider à mieux identifier

l'importance de la dominance et des variations hormonales dans la personnalité. Si des variables d'état comme l'âge ou les réserves sont associées à la taille de la bavette, il serait possible de voir émerger des liens entre la variation individuelle de la vigilance et sa plasticité et la taille de la bavette chez le mâle.

L'abondance de documentation et la disponibilité de l'espèce en milieu urbain ont facilité le choix du moineau domestique pour les projets de recherche sur la vigilance. Le deuxième chapitre du mémoire abordera l'efficacité de l'avertissement mutuel chez le moineau domestique tandis que le troisième chapitre s'attardera sur les variations individuelles de vigilance et sa plasticité chez ce petit passériforme.

Chapitre II

Spread of False Alarms in Foraging Flocks of House Sparrows

Cet article est publié et il est reproduit dans son format original: Boujja-Miljour, H., Leighton, P.A., Beauchamp, G., 2017. Spread of false alarms in foraging flocks of house sparrows. *Ethology* 123, 526-531.

Abstract

In group-foraging species with no alarm signals, the sudden departure of neighbours can be used to inform the rest of the group about the detection of a threat. However, sudden departures are ambiguous because they can be triggered by factors unrelated to predator detection. We evaluated how animals react to the sudden departure of neighbours in groups of foraging house sparrows (*Passer domesticus*). We focussed on false alarms that occurred for no apparent reasons to us because predation attempts were not frequent. Three factors can explain how the sudden departure of a neighbour can influence reaction times, namely, group size, the distance between neighbours, and predation risk. We predicted reaction times to be longer in larger groups where individual vigilance levels are low, and when group members are further apart and cannot easily monitor each other. In addition, we expected reaction times to be longer when predation risk is lower. Departures that are more temporally clumped are also expected to be less ambiguous and should trigger faster reaction times. Our results show that sparrows reacted faster, not more slowly, to the sudden departures of neighbours in larger groups, and, as predicted, more slowly when neighbours were more distant from each other. Reaction times were longer in one of the two study years in which predation risk was deemed lower. Sparrows reacted more quickly when earlier departures were more temporally clumped. The results thus provided partial support for the predictions, and future work is needed to assess how individuals react to fleeing responses by their neighbours in species with no alarm signals.

Introduction

Group foraging can provide several benefits to animals (Krause & Ruxton 2002; Beauchamp 2014). For example, it is easier for an individual in a group to find food or for the group to defend resources. Group foraging also brings antipredatory benefits through several mechanisms. In particular, if a predator can only target one group member during an attack, the risk of capture is shared amongst more individuals in larger groups (dilution effect: (Bertram 1978). Furthermore, as group size increases, more eyes and ears can detect an approaching predator before it is too late to escape (many-eyes effect: Galton 1871). The many-eyes effect can only be beneficial if individuals that detect a threat can rapidly alert the non-detectors in the group. This information transfer is known as collective detection (Pulliam 1973). Collective detection implies that individuals monitor to a certain extent the behaviour of other group members for signs of alarm (Lima 1990).

Information about incoming danger can easily spread within a group in species with visual or auditory alarm signals. Meerkats (*Suricata suricatta*), for instance, use different alarm calls to inform neighbours about different types of predators (Manser et al. 2002). This is also known in other mammals (Seyfarth et al. 1980) and in birds (Templeton et al. 2005). More passive information can also be used in other cases. As an example, whirring sounds made by the wings during takeoff can act as an alarm cue in birds (Coleman 2008; Hingee & Magrath 2009). Changes in neighbours' posture are also known to transfer information about the presence of a predator (Brown et al. 1999; Pays et al. 2013).

Although alarm calls are known in some species of birds (Griesser 2008), many avian species lack obvious cues to inform others of danger. In such species, the rapid flight to seek

cover following detection of a threat might be the only information available to non-detectors (Lima 1994). However, such cues can be ambiguous because sudden departures from a group might not always be associated with the detection of threats. Individuals, for instance, could rapidly leave the group when sated. Alarm calls, by contrast, are unlikely to be produced if no threats are perceived unless deception is involved. Consequently, the departure of a conspecific can lead to a series of false alarms, which could result in the departure of the whole group even when there is no apparent threat (Lima 1994; Proctor et al. 2001).

One convenient way to investigate collective detection in the absence of alarm signals has been to measure the time needed by individual birds to react to the hurried departure of their neighbours (Lima 1994). Longer reaction times suggest that either collective detection is less efficient due to some constraints on information use or that individuals delay their responses adaptively (Quinn & Cresswell 2005). Several factors can conceivably affect reaction times including group size, inter-individual distances, and predation risk. However, few studies have focussed on reaction times to sudden departures in species without alarm signals, and the results are often contradictory.

Longer reaction times might be predicted in larger groups because low individual vigilance in such groups could reduce the ability to perceive the flight reactions of neighbours (Lima 1994). In addition, the risk of being targeted by a predator is lower in larger groups due to the dilution effect, which would enable individuals to assess danger more fully before reacting. Longer reaction times in larger groups have been documented in one shorebird species, the redshank *Tringa totanus* (Hilton et al. 1999; Quinn & Cresswell

2005), but not in a species of frog (Martín et al. 2006) and other species of birds such as California towhees (*Pipilo crissalis*) (Fernández-Juricic et al. 2009). Longer reaction times are also expected when individuals in the group are further apart. Visual and auditory monitoring of neighbours is predicted to be less efficient when the distance between foragers increases, especially in species with no alarm calls (Proctor et al. 2003). Thus, reaction times should increase with spacing in the group (Gerkema & Verhulst 1990; Hilton et al. 1999; Pays et al. 2013) or when obstacles reduce the ability to monitor neighbours (Harkin et al. 2000).

Risk of predation could also have an influence on reaction times. When the risk of predation is high, more individuals are expected to be vigilant (Beauchamp 2015), which would facilitate the transfer of information about threats. Shorter reaction times would also be adaptive in this context since foragers could flee to safety sooner or benefit from mass departure. In redshanks, individuals avoided delayed responses when faced with high-risk stimuli (Quinn & Cresswell 2005), and in eastern grey kangaroos (*Macropus giganteus*), individuals reacted more quickly when faced with a greater safety threat (Pays et al. 2013).

Near simultaneous departures of several neighbours can also act as an indirect cue to higher predation risk as such departures are less likely to be caused by innocuous threats (Lima 1995; Cresswell et al. 2000; Proctor et al. 2001; Beauchamp & Ruxton 2007). Consequently, reaction times in the group should be quicker when early departures from the group are more temporally clumped (Lima 1994; Cresswell et al. 2000; Clément et al. 2015).

We investigated the effect of three factors (group size, inter-individual distances, and predation risk) on the spread of alarm in a group following the sudden departures of neighbours in species without alarm signals. We tested the hypothesis that reaction times following the sudden departure of neighbours increase with spacing and group size. We also tested the hypothesis that reaction times decrease when the perception of risk is higher and when sudden departures are more temporally clumped. Reaction times after the departures of several neighbours should also be shorter because multiple departures are less likely to go unnoticed and might also signal a higher risk.

We tested these predictions in the house sparrow, *Passer domesticus*, a species with no alarm calls. This is a good study species for our investigation because vigilance in house sparrows is known to vary with group size and spacing, and individuals pay attention to their neighbours (Barnard 1980; Elgar et al. 1984; Lima 1987; Tisdale & Fernández-Juricic 2009). As predation attempts rarely occurred during this study, we focussed on sudden departures with no apparent causes. Sparrows returned very quickly to the feeding site after these sudden departures, which is the reason why we refer to them as false alarms.

Methods

Study Area

The study was conducted between May 30th and August 8th in 2014 and between June 16th and August 4th in 2015 in a back alley of Montréal (Québec, Canada: 45.43° N, 73.60° W). The back alley, which was approximately 15 m long and 4 m wide, was bordered by house fences on the two long sides. This particular back alley was chosen because it was rarely disturbed by cars or pedestrians. Local residents maintained several bird feeders in

the area, which helped sustain a fairly large population of house sparrows. Grass covered most of the back alley except for an asphalted patch (approximately 1 m²). We supplied this cleared area with millet seeds on a daily basis to attract house sparrows. One of us (HB-M) monitored the feeding patch from behind a nearby tree with a digital camera approximately 4 m away. At that distance, feeding sparrows showed no obvious signs of reaction to the observer's presence. Other avian species occasionally visited the patch. Cats and birds of prey were also present during the two study years.

Sampling

Sampling took place from Mondays to Fridays during morning hours (from 7h00 to 10h00 approximately) to reduce external disturbances. Observations started when the first sparrow landed on the provisioned feeding patch and lasted for about 3 hours. Typically, multiple sparrows sequentially landed on the patch. Back and forth movements between the patch and nearby fences ceased after a few seconds and all individuals present started to feed. Because of grass nearby and lack of food, individuals rarely moved away from the patch when on the ground. For our purposes, a flock was the set of all individuals feeding on the provisioned patch at a given time.

The whole flock often left hurriedly from the patch for no apparent reason. We refer to these events as false alarms. We are quite confident that these alarms were not caused by predators because the study area was small and partially enclosed, which made it quite easy for us to detect terrestrial or aerial predators.

We extracted false alarm sequences from the video recordings. To increase homogeneity in our samples, we did not retain cases in which other species fed from the

patch at the same time. Also, we only retained false alarms that occurred after the flock fed uninterrupted from the patch for at least 15 s. This delay ensured that the whole flock was feeding when false alarms occurred. We did not retain sequences in which the birds left behind after sudden departures resumed feeding before leaving as this would indicate a lack of response to the initial departures. For each false alarm, we recorded initial flock size and the elapsed time since the beginning of recording for that day. As a measure of initial flock spacing, we evaluated the distance between the two most distant flock members. Set near the patch, a marker of known size helped gauge individual spacing.

We played video sequences frame by frame (1 frame = 33 msec) to measure reaction times between sequential departures in retained false alarm sequences. The first reaction time in a sequence was measured relative to the sparrow that initiated the alarm. Subsequent reaction times were measured relative to the sparrow that left immediately before. When measuring reaction times, time 0 represented the moment when both feet of a fleeing sparrow cleared the ground. The reaction time was the time that elapsed from time 0 (counted as frame numbers) until both feet of the sparrow that flew next cleared the ground. We measured all reaction times in this fashion until no more sparrows were left. Occasionally, two sparrows left in the same frame. We assumed that those birds independently reacted to the previous departure and counted the simultaneous departures as one event.

Statistical Analysis

Prior to analysis, the \log_{10} transformation was applied to all variables to normalize distributions. For the analysis of group size and spacing, we used a linear mixed model with

year and time elapsed since the beginning of a recording session on a given day as fixed factors and day as a random factor. The interaction between year and elapsed time was also considered, but removed if not statistically significant. Year was treated as a fixed factor in this and subsequent models to evaluate whether trends were similar between study years. Elapsed time was considered an indirect measure of predation risk as birds might perceive a lower risk after several false alarms in a row during the same morning.

For the first reaction time, we used a linear mixed model with year, spacing, elapsed time and number of birds left behind after the first departure (total group size minus 1) as fixed factors and day as a random factor. Interactions between year and spacing or remaining group size were considered, but dropped when not significant. For the second reaction time, we used the same linear mixed model but added the first reaction time as a co-factor. For the third and fourth reaction times, we included the sum of the two first reaction times as a co-factor. Notice that sample size decreases with each reaction time since larger groups were less common. Standard linear regression diagnostic tools did not reveal multicollinearity issues amongst the independent variables.

The final analysis focused on larger groups where it was possible to record the first four reaction times within the same groups (group size ≥ 5). The sequence of reaction times (labelled 1 to 4) was analyzed with a linear mixed model with year, spacing, initial group size, elapsed time and number in the sequence as fixed factors and group id as a random factor. Tukey's post-hoc tests were used to compare pairs of means subsequently. Back-transformed means (95% C.I.) are provided below.

Results

The dataset consisted of 117 false alarm sequences in 2014 and 33 sequences in 2015. Despite a similar sampling effort (21 days in 2014 and 18 in 2015), fewer sequences in 2015 met the inclusion criteria of stable group membership over the set time limit.

Groups included in the analysis ranged in size from 2 to 23 with a median value of 5 in 2014 and 4 in 2015. The mean size of the groups did not differ between the two study years (2014: 3.97 (3.28, 4.8), 2015: 4.23 (3.32, 5.37); $F_{1,32.7}=0.02$, $p = 0.90$), but increased with elapsed time during a recording session ($\beta[\text{SEM}]=0.11$ [0.047], $F_{1,112}=5.3$, $p = 0.02$). Mean spacing was significantly lower in 2015 than in 2014 (2014: 6.92 (5.74, 8.34), 2015: 4.28 (3.32, 5.51); $F_{1,116}=8.4$, $p = 0.005$). There was a significant interaction between elapsed time during a recording session and year ($F_{1,120}=5.0$, $p = 0.02$): mean spacing thus increased with elapsed time in 2015 ($\beta[\text{SEM}]=0.17$ [0.089], $t=2.2$, $p=0.03$) but not in 2014 ($\beta[\text{SEM}]=-0.038$ [0.051], $t=-0.74$, $p=0.46$).

The first reaction time ranged between 0.033 and 4.6 s with a median value of 0.1 s both years. The mean did not statistically vary with year, spacing and elapsed time (Tableau 2.1), but decreased with remaining group size indicating faster reaction times in larger groups (Fig. 2.1). The second reaction time ranged between 0.03 and 1.6 s with a median value of 0.066 s in 2014 and 0.033 in 2015. The mean did not statistically vary with year, spacing and elapsed time (Tableau 2.1), but decreased with remaining group size and increased with the duration of the first reaction time. The third reaction time ranged between 0.033 and 1.03 s with a median value of 0.033 s both years. The mean did not statistically vary with year, spacing, elapsed time, remaining group size and the sum of the

Tableau 2.1: Statistical analysis of reaction times during false alarms in foraging groups of house sparrows

Reaction time (s)	Year ¹			Spacing		Remaining group size		Elapsed time		Previous reaction time	
	2014	2015	F-test	β (SEM)	F-test	β (SEM)	F-test	β (SEM)	F-test	β (SEM)	F-test
1	0.12 (0.099, 0.15)	0.090 (0.065, 0.12)	$F_{1,43.2}=2.3$, $p = 0.13$	0.19 (0.13)	$F_{1,92.5}=2.3$, $p = 0.13$	-0.27 (0.10)	$F_{1,72.5}=6.8$, $p = 0.01$	-0.018 (0.061)	$F_{1,124}=0.09$, $p = 0.77$	-	-
2	0.063 (0.050, 0.079)	0.043 (0.031, 0.059)	$F_{1,37.9}=7.5$, $p = 0.07$	0.25 (0.15)	$F_{1,88.1}=2.7$, $p = 0.10$	-0.26 (0.11)	$F_{1,87.6}=5.7$, $p = 0.02$	-0.039 (0.063)	$F_{1,91}=0.39$, $p = 0.53$	0.26 (0.084)	$F_{1,86.4}=6.7$, $p = 0.003$
3	0.073 (0.049, 0.11)	0.039 (0.025, 0.062)	$F_{1,20.5}=4.1$, $p = 0.06$	0.086 (0.23)	$F_{1,72.9}=0.14$, $p = 0.71$	-0.19 (0.14)	$F_{1,71.6}=1.9$, $p = 0.17$	-0.11 (0.086)	$F_{1,73}=1.5$, $p = 0.22$	-0.035 (0.12)	$F_{1,65.8}=0.08$, $p = 0.77$
4	0.067 (0.051, 0.086)	0.047 (0.026, 0.084)	$F_{1,49}=1.2$, $p = 0.29$	0.42 (0.37)	$F_{1,49}=1.3$, $p = 0.26$	-0.083 (0.20)	$F_{1,49}=0.17$, $p = 0.68$	0.044 (0.1)	$F_{1,49}=0.16$, $p = 0.69$	0.0037 (0.17)	$F_{1,49}=0.0$, $p = 0.96$

¹ Reaction times were analyzed with a linear mixed model with year, spacing, number of birds left behind after the first departure (total group size minus 1), and elapsed time since the beginning of observations on a given day as fixed independent variables and day as a random factor. For the second, third and fourth reaction times, we also tested the effect of the previous reaction time in the same sequence. Back-transformed means (95% CI) are shown. Bold p-values are statistically significant.

previous two reaction times (Tableau 2.1) The fourth reaction time ranged between 0.033 and 1.50 s with a median value of 0.05 s in 2014 and 0.033 s in 2015. The mean did not vary according to year, spacing, elapsed time, remaining group size and the sum of the previous two reaction times (Tableau 2.1). Although the year effect was not statistically significant in each of the above four models, mean values were typically 25% lower in 2015 than in 2014 (Tableau 2.1).

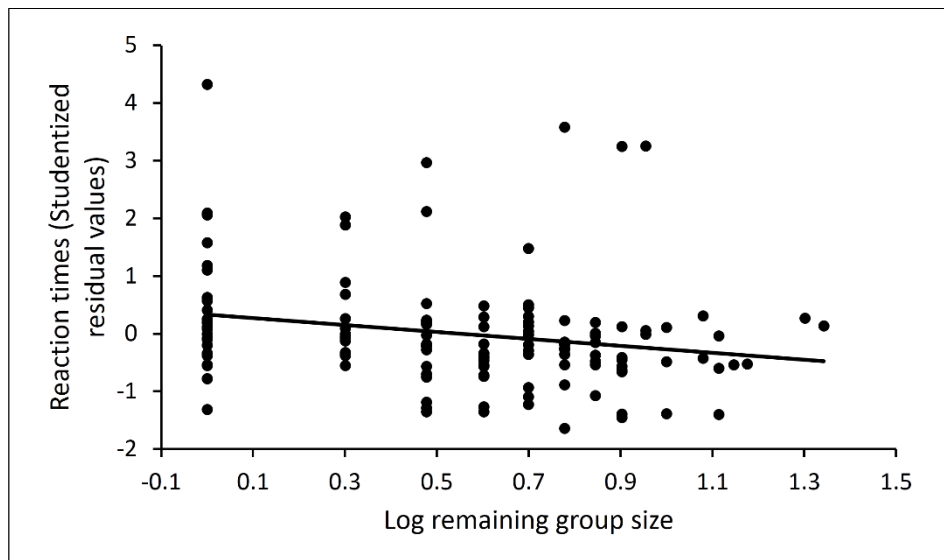


Fig. 2.1: The mean time to react (s) to the sudden departure of a neighbour decreased inversely proportionally to group size. Studentized residuals from a mixed linear model including year, spacing, and elapsed time from the beginning of a recording session on a given day as fixed factors and day as a random factor, but excluding remaining group size, are plotted against remaining group size. The linear trend is shown with the line.

In the analysis comparing the first four reaction times within the same large groups, the overall mean was significantly larger in 2014 than in 2015 (Fig. 2.2), increased with spacing (β [SEM]: 0.29 [0.14]; $F_{1,86.4}=4.2$, $p=0.04$) but did not vary with initial group size (β [SEM]: -0.14 [0.17]; $F_{1,85.2}=0.68$, $p=0.41$) and elapsed time (β [SEM]: 0.0052 [0.048]; $F_{1,86}=0.01$, $p=0.91$). The mean also varied with the sequence of reaction times ($F_{3,186}=10.5$,

$p < 0.0001$; Fig. 2.2) and was significantly larger for the first reaction time than for the remaining three reaction times.

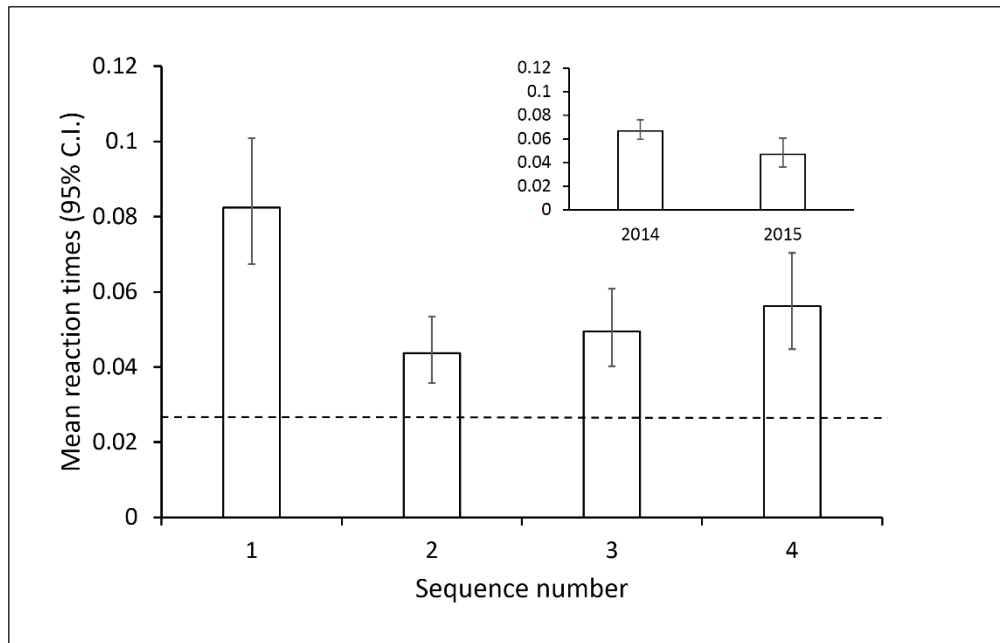


Fig. 2.2: Mean reaction times (s) decreased when further down the sequence of consecutive responses in groups of house sparrows. The inset illustrates the difference in overall mean between the two study years (2014 and 2015). Back-transformed least-squares means are shown along with the 95% confidence intervals. The resolution of the video camera was 33 msec (dashes).

Discussion

In this study, the spread of false alarms following the sudden departures of neighbours was quicker in larger groups. Indeed, in general, reaction times to previous departures tended to decrease with the number of individuals left behind. Based on the dilution effect and the lower vigilance of group members in larger groups, we expected reaction times to increase in larger groups, but observed the opposite. Redshanks, by contrast, reacted more slowly in larger groups (Hilton et al. 1999; Quinn & Cresswell 2005). In redshanks, predators tend to target smaller groups or more isolated foragers (Cresswell & Quinn 2004; Quinn & Cresswell

2006). It is perhaps the case that larger groups of house sparrows faced a higher rather than lower predation risk, which would favour quicker responses to departures in such groups. Predator preference for larger groups has been documented in other species (Lindstrom 1990; Krause & Godin 1995; Hebblewhite & Pletscher 2002). More data on attack rate as a function of group size is required to assess this hypothesis in house sparrows.

Another possible explanation is that despite the presumably lower individual vigilance in larger groups, the level of collective vigilance achieved at the group level, that is, how frequently at least one group member is vigilant at any given time, was actually higher in such groups. This higher collective vigilance would allow quicker detection of sudden departures and thus a reduction in reaction times in larger groups. In other species, levels of collective vigilance often are higher in larger groups (Ebensperger et al. 2006; Pays et al. 2012; Whiteside et al. 2016). Data on collective vigilance in sparrow groups are needed to assess this hypothesis more fully.

Within the same groups, reaction times increased with spacing. House sparrows do not rely on auditory cues to warn the rest of the group; takeoff of previous group members is the only known warning about external threats. When individuals are further away, it becomes harder to monitor conspecifics and alarm flights (Harkin et al. 2000), and longer reaction times might simply betray a constraint on information use. However, the value of information given by a detector is thought to decrease as inter-individual distances increase (Seppänen et al. 2007). Consequently, individuals could pay less attention to the less relevant information provided by more distant neighbors. A positive relationship between spacing and reaction times has been documented in other species without alarm calls

(Hilton et al. 1999; Quinn & Cresswell 2005; Pays et al. 2013). The occurrence of tighter groups in 2015 could also explain why reaction times tended to be shorter that year controlling for group size.

Reaction times also varied with the perception of predation risk. Consistent with the expectation that clumped departures signal a higher risk (Lima 1994; Cresswell et al. 2000; Proctor et al. 2001), reaction times decreased when the first two birds left closer in time although the effect did not persist for subsequent reaction times. After witnessing several hurried departures from the group, sparrows further down the reaction chain probably assumed the worst and all departed quickly. This could also explain the observation that within the same group reaction times tended to be quicker for the birds responding later.

We expected reaction times to increase as the day progressed because repeated false alarms might induce a reduction in the perception of predation risk. While this was not the case here, we point out that it was not possible to ascertain how long each bird remained at the patch. The prediction would be best tested by comparing reaction times by individually marked birds across time. Studies with marked individuals would also make it possible to determine whether some individuals tend to occur together in the same flocks (mates and offspring for instance) and whether this has an impact on reaction times.

Interesting differences emerged between the two study years. House sparrows reacted faster in 2015 than in 2014 controlling for group size and spacing. Together with the findings that spacing increased over time during a given day in 2015 and that groups were also less stable that year, the results suggest that the perception of risk was higher in 2015, which would explain faster reaction times. Our casual observations indicate that more cats

roamed the area in 2015, perhaps explaining the greater flightiness that year. In future studies, experimental manipulation of predation risk would provide more direct evidence for a role of predation risk on reaction times.

In conclusion, our study showed that many variables, such as group size, inter-individual distances, and predation risk, can affect reaction times following the sudden departures of neighbours, but not always in the direction predicted. Further studies are needed to understand how species without alarm signals are able to assess predation risk from their neighbours.

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Chapitre III

Individual Vigilance Profiles in Flocks of House Sparrows

Cet article sera soumis pour publication dans la revue *Ethology* en automne 2017 et est reproduit dans le format de cette revue: Boujja-Miljour, H., Leighton P. A., & Beauchamp G. Individual vigilance profiles in flocks of house sparrows.

Abstract

In group-foraging species, a decrease of individual vigilance with flock size is often seen. However, the group size effect explains only a small percentage of vigilance variation which suggests the importance of individual differences (i.e. personality trait). Individuals could show constancy in their vigilance level but also be able to adapt to different situations (i.e. plasticity). We investigated individual variations in vigilance and plasticity in house sparrows (*Passer domesticus*). We evaluated repeatability and plasticity at the same time by using a linear model of vigilance as a function of group size using multiple observations of the same individuals in groups of different sizes. Our results showed the well-known group size effect at the population level. In addition, vigilance differences were seen between months which may shed light on differences in drivers of vigilance (e.g. presence of juveniles and temperature). Sex of individuals did not influence vigilance. Individual sparrows had consistent differences in vigilance and plasticity. Furthermore, sparrows with larger bills (bill size correlates with dominance and age) were less vigilant and had a higher feeding rate. This could support one of the theories explaining consistent profiles of vigilance: the state-dependent hypothesis. According to this hypothesis, individuals adjust their behaviour to their state (e.g. age in our study), which varies in the population and therefore creates different profiles of vigilance. In conclusion, we found evidence for consistent individual variations in vigilance and plasticity in response to variation in flock size. Future work is needed to discover the underlying mechanism maintaining vigilance profiles.

Introduction

Vigilance represents the action of keeping watch for danger or other difficulties (Stevenson 2010). When scanning the surroundings for predators, individuals that forage in groups can maintain a lower vigilance without incurring a higher risk of predation (group-size effect: Pulliam 1973). This advantage of group foraging prevails in many species of animals (Caro 2005). The many-eyes effect and risk dilution are two of the main hypotheses explaining the negative relationship between vigilance and group size. As group size increases, more eyes and ears are available to detect predators (many-eyes effect: Caraco et al. 1980), and information about detection can rapidly spread in the group to alert neighbours about the incoming threat (collective detection: Lima 1996). Furthermore, the odds that a predator targets a specific individual are lower in a larger group (dilution: Bertram 1978).

Models of antipredator vigilance predict the decline in vigilance as a function of group size for an average individual. Group size, however, often explains a relatively small amount of the variation in vigilance in many species (Blumstein 1996; Beauchamp 2008). Plots of the relationship between vigilance and group size also reveal important heterogeneity (Beauchamp 2013). These findings suggest that the group-size effect on vigilance might vary for different subsets of individuals. For instance, males might maintain more vigilance against neighbours than females during the reproductive season and show a shallower decline of vigilance with group size (Childress & Lung 2003; Li et al. 2012). A shallower group-size effect on vigilance is also expected for individuals with more energy reserves (McNamara & Houston 1992).

Heterogeneity in the group-size effect on vigilance might also reflect individual differences. Indeed, regardless of group size, some individuals might be consistently more vigilant than others. Recent studies have documented stable individual vigilance profiles in mammals (Carter et al. 2009; Pangle & Holekamp 2010; Rieucan et al. 2010; Dannock and 2013; Edwards et al. 2013; Hoogland et al. 2013; Favreau et al. 2014) and in birds (Couchoux & Cresswell 2012; Roche & Brown 2013). In addition to consistent differences in overall vigilance, individuals could also show differences in the level of adjustment of vigilance to group size or more generally to any factor related to predation risk. Various terms describe this component of individual responses including plasticity but also flexibility, responsiveness, coping style or reactivity (Wolf et al. 2008). Two studies revealed consistent individual differences in plasticity with respect to a gradient in predation risk (Mathot et al. 2011; Couchoux & Cresswell 2012). The results are mixed for studies investigating the group-size effect on vigilance with evidence for plasticity in one case (Carter et al. 2009) but not in others (Rieucan et al. 2010; Dannock et al. 2013; Favreau et al. 2014).

What might explain consistent individual differences in vigilance and plasticity? One explanation relies on state-dependent behaviour. Individuals adjust their behaviour according to their state (e.g. energy reserves), which varies consistently among individuals, and differences between individuals tend to increase or to decrease when predation risk changes thus inducing different levels of plasticity amongst individuals along the predation risk gradient (Sih et al. 2015). Another explanation emphasizes negative frequency-dependent payoffs associated with different behavioural options. Flexible individuals that adjust their vigilance to predation risk can benefit the whole group because vigilance

payoffs are shared through collective detection. This mechanism allows the coexistence of flexible and less flexible individuals with respect to how vigilance is adjusted to predation risk (Mathot et al. 2011).

Overall, few studies have investigated individual vigilance profiles as a function of group size. Thus far, the evidence for consistent individual differences in vigilance and for plasticity in the group-size effect on vigilance is mixed. In most cases, it is not clear which mechanism underlies individual variation. If vigilance represents an individual trait, we expect variation among individuals in the population, repeatability and heritability (Reale et al. 2007). Our study conducted over one field season addresses the first two features. To evaluate repeatability and plasticity at the same time, we used a linear model of vigilance as a function of group size using multiple observations of the same individuals in groups of different sizes (Dingemanse et al. 2010). In this model, we sought evidence for statistical heterogeneity in individual intercept values, which would indicate repeatability of vigilance at the time scale of the study, and heterogeneity in individual slope values, which would suggest individual variation in plasticity.

We investigated individual vigilance profiles in flocks of the house sparrow, *Passer domesticus*, a model species for vigilance (Anderson 2006). Sparrows typically feed on seeds in small flocks and often interrupt their feeding to scan the surroundings for signs of danger. Their lateral eyes allow detection of threats when foraging head down (Fernández-Juricic et al. 2008), but postures with the head up are commonly used to handle food and to scan for threats (Liker & Barta 2002; Tisdale & Fernández-Juricic 2009). Vigilance in house sparrows decreases with flock size (Studd et al. 1983; Elgar et al. 1984), and also varies as a function

of sex and temperature (Beveridge & Deag 1987) and the density of food (Johnson et al. 2001). During the reproductive season, house sparrows tend to be territorial (Lowther & Cink 2006), making it easier to follow the same individuals over time at the same location. Males possess a black bib whose size correlates with dominance and age (Nakagawa et al. 2007), two state-dependent variables that might explain how stable individual vigilance profiles can arise in males of this species.

Methods

Study Area

We conducted the study between May 27th and August 5th in 2016 on the balcony of a third-floor apartment in the city of Montréal (Québec, Canada: 45.27° N, 73.33° W). The apartment building was located on a small street with few disturbances. Trees located across the street from the apartment building provided a refuge for the feeding sparrows. We placed a 1m X 1m feeder on the balcony flush with the railings so that the sparrows could land directly on the feeder to access resources. We supplied the feeder with a large amount of white millet seeds on a daily basis to attract sparrows. A large population (>50) of sparrows inhabited the area and regularly visited the feeder.

Prior to the start of the study, we captured sparrows directly on the balcony using a small trap that could hold several sparrows simultaneously. We set the trap next to the feeder for about three hours daily. The trap had a small landing area supplied with white millet seeds. For one week, we blocked the chute mechanism underneath the landing area to entice as many sparrows as possible to visit the trap. We captured sparrows after this habituation phase by unblocking the chute mechanism for a period of 10 days. We fitted

captured bird with coloured metal leg bands for individual identification. Using pictures taken with a digital camera, we measured the width and length of the black bill in males. For these measurements, we selected pictures of the birds in the high vigilance posture (see below) directly facing the camera and located at the same distance from the camera. We used bill size (10 mm) as a marker to convert our screen measurements to bill area (Møller 1987). The study was approved by the Animal Care and Use committee of the Faculté de médecine vétérinaire of the Université de Montréal.

Behavioural sampling

We monitored the feeder during the workweek in the morning for about three hours daily. We videotaped flocks of sparrows with a digital camera from behind a one-way mirror located on the balcony door whenever a banded sparrow landed on the feeder. Given the small size of the feeder, the total number of sparrows present on the feeder at the time of an observation defined a flock.

We retained for analysis video sequences with banded sparrows during which flock size remained constant for at least 10 s. This ensured that all sparrows foraged at the time of observation. If two or more banded sparrows occurred at the feeder at the same time, which rarely happened, we randomly chose a focal subject from those present. Observations stopped when the focal banded sparrow left the feeder or after 30 s, whichever came first.

We replayed video sequences frame by frame (1 frame = 33 msec) to gather data for each banded sparrow. Sparrows pecked at the seeds with the head pointing down and raised the head to scan the surroundings. A vigilance bout started when the feeding sparrow

held its bill horizontally and ended when the bird started to move the head down. We distinguished two types of vigilance postures during a vigilance bout. In the low vigilance posture, the long axis of the body from the tail to the bill was near horizontal. In the high vigilance posture, the sparrow raised its head up so that the long axis of the body was more inclined. Notice that sparrows frequently switched from low to high vigilance postures during the same vigilance bout. Sparrows handled all seeds in the low vigilance posture and stopped handling during high vigilance.

For each focal observation with a banded sparrow, we recorded the duration of each vigilance bout and the overall frequency of high vigilance postures. Using focal observation duration, we calculated the percentage of time spent vigilant, the frequency of vigilance bouts per min and the frequency of high vigilance postures per min. We obtained average duration of a vigilance bout by dividing total time spent vigilant by the frequency of vigilance bouts in a focal observation. In addition to vigilance, we also counted the number of seeds collected during the focal observation from which we calculated food intake rate over one minute. Contextual information included flock size, the sex of the banded bird, the date, and the month (June or July). We included month of the year as the size of the flocks increased in July following the recruitment of juveniles to the feeding flocks. Due to the small size of the flocks, it was not possible to reliably determine the relative spatial position of a focal bird on the feeder (central or at the periphery).

Statistical analysis

For the analysis of flock sizes, we used a linear mixed model with \log_{10} transformed flock size as the dependent variable, id and date as random factors, and sex and month as fixed factors.

For the analysis of individual profiles, we applied the following procedure to each of the following dependent variables after a suitable transformation: logit-transformed percentage of time spent vigilant, frequency of vigilance bouts, frequency of high vigilance postures, \log_{10} transformed duration of vigilance bouts, and \log_{10} transformed food intake rate. The random coefficients models all included date as a random factor and the set of independent variables described earlier. We added id as a random factor (random intercepts) and tested its statistical significance using a likelihood ratio test with one degree of freedom. We then added random slopes for each individual and tested the statistical significance of this factor using a likelihood ratio test with two degrees of freedom this time (one for the slope and one for the covariance between slopes and intercepts). The minimum sample size to reliably detect heterogeneity in intercepts and slopes in random regression models is 200 with a ratio between the number of individuals and the number of observations per individual greater than 0.5 (Martin et al. 2011). Our study met these criteria (see Results) thus providing sufficient power to measure individual differences. We also tested for non-linear trends in the relationships between our dependent variables and flock size using a polynomial regression. As we found no evidence for non-linear relationships, second-degree terms were dropped for the final models. When reporting the

fixed effects below, we only retained the statistically significant random effects. Results below show back-transformed least squares means (95% CI).

Results

We captured 18 individuals and discarded data from four sparrows with only one or two observations. The remaining set contained six adult females and eight adult males. We gathered 283 focal observations, and the number of observations for each individual ranged between 6 and 40 with a median of 17. The overall ratio between number of subjects and number of observations per subject was 0.82. Group size ranged from one to 13 with a median of three. The average size of a flock increased from June to July ($F_{1,232} = 25.0$, $p < 0.0001$; Fig. 3.1), but was not associated with sex of the focal individual ($F_{1,232} = 0.45$, $p = 0.50$).

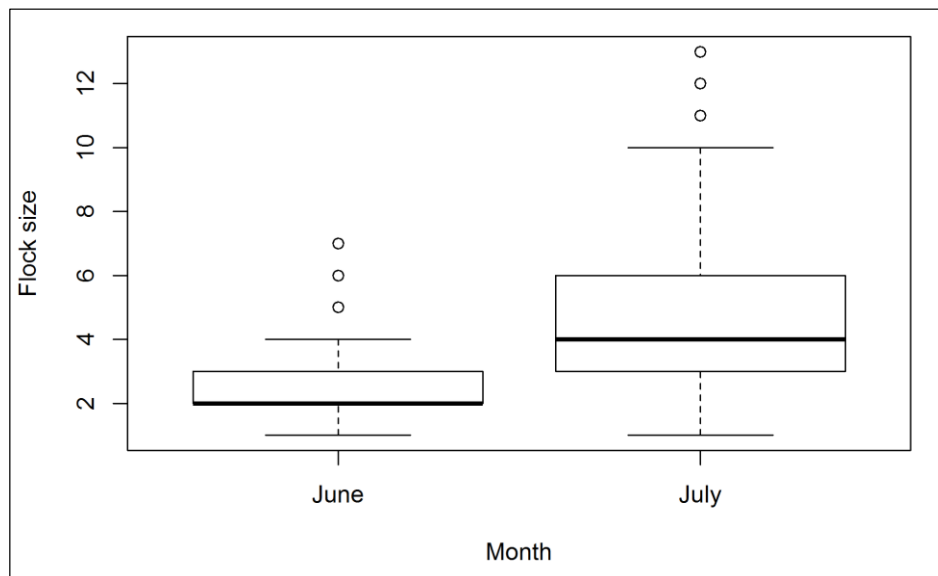


Fig. 3.1: Changes in the size of house sparrow flocks during the two months of the study. The bar in the box corresponds to median flock size and the box extends from the 25th to the 75th percentile. Whickers extend to 1.5 times the interquartile range and outliers are shown with dots.

The percentage of time spent vigilant decreased with flock size ($F_{1,231} = 42.1$, $p < 0.0001$; Fig. 3.2), was higher in July (72.0%; 66.5%, 77.0%) than in June (61.5%; 56.5%, 66.3%) ($F_{1,231} = 12.5$, $p = 0.0005$), but was not associated with sex ($F_{1,231} = 0.07$, $p = 0.79$). Sparrow id explained 12.7% of the variation in time spent vigilant, a significant effect (random intercepts: $\chi_1 = 19.7$, $p < 0.0001$). There was no evidence for individual variation in the strength of the flock size effect (random slopes: $\chi_2 = 0.2$, $p = 0.90$; Fig. 3.3).

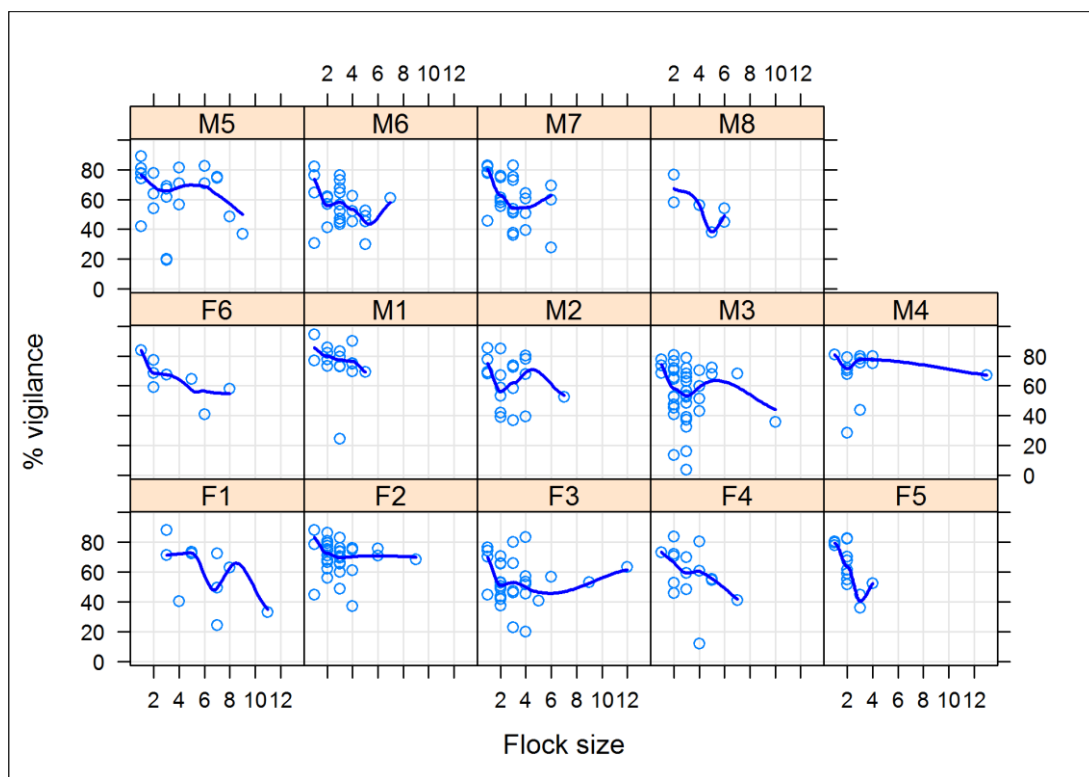


Fig. 3.2: Individual variation in the relationship between time spent vigilant (%) and flock size in six female (F1 to F6) and eight male (M1 to M8) house sparrows. A loess curve was fitted for each individual.

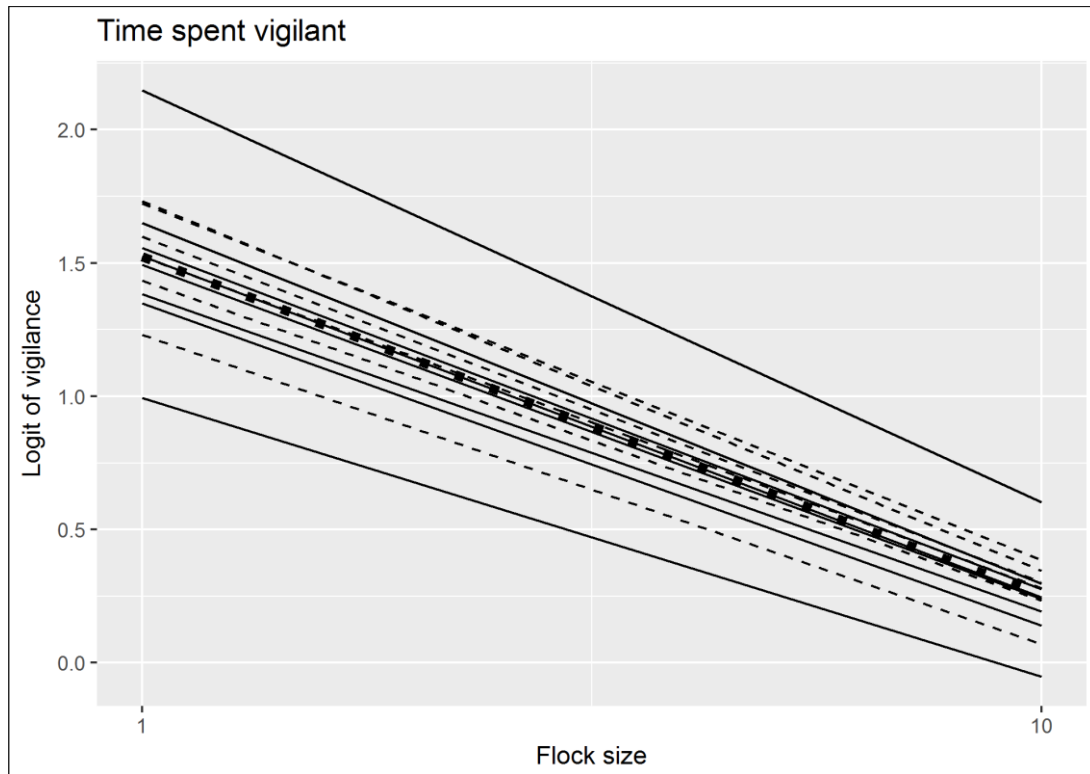


Fig. 3.3: Predicted relationships between the logit of the % of time spent vigilant and flock size in six female (dashes) and eight male (black lines) house sparrows. The large dotted line represents the average for the sample. Predicted values are derived from a linear mixed effect model of vigilance including random slopes and intercepts.

The frequency of vigilance bouts per min. ranged between 1.4 and 61.4 with a mean of 32.1. The frequency of vigilance bouts was not associated with flock size ($F_{1,231} = 0.10$, $p = 0.76$), sex ($F_{1,231} = 0.23$, $p = 0.63$) or month ($F_{1,231} = 0.39$, $p = 0.53$). Sparrow id explained 15.9% of the variation in the frequency of vigilance bouts, a significant effect (random intercepts: $\chi_1 = 20.1$, $p < 0.0001$). There was no evidence for individual variation in the strength of the flock size effect (random slopes: $\chi_2 = 2.0$, $p = 0.37$).

The frequency of high vigilance postures per min. decreased with flock size ($F_{1,231} = 29.8$, $p < 0.0001$), was higher in July (21.6; 17.8, 25.4) than in June (17.6; 14.3, 20.9) ($F_{1,231} = 5.8$, $p = 0.02$), but was not associated with sex ($F_{1,231} = 0.09$, $p = 0.76$). Sparrow id explained

a significant amount of the variation in the frequency of high vigilance postures (random intercepts: $\chi_1 = 72.1$, $p < 0.0001$). In flocks including one or two individuals, sparrow id explained 19.7% of the variation in the frequency of high vigilance postures. There was evidence for individual variation in the strength of the flock size effect (random slopes: $\chi_2 = 6.6$, $p = 0.04$; Fig. 3.4).

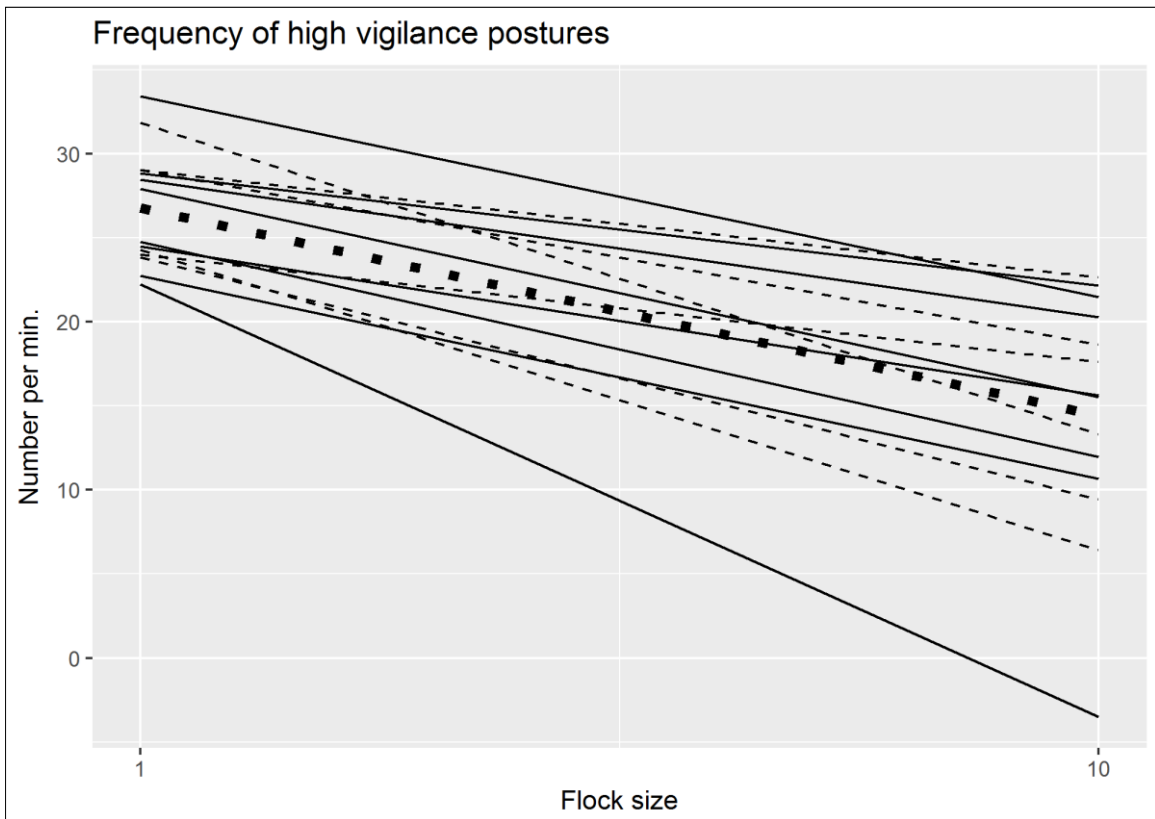


Fig. 3.4: Predicted relationships between the frequency of high vigilance postures (number per min.) and flock size in six female (dashes) and eight male (black lines) house sparrows. The large dotted line represents the average for the sample. Predicted values are derived from a linear mixed effect model of vigilance including random slopes and intercepts.

The duration of vigilance bouts in seconds decreased with flock size ($F_{1,231} = 20.1$, $p < 0.0001$), was higher in July (1.4; 1.2, 1.6) than in June (1.2; 1.0, 1.3) ($F_{1,231} = 9.5$, $p = 0.002$), but was not associated with sex ($F_{1,231} = 0.02$, $p = 0.88$). Sparrow id explained 21.6% of the variation in the duration of vigilance bouts, a significant effect (random intercepts: $\chi_1 = 39.1$,

$p < 0.0001$). There was no evidence for individual variation in the strength of the flock size effect (random slopes: $\chi^2 = 1.5$, $p = 0.47$).

Food intake rate (number of seeds per min.) increased with flock size ($F_{1,231} = 9.2$, $p = 0.003$), was lower in July (33.9; 29.4, 39.1) than in June (38.8; 34.7, 43.5) ($F_{1,231} = 4.4$, $p = 0.04$), but did not differ between the sexes ($F_{1,231} = 0.0$, $p = 0.97$). Sparrow id explained 17.2% of the variation in food intake rate, a significant effect (random intercepts: $\chi^1 = 28.5$, $p < 0.0001$). There was no evidence for individual variation in the strength of the flock size effect (random slopes: $\chi^2 = 0$, $p = 1$). Based on the intercept values from the above random coefficient models, sparrows that spent more time vigilant obtained food at a lower rate ($r = -0.83$, $p = 0.0003$, $n = 14$; Fig. 3.5).

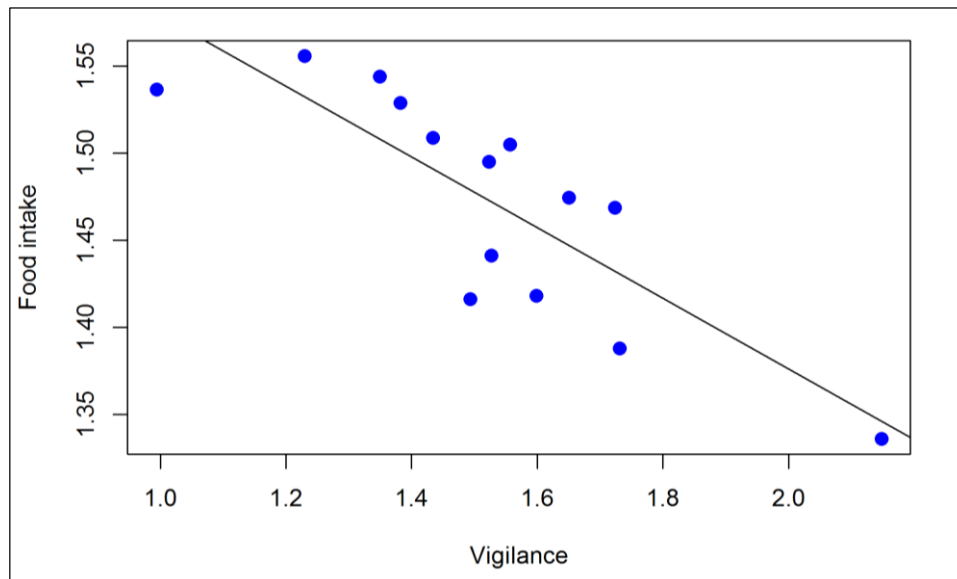


Fig. 3.5: More vigilant house sparrows obtained food at a lower rate ($n = 14$). The logarithm of food intake rate is plotted against the logit of the % of time spent vigilant. Values in the graph represent the intercepts of a linear mixed effect model including random slopes and intercepts.

Using intercept values from the random coefficient models, males with a larger bib spent less time vigilant ($r = -0.62$, $p = 0.10$, $n = 8$) and obtained food at a higher rate ($r = 0.73$, $p = 0.035$, $n = 8$). There was a positive correlation between intercepts and slopes for the frequency of high vigilance postures, but this was not statistically significant ($r = 0.48$, $p = 0.22$, $n = 8$).

Discussion

We uncovered several correlates of vigilance in house sparrow flocks, including well-known ones like flock size. In addition, we found evidence for consistent individual vigilance profiles over the time course of the study and evidence for different levels of plasticity amongst individuals in the group-size effect on vigilance. We discuss these different correlates in turn.

The percentage of time spent vigilant, the frequency of high vigilance postures, and the duration of vigilance bouts significantly decreased with flock size. The group-size effect on vigilance has also been documented in several other populations of house sparrows (e.g. Barnard 1980; Elgar 1989). Lower levels of vigilance probably reflect a lower perception of predation risk in larger flocks. Because sparrows foraged in small flocks and had access to a large supply of food, scramble competition for resources is probably less likely to explain why vigilance decreased with flock size (Beauchamp 2003).

Males and females showed the same level of vigilance and obtained food at the same rate. In addition, food intake rate for the two sexes increased monotonously with flock size. An earlier study found that female sparrows maintained more vigilance than males (Beveridge & Deag 1987), suggesting that females might spend time monitoring

threatening conspecifics as well as predators. Using a feeder the same size as ours, Johnson et al. (2004) found that food intake rate increased monotonously with flock size, suggesting little interference competition under such conditions and less need to monitor neighbours. The results suggest that interference competition was not acting strongly in our study, and that monitoring neighbours was not a priority.

Sparrows were more vigilant and fed at a lower rate in July compared to June despite no changes in food density. Other drivers of vigilance might have varied between the two months. We noted larger flocks later in the season and begging behaviour by some individuals, which suggest recruitment of juveniles to the flocks. Increased vigilance by adult sparrows (controlling for flock size) might be needed to protect vulnerable offspring. Mammals and birds have been shown to be more vigilant in the presence of juveniles (e.g. Seddon & Nudds 1994; Hunter & Skinner 1998; Treves et al. 2001; Di Blanco & Hirsch 2006; Lashley et al. 2014). Higher vigilance can also reflect warmer temperatures later in the study as sparrows would need less energy to maintain their temperature (i.e. lower feeding rates are needed, more time for vigilance) (Pravosudov & Grubb 1998).

Males with a larger bib tended to be less vigilant and fed at a higher rate. Bib size in sparrows increases with age and is also correlated with dominance status (Hein et al. 2003). In another study, males with larger bibs tended to be more dominant but displayed less aggression (Hein et al. 2003). The time thus saved could be used to obtain more food. Lower vigilance might also betray less need to monitor threatening neighbours (Pravosudov & Grubb 1999). However, as noted earlier, we found little evidence for interference competition in our flocks, suggesting that other correlates of bib size might be more

relevant. In Eurasian siskins (*Carduelis spinus*), males with larger bibs spent more time vigilant but obtained food at the same rate as other males (Pascual & Senar 2014). More vigilance might be expected for siskins with larger bibs because bib size is correlated with higher risk taking in this species. It is not clear whether bib size also correlates with risk taking in house sparrows.

We found evidence for consistent individual differences in overall time spent vigilant, in the frequency of vigilance, and in the duration of vigilance bouts. Food intake rate also varied significantly amongst individuals. Up to about 20% of the variation in vigilance could be explained by individual variation. In addition, we documented individual variation in the relationship between the frequency of high vigilance postures and flock size, thus providing evidence for plasticity in the group-size effect on vigilance. Sparrows can maintain vigilance when handling seeds with the head up. Stretching the body to maintain high vigilance is more costly because individuals stop feeding during such bouts. This is probably why individual variation in the willingness to take risk was more apparent with the vigilance posture associated with the highest cost.

Many species show consistent individual variation in vigilance including eastern grey kangaroo (*Macropus giganteus*) (Favreau et al. 2014) and the redshank (*Tringa totanus*) (Couchoux & Cresswell 2012). Few studies, however, have focused on plasticity in the group-size effect on vigilance. One study found evidence for plasticity (Carter et al. 2009), but not the others (Rieucou et al. 2010; Dannock et al. 2013; Favreau et al. 2014). It is not clear whether the contrasting results indicate differences in statistical power or methodology or whether plasticity in the group-size effect on vigilance can vary across

species. Individual variation in food intake rate has been noted in several other species including house sparrows (Johnson et al. 2001).

Individual variation in vigilance could be explained by stable differences in state-dependent variables such as energy reserves, size, and/or condition in the population (State-dependent hypothesis : Sih et al. 2015) and/or by negative frequency-dependent payoffs. State-dependent explanations predict a correlation between slopes and intercepts in the random coefficient models. We found evidence for a large positive correlation between slopes and intercepts for the high vigilance posture ($r = 0.48$), but this remains to be validated with a larger sample size. One potential state variable to consider in this study is age. Older individuals could invest less in vigilance and show less adjustment in vigilance with flock size (Sih et al. 2015). This fits with the finding that males with larger bills, which are presumably older, invested less in vigilance. Future studies with marked birds of known ages are needed to confirm this hypothesis.

In our study, more vigilant individuals obtained food at a lower rate, which is not immediately obvious given that in sparrows much of the feeding occurs in the vigilant posture. Models suggest that vigilance levels increase with energy reserves (McNamara & Houston 1992). In this case, the negative relationship between vigilance and food intake rate would predict a gradual convergence of energy reserves across individuals over time. Therefore, we would not expect to see stable individual differences in vigilance based on energy reserves in this population unless other factors influence energy reserves. For instance, more dominant individuals could limit access to resources to subordinates, which would maintain their reserves at a consistently low level (Sih et al. 2015). With our large

feeder, we saw few aggressive interactions amongst individuals. With a smaller feeder, the need to monitor neighbours might increase and dominance could have an impact on energy reserves, which could contribute to individual differences in vigilance and plasticity.

In conclusion, we found evidence for consistent individual variation in vigilance and plasticity in response to variation in flock size. We also present evidence that such differences might be associated with state-dependent variables. Future work is needed to determine the mechanisms responsible for the maintenance of consistent individual differences in vigilance.

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Chapitre IV : Discussion générale

Tel qu'élaboré dans l'introduction, la vie en groupe permet de diminuer le risque de prédation pour un individu grâce plusieurs mécanismes comme l'effet de dilution, l'effet de confusion, la détection hâtive ainsi que l'avertissement mutuel. Cependant, l'efficacité du transfert d'informations chez les espèces sans cris d'alarme reste très peu étudiée. En effet, plusieurs articles publiés à ce sujet dans la littérature semblent contradictoires. Le chapitre 2 du mémoire démontre l'efficacité de l'avertissement mutuel chez le moineau domestique. Un autre questionnement en lien à la vigilance est abordé dans l'introduction : l'hétérogénéité de l'effet de la taille du groupe. À maintes reprises, une relation inversement proportionnelle entre la taille du groupe et la vigilance a été observée chez différentes espèces animales. Néanmoins, l'ampleur de cet effet, voire sa présence, varie d'une espèce à l'autre et parfois même entre différentes populations. Un élément pouvant contribuer à cette discordance est la personnalité animale. Il pourrait donc y avoir différents profils de vigilance dans une population indépendamment de l'environnement présent. Une variation individuelle de plasticité, c'est-à-dire une capacité d'adaptation à l'environnement, est aussi possible. La présence de l'effet de la taille du groupe chez le moineau domestique est montrée en outre dans le troisième chapitre de même que, la présence de profils de vigilance et de plasticité individuels différents.

Les deux projets de recherche ont permis de faire la lumière sur plusieurs facteurs qui influencent les bénéfices reliés à la vie en groupe chez le moineau domestique. Le premier projet s'attardait à l'avertissement mutuel et plus particulièrement à la relation

entre les temps de réaction dans un groupe suite à une fausse alarme et trois facteurs : la taille du groupe, l'étalement entre les individus et le risque de prédation. Selon nos résultats, l'avertissement mutuel semble efficace chez le moineau malgré l'absence de cris d'alarme. En effet, il y a un raccourcissement des temps de réaction et un étalement moindre dans le groupe lorsque le risque de prédation est plus élevé, suggérant que les moineaux retirent des avantages de l'avertissement mutuel. De façon plus surprenante, les temps de réaction étaient plus courts dans les grands groupes alors que les individus dans ces grands groupes sont supposément plus à l'abri de la prédation. Toutefois, il se peut que ces grands groupes attirent plus les prédateurs. De plus, le niveau de vigilance au niveau du groupe peut être plus élevé en dépit de la réduction de la vigilance individuelle ce qui favoriserait des temps de réaction plus courts. Une étude plus approfondie de l'impact du risque de prédation sur la vigilance est nécessaire pour confirmer cette hypothèse chez le moineau domestique.

Le deuxième article se penchait sur l'évaluation de la vigilance comme un trait de personnalité et sa plasticité chez le moineau domestique. Des profils de vigilance différents ont été identifiés chez 14 individus. De plus, une variation de la plasticité de la vigilance en fonction de la taille du groupe a été observée en lien à l'évaluation de la posture de haute vigilance. Ainsi, tous les individus ne semblent pas bénéficier des mêmes avantages de la vie en groupe. L'état d'un individu (e.g. âge, réserve énergétique) est possiblement responsable de l'apparition et du maintien de ces différences individuelles. Plus de travaux sont nécessaires afin d'évaluer les mécanismes derrière l'établissement de celles-ci.

Les observations présentées dans ce travail ont été concentrées sur une espèce dans son milieu. Les études éthologiques dans de tels cas améliorent notre compréhension des différentes questions proposées par Tinbergen. Cette recherche est fondamentale en principe mais peut être appliquée aux espèces domestiques ou de production. La discipline du comportement animal appliqué, qui se concentre sur le comportement des espèces domestiques comme le chien ou de production comme la vache, se fonde sur les résultats d'études plus fondamentales chez des espèces comme le moineau afin d'améliorer leur mieux-être. Il est clair qu'une connaissance de l'éthologie est utile en médecine vétérinaire (Sambraus 1998). Par exemple, la vigilance chez la vache peut nous informer sur la présence de peur (Welp et al. 2004). La vigilance et l'approvisionnement en nourriture sont souvent considérés mutuellement exclusifs. Ainsi, une vache ayant une vigilance élevée (peur augmentée) risque de présenter une production laitière diminuée. Bref, une connaissance du comportement normal de nos animaux nous aidera grandement à déceler l'anormal et à améliorer leur bien-être.

Conclusion

Ce mémoire se penche sur les différents mécanismes permettant une diminution du risque de prédation chez des espèces grégaires. Les chapitres 2 et 3 montrent plusieurs faits saillants de la vigilance chez le moineau domestique. Tout d'abord, l'avertissement mutuel semble être efficace malgré l'absence de cris d'alarme particulièrement chez les grands groupes. De plus, différents profils de vigilance et de plasticité nuancent l'importance de

l'effet de la taille du groupe chez l'individu ainsi que ses bénéfices associés. Finalement, l'éthologie est primordiale en médecine vétérinaire afin d'élargir notre arsenal de connaissances permettant de mieux aider nos patients.

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