Université de Montréal

Effets de la consanguinité dans des modèles de sélection pour des populations structurées en familles

par

Ghislain Rocheleau

Département de mathématiques et de statistique

Faculté des arts et sciences

Thèse présentée à la Faculté des études supérieures

en vue de l'obtention du grade de

Ph.D. en statistique

Décembre 2002

Université de Montréal

Faculté des études supérieures

Cette thèse intitulée

Effets de la consanguinité dans des modèles de sélection pour des populations structurées en familles

présentée par

Ghislain Rocheleau

a été évaluée par un jury composé des personnes suivantes:

.....

président-rapporteur

.....

directeur de recherche

.....

membre du jury

.....

examinateur externe

.....

représentant du doyen de la FES

Résumé

Cette thèse est consacrée à l'étude des effets de la consanguinité et de la sélection dans les modèles avec consanguinité partielle. Le Chapitre 1 entreprend une analyse détaillée du modèle d'autofécondation partielle avec sélection pour un locus à deux allèles. On montre qu'un équilibre polymorphique ne peut exister que dans les cas de surdominance ou de sousdominance des hétérozygotes et seulement pour certaines valeurs du taux d'autofécondation. Lorsqu'il existe, on montre l'unicité d'un tel équilibre. Une analyse de stabilité locale de l'équilibre polymorphique et des états de fixation est effectuée et révèle que seule la surdominance peut maintenir un polymorphisme dans la population. Lorsque l'analyse linéaire est non concluante, une analyse quadratique est réalisée. Pour certaines combinaisons de valeurs sélectives, on démontre la convergence globale. Finalement, on compare les résultats obtenus dans ce modèle avec ceux du modèle panmictique.

Confronté à la complexité de conduire une étude semblable dans le modèle avec accouplement frère-soeur partiel, une formule générale pour l'approximation dans le changement de fréquence d'un allèle mutant est déduite et rigoureusement prouvée sous l'hypothèse de sélection faible. On suppose que l'allèle est introduit en petite quantité dans une population originalement à l'état de fixation. Des conditions exactes d'invasion de cet allèle sont déduites pour un locus autosome dans le modèle d'autofécondation partielle, ainsi que pour un locus autosome et un locus lié au sexe dans le modèle d'accouplement frère-sœur partiel. On montre que ces conditions impliquent des coefficients d'apparentement entre les individus d'un couple reproducteur. Ceci peut s'interpréter comme un effet dû à la sélection de parentèle causé par la consanguinité, même si aucune interaction intra-familiale n'affecte leur viabilité.

Dans le Chapitre 3, on étend les résultats obtenus au chapitre précédent en considérant des valeurs sélectives basées sur des stratégies mixtes. Des interactions deux-à-deux, classiques dans la théorie ESS, sont admises quoique restreintes aux

individus d'une même fratrie. Deux hypothèses de sélection faible sont considérées: une première supposant de petites différences dans les valeurs génotypiques déterminant les stratégies mixtes, et une deuxième admettant de petites différences dans les viabilités. Sous la première hypothèse, on montre que les conditions de protection d'un allèle mutant rare équivalent à des conditions d'invasion initiale obtenues dans les modèles additifs de sélection de parentèle. Dans un contexte particulier d'altruisme, on fournit des intervalles de valeurs pour la proportion d'accouplements consanguins, basés sur un rapport coût-bénéfice, permettant l'invasion de cet allèle dans la population. Sous la deuxième hypothèse, on ne peut obtenir de tels intervalles à moins d'imposer de sévères restrictions sur les paramètres de viabilité. L'analyse confirme que la consanguinité ne favorise pas nécessairement l'altruisme.

Enfin, une généralisation possible appliquée à des populations structurées en petits groupes est discutée. Une étude exploratoire des modèles avec migration partielle avant ou après accouplement est effectuée et suggère qu'un coefficient d'apparentement indépendant des fréquences alléliques et des valeurs génotypiques pourrait être utilisé dans la formule du changement de fréquence d'un allèle mutant rare sous la sélection faible.

Mots clés: Autofécondation – Accouplement frère-sœur – Convergence globale – Topographie adaptative – Parentèle – Dispersion

Summary

This thesis is devoted to the study of the effects of inbreeding and selection in partial inbreeding models. Chapter 1 undertakes a detailed analysis of the one-locus two-allele partial selfing selection model. It shows that a polymorphic equilibrium can exist only in the cases of overdominance or underdominance of heterozygotes and only for a certain range of selfing rates. When it exists, the polymorphic equilibrium is shown to be unique. A local stability analysis of the polymorphic equilibrium and fixation states is carried out and reveals that only overdominance can maintain polymorphism in the population. When the linear analysis is inconclusive, a quadratic analysis is performed. For some sets of selective values, global convergence is demonstrated. Finally, a comparison between results obtained under this model and those under the random mating model is done.

Due to the complexity of conducting a similar study in the partial sib-mating model, a general formula approximating the change in frequency of a mutant allele under weak selection is deduced and rigorously proven. It is assumed that this allele is introduced in small frequency into a population previously at a fixation state. Exact conditions for invasion of this allele are deduced at an autosomal locus in the partial selfing model and at an autosomal as well as a sex-linked locus in the partial sib-mating model. It is shown that these conditions involve relatedness coefficients between mates. This can be interpreted as a kin selection effect caused by inbreeding, even if no interaction between kin affects their viability.

In Chapter 3, results obtained in the preceding chapter are extended to selective values based on mixed strategies. Pairwise interactions, classical in ESS theory, are assumed but restricted to individuals within the same sibship. Two different hypotheses of weak selection are considered, one applied through small differences in genotypic values determining mixed strategies, the other through small differences in viabilities. Under the first hypothesis, it is shown that conditions for protection of a rare mutant allele are tantamount to conditions for initial increase in

frequency obtained in additive kin selection models. In a particular context of altruism, explicit ranges of values for the proportion of inbred matings, based on cost-benefit ratios, allowing the spread of this allele in the population are provided. Under the second hypothesis, such ranges of values cannot be obtained unless stringent restrictions are imposed on viability parameters. The analysis confirms that inbreeding does not necessarily promote altruism.

Finally, a possible generalization to populations structured in small mating groups is discussed. An exploratory study of models with partial migration before or after mating is accomplished and suggests that a relatedness coefficient independent of allelic frequencies and genotypic values could be used into the formula for the change in frequency of a rare mutant allele under weak selection.

Key words: Selfing – Sib-mating – Global convergence – Adaptive topography – Kin – Dispersion

Table des matières

Liste des Tableaux x

Liste des Figures xi

Remerciements xii

INTRODUCTION 1

CHAPITRE 1: ***STABILITY ANALYSIS OF THE PARTIAL SELFING SELECTION MODEL***

ABSTRACT 16

1.1 *INTRODUCTION* 17

1.2 *MODEL* 19

1.3 *EQUILIBRIUM CONDITIONS* 22

1.4 *STABILITY OF POLYMORPHIC EQUILIBRIA* 30

1.4.1 *Case of overdominance without symmetry* 31

1.4.2 *Case of underdominance without symmetry* 33

1.5 *STABILITY OF THE FIXATION STATES* 35

1.5.1 *Case of overdominance without symmetry* 35

1.5.2 *Case of underdominance without symmetry* 40

1.6 *SPECIAL CASES* 42

1.6.1 *Case of directional selection* 42

1.6.2 *Case of complete dominance* 43

1.6.3 *Case of symmetric selection* 44

1.6.4 *Case of a lethal homozygote* 47

1.6.5 *Case of a lethal heterozygote* 49

1.7 *DISCUSSION* 52

1.8 *SUMMARY* 58

CHAPITRE 2: ***CHANGE IN FREQUENCY OF A RARE MUTANT ALLELE: A GENERAL FORMULA AND APPLICATIONS TO PARTIAL INBREEDING MODELS***

ABSTRACT 60

2.1 *INTRODUCTION* 61

2.2 *FRAMEWORK AND BASIC RESULTS* 63

2.3 *PARTIAL SELFING MODEL* 66

2.4 *PARTIAL SIB-MATING MODEL* 70

2.5 *PARTIAL SIB-MATING MODEL FOR SEX-LINKED GENES* 77

2.6 *DISCUSSION* 82

CHAPITRE 3: ***NEW INSIGHTS INTO KIN SELECTION THEORY IN FAMILY-STRUCTURED POPULATIONS WITH INBREEDING***

ABSTRACT 86

3.1 *INTRODUCTION* 87

3.2 *FAMILY-SPECIFIC FITNESSES BASED ON STRATEGIES* 92

3.3 *RECURRENCE EQUATIONS UNDER REGULAR SYSTEMS OF MATING* 95

3.3.1 *Partial selfing model* 95

3.3.2 *Partial sib-mating model: case of an autosomal locus* 96

3.3.3 *Partial sib-mating model: case of a sex-linked locus* 97

3.4 *CONDITIONS FOR PROTECTION OF A RARE MUTANT ALLELE UNDER WEAK SELECTION* 100

3.4.1 *Case of small differences in mixed strategies* 100

3.4.2 *Case of small differences in viabilities* 103

3.5 *A KIN SELECTION PERSPECTIVE* 107

3.5.1 *Case of small differences in mixed strategies* 107

3.5.2 *Case of small differences in viabilities* 112

3.6 *DISCUSSION* 116

CONCLUSION 121

BIBLIOGRAPHIE 128

Appendice A: Preuves du Chapitre 1

A.1 *Proof of Result 1.5* xiii

A.2 *Proof of Result 1.6* xv

A.3 *Proof of Result 1.8* xv

A.4 *Proof of Result 1.10* xvii

A.5 *Proof of Result 1.11* xviii

A.6 *Proof of Result 1.12* xx

A.7 *Proof of Result 1.13 and 1.14* xx

Appendice B: Preuves et compléments du Chapitre 2

B.1 *Proof of Result 2.1* xxv

B.2 *Proof of Result 2.2* xxvii

B.3 *Coefficients of regression for the partial sib-mating models* xxxiii

B.4 *Matrix of linear approximation for autosomal genes in partial sib-mating populations* xxxv

Appendice C: Matrices d'approximation linéaire pour les modèles d'accouplement frère-sœur partiel du Chapitre 3

C.1 *Case of small differences in mixed strategies (autosomal locus)* xxxvi

C.2 *Case of small differences in mixed strategies (sex-linked locus)* xxxvii

C.3 *Case of small differences in viabilities (autosomal locus)* xxxviii

C.4 *Case of small differences in viabilities (sex-linked locus)* xxxix

Appendice D: Calcul des coefficients d'identité et d'apparentement utilisés dans les Chapitres 1, 2 et 3

D.1 Coefficients d'identité par descendance xl

D.2 Coefficients d'apparentement xlvii

D.3 Coefficients d'apparentement avec consanguinité partielle liv

Appendice E: Coefficients d'apparentement pour populations structurées lviii

Liste des Tableaux

Table 1.1 *Conditions for a (unique) polymorphic equilibrium to exist* 28

Table 1.2 *Comparative results under the panmictic model and the partial selfing model* 53

Table 2.1 *Male × female mating types in the current generation and male × female couples of sibs produced in the next generation* 71

Table 2.2 *Mating types in the current generation and couples of sibs produced in the next generation for a sex-linked locus* 77

Table 3.1 *Conditions for protection of a rare mutant allele under three partial inbreeding models* 111

Tableau D.1 Distributions conjointe et marginales des génotypes de deux individus *I* et *J*, avec la fréquence du gène A_1 et la valeur génotypique correspondantes xlviii

Tableau D.2 Distributions conjointe et marginales des génotypes (a) d'une femelle *I* et d'un mâle *J*, (b) de deux mâles J_1 et J_2, avec la fréquence du gène A_1 et la valeur génotypique correspondantes li

Tableau E.1 Valeurs numériques des rapports de probabilités dans le modèle de dispersion après accouplement lxxxii

Tableau E.2 Valeurs numériques des rapports de probabilités dans le modèle de dispersion avant accouplement lxxxiii

Liste des Figures

Figure 1.1 *Life cycle and notation*.....21

Figure 2.1 *Life cycle and notation for genotypic and allelic frequencies in the partial selfing model*.....67

Figure 2.2 *Life cycle and notation for frequencies in males and females in the partial sib-mating model*.....70

Figure D.1 Situations restreintes d'identité entre les gènes de I et J.....xl

Figure D.2 (a) Situations restreintes d'identité entre les gènes d'une femelle I et d'un mâle J (b) Situations restreintes d'identité entre les gènes de deux mâles J_1 et J_2.....xlv

Figure E.1 Courbes des rapports de probabilités $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ obtenus dans le modèle diploïde de dispersion après accouplement, en fonction du paramètre κ et pour certaines valeurs fixées de N.....lxxix

Figure E.2 Courbes des rapports de probabilités $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ obtenus dans le modèle diploïde de dispersion avant accouplement, en fonction du paramètre $\kappa = \kappa_1 = \kappa_2$ et pour certaines valeurs fixées de N. Pour $N = 1$, les trois courbes sont en tous points identiques.....lxxix

Figure E.3 Courbes des rapports de probabilités (a) $\hat{f}_{I_1I_2}/\hat{f}_{I_1I_1}$, $\hat{\delta}_{I_1I_2}/\hat{\delta}_{I_1I_1}$ et $\hat{\gamma}_{I_1I_2}/\hat{\gamma}_{I_1I_1}$ pour deux individus diploïdes I_1 et I_2, (b) $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ pour un individu diploïde I et un individu haploïde J, obtenus dans le modèle haplo-diploïde de dispersion après accouplement, en fonction du paramètre κ et pour certaines valeurs fixées de N.....lxxx

Figure E.4 Courbes des rapports de probabilités (a) $\hat{f}_{I_1I_2}/\hat{f}_{I_1I_1}$, $\hat{\delta}_{I_1I_2}/\hat{\delta}_{I_1I_1}$ et $\hat{\gamma}_{I_1I_2}/\hat{\gamma}_{I_1I_1}$ pour deux individus diploïdes I_1 et I_2, (b) $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ pour un individu diploïde I et un individu haploïde J, obtenus dans le modèle haplo-diploïde de dispersion avant accouplement, en fonction du paramètre $\kappa = \kappa_1 = \kappa_2$ et pour certaines valeurs fixées de N. Pour $N = 1$, les trois courbes en (a) d'une part, et les trois courbes en (b) d'autre part, sont en tous points identiques.....lxxxi

Remerciements

Cette thèse représente le fruit d'un travail laborieux échelonné sur quelques années et j'en suis particulièrement fier. Il m'a fallu énormément de patience et de persévérance, surtout dans la dernière année de rédaction. Mais je n'aurais pu y arriver sans le soutien moral et financier de mon directeur de thèse, Sabin Lessard, qui a fait preuve lui aussi de beaucoup de patience. Durant ces quelques années de collaboration, il a su m'inculquer des valeurs essentielles à la recherche, notamment la rigueur et l'intégrité. Je ne saurais trop le remercier à cet égard. Je remercie également ma conjointe, Marie-Eve, pour son appui indéfectible et ses encouragements. Elle m'a également fourni une aide précieuse dans la confection du tapuscrit de cet ouvrage. Enfin, un merci tout personnel à mes enfants, Anne-Elyse et Louis-Simon, qui m'ont apporté d'intenses moments de plaisir et de joie, fortement appréciés tout au long de l'élaboration de cette thèse.

Introduction

La structure génétique d'une population peut varier en fonction d'un grand nombre de facteurs évolutifs tels que la mutation génique, la migration, la sélection, pour n'en nommer que quelques-uns. Ces facteurs (et beaucoup d'autres) modifient la structure génique de la population en favorisant, par exemple, la fréquence d'un gène au détriment des autres gènes. Ainsi, un état polymorphique (où plus d'un allèle est présent dans la population) soumis aux pressions évolutives de ces facteurs pourrait éventuellement disparaître au profit d'un des états de fixation (où un et un seul allèle est présent dans la population). Un autre facteur modifiant la structure génétique d'une population est la consanguinité. La consanguinité résulte principalement d'un accouplement entre individus apparentés. Étant donné que ces individus partagent un ou plusieurs ancêtres communs dans leur pedigree respectif, un rejeton issu de ce couple aura donc tendance à hériter de gènes "semblables" (on donnera plus loin une définition précise de cette similarité entre gènes).

Cette thèse par articles est consacrée à l'étude de modèles dynamiques où interviennent conjointement la sélection et la consanguinité. La sélection est appliquée au stade zygotique et s'exprime par des différences de viabilité entre les génotypes. Plus précisément, ces différences signifient que la probabilité de survie d'un individu du moment de sa conception jusqu'au stade adulte (pré-reproducteur) dépend de son génotype au locus concerné. La consanguinité, quant à elle, est engendrée par des accouplements entre individus apparentés, lesquels accouplements sont donnés explicitement dans les modèles étudiés. Ces modèles, classiques en génétique des populations, font partie d'une classe de modèles dits de consanguinité partielle. Dans cette thèse, deux modèles avec consanguinité partielle sont étudiés: un premier modèle avec autofécondation partielle (traduction libre de *partial selfing model*) et un deuxième avec accouplement frère-sœur partiel (traduction libre de *partial sib-mating model*). Essentiellement, ces deux modèles supposent que la population est de taille infinie (les fluctuations aléatoires étant donc réputées négligeables), que les générations sont discrètes et séparées (chaque individu

appartient à une et une seule génération) et que la transmission des gènes d'une génération à la suivante s'effectue par ségrégation Mendélienne.

Dans le modèle avec autofécondation partielle, chaque individu peut se reproduire, soit par autofécondation (union de deux gamètes produits par le même individu) avec une certaine probabilité, soit par fécondation au hasard (union de deux gamètes produits par deux individus différents non-apparentés) avec probabilité complémentaire. Dans le monde végétal, il n'est pas rare d'assister à l'autofécondation, bien que chez certaines espèces, plusieurs mécanismes existent pour empêcher ce mode de reproduction. Mise à part la parthénogenèse, l'autofécondation conduit à l'une des formes les plus extrêmes de consanguinité. Dans le modèle avec accouplement frère-sœur partiel, chaque individu peut s'accoupler soit avec un membre de sa fratrie (frère ou sœur, selon le cas) avec une certaine probabilité, soit avec un individu non-apparenté, choisi au hasard dans la population, avec probabilité complémentaire. L'accouplement frère-sœur représente la forme la plus extrême de consanguinité impliquant deux individus distincts appartenant à la même génération. Ce type d'accouplement est d'usage courant dans l'élevage animal, par exemple, lorsqu'on désire obtenir une lignée plus "pure" relativement à un caractère fortement recherché.

Conséquences de la consanguinité

Les modèles avec consanguinité partielle décrits ci-haut engendrent de la consanguinité du seul fait qu'ils permettent l'accouplement entre individus apparentés. Cependant, contrairement à la sélection, la consanguinité seule ne modifie pas les fréquences des gènes dans une population de taille infinie; tout au plus, elle occasionne une redistribution plus stable des gènes entre les individus de la population. En effet, en absence de sélection, les équations de récurrence décrivant le passage d'une génération à la suivante convergent vers un état polymorphique qui ne dépend que des fréquences des gènes initialement présents dans la population (voir, par exemple, Karlin, 1968). Toutefois, ce réarrangement de gènes favorise les

génotypes homozygotes au détriment des génotypes hétérozygotes. Il en résulte alors une perte d'hétérozygotie dans la population, les fréquences génotypiques ne se conformant plus aux proportions espérées par le principe de Hardy-Weinberg. Cette perte d'hétérozygotie peut être mesurée à l'aide d'un indice de fixation (aussi appelé indice d'écart à la panmixie) (Wright, 1951). Cet indice représente la réduction en hétérozygotes dans la population à une génération donnée relativement à la proportion d'hétérozygotes espérée par le principe de Hardy-Weinberg. Dans les modèles de consanguinité partielle évoqués plus haut et en absence de différences sélectives entre les génotypes, cet indice tend vers une valeur limite, exprimée comme une fonction de la probabilité d'un accouplement consanguin, à mesure que le nombre de générations écoulées devient de plus en plus grand (voir, p. ex., Karlin, 1968). Dans tous ces modèles, cet indice de fixation, en absence de sélection, ne dépend pas de la composition génique de la population mais plutôt de l'identité entre les gènes formant un individu.

Mesures de la consanguinité

Il existe plusieurs façons de mesurer la consanguinité, car l'appellation même de consanguinité est un terme quelque peu galvaudé, servant à décrire diverses situations en apparence similaires (Jacquard, 1975). Dans cette thèse, trois mesures particulières sont utilisées: le coefficient de consanguinité, le coefficient de parenté et le coefficient d'apparentement. Bien que les vocables les désignant semblent décrire une même réalité et par conséquent, peuvent porter à confusion, chaque coefficient exprime une facette particulière de la consanguinité.

Le coefficient de consanguinité F a été introduit par Wright (1922) pour calculer explicitement la proportion par laquelle est réduite l'hétérozygotie dans la population. Lorsque $F = 0$, il n'y a aucune perte d'hétérozygotie et les fréquences des génotypes dans la population respectent les proportions de Hardy-Weinberg. Lorsque $F = 1$, la perte en hétérozygotes est totale, si bien qu'il ne subsiste dans la population que des individus homozygotes. À l'origine, l'auteur avait déduit ce coefficient en

exploitant les liens statistiques entre individus apparentés. De ce point de vue, le coefficient de consanguinité peut s'interpréter comme le coefficient de corrélation entre deux gamètes qui s'unissent pour former un individu (voir, p. ex., Crow & Kimura, 1970). Plus tard, une approche alternative fondée sur la théorie des probabilités a défini F comme étant la probabilité que les deux gènes portés par les gamètes formant un individu soient identiques par descendance. Par définition, deux gènes homologues sont dits identiques par descendance si ces deux gènes sont des copies d'un même gène provenant d'un ancêtre commun. Il ne faut pas confondre le concept d'identité par descendance avec celui, moins restrictif, d'identité allélique (Gillois, 1965). Ainsi, deux gènes peuvent produire le même effet, c'est-à-dire appartenir à une même classe allélique, sans être les copies d'un même gène ancestral.

Le coefficient de consanguinité F_I d'un individu I permet donc de mesurer la consanguinité propre à un seul individu. Le coefficient de parenté f_{IJ}, quant à lui, mesure la consanguinité entre deux individus I et J (les indices I et J pouvant désigner un même individu). Il est défini comme la probabilité qu'un gène choisi au hasard chez I soit identique par descendance à un gène choisi au hasard au même locus chez J (Malécot, 1948). Habituellement, le calcul de cette probabilité est effectué en considérant toutes les situations possibles d'identité par descendance entre les quatre gènes homologues de deux individus diploïdes I et J (Gillois, 1964). En ne tenant pas compte de l'origine (paternelle ou maternelle) de chacun des gènes, les situations d'identité pour une population diploïde se réduisent à neuf situations restreintes d'identité (Jacquard, 1974). À chacune de ces situations restreintes d'identité est attachée une probabilité de réalisation Δ_i (i = 1, 2, ..., 9) appelée coefficient restreint d'identité. Dans une population haplo-diploïde ou dans le cas d'un locus lié au chromosome X, les mâles étant haploïdes et les femelles diploïdes, il faut cependant considérer toutes les situations d'identité entre deux individus diploïdes, entre un individu diploïde et un individu haploïde et enfin, entre deux individus haploïdes. Dans l'appendice D, ces situations d'identité ainsi que les coefficients restreints d'identité s'y rapportant sont clairement précisés. On montre également la procédure utilisée pour établir les valeurs limites des coefficients d'identité dans les modèles

avec consanguinité partielle. L'auteur du présent ouvrage n'a pas pu retracer dans la littérature le calcul de ces limites dans les modèles susmentionnés et, à cet égard, désirait les incorporer dans celui-ci.

Le coefficient d'apparentement est apparu dans les travaux marquants de William D. Hamilton sur l'évolution des comportements sociaux (altruisme, soins parentaux, caste d'ouvrières stériles chez les insectes sociaux, etc.). Dans sa définition de valeur sélective globale, Hamilton (1963, 1964) suggérait l'emploi du coefficient de relation de Wright pour décrire "l'apparentement" entre altruistes et bénéficiaires. Toutefois, ce coefficient s'avérait insuffisant pour décrire les liens génétiques entre individus dans des modèles avec consanguinité. Par la suite (voir, p. ex., Michod & Hamilton, 1980, Seger, 1981), dans les modèles d'altruisme à un locus et deux allèles, le coefficient d'apparentement $R_{I\to J}$ d'un individu I à un autre individu J a été défini plus généralement comme le rapport de deux covariances: la covariance entre la fréquence de l'allèle altruiste chez J et la valeur génotypique de I sur la covariance de ces deux quantités chez I. Dans ces modèles, la valeur génotypique d'un individu représente "... *la propension à l'altruisme, mesurée par la probabilité d'adopter un comportement altruiste selon le génotype au locus en question*" (Lessard, 1996). En s'inspirant de Michod & Hamilton (1980), l'appendice D propose une méthode basée sur les coefficients restreints d'identité, applicable autant dans une population haplo-diploïde que dans une population diploïde.

Dans les modèles avec consanguinité partielle, du moins ceux impliquant autofécondation ou accouplement frère-sœur, Lessard (1992) a montré que le coefficient d'apparentement $R_{I\to J}$, en absence de sélection, se réduisait à un indice basé sur le pedigree de I et J, indépendamment des valeurs génotypiques individuelles et des fréquences alléliques dans la population. Cet indice s'exprime comme le rapport du coefficient de parenté entre I et J sur le coefficient de parenté de I avec lui-même. En outre, cet indice correspond exactement au coefficient de régression de la fréquence d'un allèle donné chez J sur la fréquence de ce même allèle chez I. Dans l'appendice D, les coefficients d'apparentement apparaissant dans les modèles avec

consanguinité partielle étudiés dans cette thèse sont donnés de façon explicite. Dans l'Appendice E, ces coefficients sont étudiés dans le cas plus général de populations structurées en petits groupes avec migration partielle avant ou après accouplement.

Conséquences de la sélection

Tel que mentionné précédemment, la sélection est rendue par des différences de viabilité entre les génotypes. Ces différences s'expriment à travers des coefficients, appelés valeurs sélectives génotypiques, proportionnels aux probabilités de survie de la conception à l'âge adulte. À des fins de simplification, ces valeurs sélectives sont généralement réputées constantes d'une génération à l'autre. Dans le Chapitre 1, la valeur sélective d'un individu ne dépendra que de son génotype au locus concerné, tandis que dans le Chapitre 2, celle-ci variera à la fois en fonction du génotype et du sexe de l'individu. Dans le Chapitre 3, la valeur sélective d'un individu dépendra, non seulement de son génotype et de son sexe, mais aussi de la stratégie adoptée par celui-ci, une stratégie étant définie comme un comportement (phénotype) adopté par l'individu, généralement en forte corrélation avec son génotype au locus en question. La valeur sélective de cet individu dépendra aussi de la stratégie adoptée par ses frères et sœurs. Cette dernière forme de sélection (*frequency-dependent selection*) impliquant des interactions entre individus apparentés s'inspire fortement de la théorie sur les stratégies "évolutionnairement" stables (*ESS theory*, Maynard Smith & Price, 1973).

Peu importe la forme que prend la sélection, son effet le plus marquant est de modifier les fréquences des gènes dans la population. En absence de sélection, on peut facilement montrer que, dans les modèles avec consanguinité partielle considérés dans cette thèse, les fréquences des génotypes se "réarrangent" selon une configuration plus stable mais que les fréquences des gènes demeurent inchangées. En présence de sélection toutefois, les équations de récurrence décrivant le passage d'une génération à la suivante deviennent des transformations non linéaires, d'où la difficulté accrue de déterminer de façon analytique les points d'équilibre et la stabilité de tels points.

Néanmoins, dans le Chapitre 1, une étude approfondie du modèle d'autofécondation partielle avec sélection pour un locus à deux allèles est proposée. Un examen exhaustif de toutes les combinaisons de valeurs sélectives permet de dégager des conditions exactes pour lesquelles un équilibre polymorphique existe et l'unicité d'un tel point. Ces nouveaux résultats complètent ainsi ceux présentés, notamment, par Workman & Jain (1966), Jain & Workman (1967), Weir (1970), Kimura & Ohta (1971), Overath & Asmussen (1998). Une analyse locale de l'équilibre polymorphique et des points de fixation est également effectuée, à défaut de pouvoir réaliser une analyse globale des équations de récurrence du modèle. Cette analyse locale est conduite en considérant la matrice des approximations linéaires des équations de récurrence près du point d'équilibre. La stabilité locale d'un tel point est déduite en examinant le module de la plus grande valeur propre ρ de la matrice des approximations linéaires. Si le module de ρ est plus petit que 1, alors le point d'équilibre est localement stable; au contraire, si le module de ρ est plus grand que 1, alors le point d'équilibre est localement instable. Enfin, si le module de ρ égale exactement 1, il faut alors effectuer une analyse plus fine, basée sur les termes quadratiques des équations de récurrence près du point d'équilibre (voir Lessard & Karlin, 1982). L'appendice A expose deux cas critiques nécessitant une telle analyse. Bien que ce type d'analyse linéaire et quadratique soit largement courant en génétique des populations, elle n'avait jamais été réalisée de façon complète dans le modèle avec autofécondation partielle.

Pour certaines combinaisons particulières de valeurs sélectives, par exemple, égalité de valeurs sélectives ou une des valeurs sélectives égale à 0, une analyse globale rigoureuse du modèle s'est avérée possible, ce qui représente une contribution majeure à l'étude de ce modèle. Cette analyse est particulièrement intéressante puisqu'elle permet d'établir une comparaison entre les résultats classiques du modèle panmictique et ceux obtenus dans ce modèle. En somme, l'introduction d'accouplement par autofécondation semble compromettre la possibilité d'un polymorphisme dans une population initialement sous régime panmictique.

Il ne faudrait pas passer sous silence la contribution récente de Nagylaki (1997) concernant le modèle d'autofécondation partielle avec sélection faible. L'hypothèse de sélection faible est couramment employée dans l'étude de modèles en génétique des populations. Cette hypothèse, généralement plausible dans l'échelle de temps du point de vue de l'évolution, stipule que les différences de viabilité entre les génotypes sont petites, ce qui a pour effet habituellement de simplifier l'analyse mathématique des modèles en question. En s'appuyant ainsi sur une hypothèse de sélection faible, Nagylaki (1997) a produit une étude complète de la dynamique du modèle avec autofécondation partielle au moyen d'équations différentielles décrivant les changements, dans le temps, des fréquences des allèles dans la population. Les résultats obtenus par cet auteur s'inscrivent comme un cas particulier des résultats présentés au Chapitre 1.

Fort d'une étude rigoureuse du modèle avec autofécondation partielle, l'analyse du modèle d'accouplement frère-sœur partiel avec sélection a été envisagée. Malheureusement, les équations de récurrence sur les fréquences génotypiques s'avèrent insuffisantes pour décrire l'évolution génétique de la population, d'une génération à la suivante. Il faut alors utiliser des équations de récurrence sur les couples reproducteurs, d'où la nécessité, entre autres, d'invoquer une hypothèse de sélection faible pour simplifier le traitement analytique de ces équations. Par ailleurs, confronté à la complexité de déterminer les points d'équilibre et leur stabilité, l'auteur de cette thèse a plutôt recherché des conditions d'invasion d'un gène rare, sous l'hypothèse de sélection faible dans la population, ce qui revient essentiellement à examiner la stabilité locale des points de fixation.

Étude du changement de la fréquence d'un gène

Un outil théorique fort important dans l'étude du changement de la fréquence d'un gène dans la population est fourni par la formule de covariance de Li-Price (Li, 1967, Price, 1970):

$$\Delta Q^{(k)} = \frac{\mathrm{Cov}(q^{(k)}, \mathrm{W})}{\overline{\mathrm{W}}},$$

où $q^{(k)}$ est la fréquence de l'allèle $A^{(k)}$ chez un individu, $Q^{(k)}$ est la fréquence de $A^{(k)}$ dans la population, W est la valeur sélective de l'individu et $\overline{\mathrm{W}}$ est la valeur sélective moyenne dans la population. La quantité $\Delta Q^{(k)}$ décrit l'augmentation ou la diminution dans la fréquence de $A^{(k)}$ entre deux générations successives. Quoique cette formule soit exacte sous toutes conditions, il faut néanmoins définir explicitement et rigoureusement la valeur sélective W d'un individu, ce qui s'avère délicat notamment en présence d'interactions entre individus apparentés dans une population non panmictique, telles qu'introduites au Chapitre 3. À ce sujet, il faut mentionner les travaux de Taylor (1988a, 1989) pour obtenir une approximation de la formule de Li-Price pour un allèle mutant dans le cas de sélection faible. En accord avec les travaux de cet auteur, une approche plus directe et rigoureuse pour décrire le changement dans la fréquence d'un gène rare, lorsqu'introduit en petite quantité dans une population soumise à la sélection faible, est explicitée au Chapitre 2.

Dans les modèles de consanguinité partielle avec sélection faible, Wright (1942) avait suggéré l'emploi d'une "topographie adaptative" approximative. Selon l'interprétation de Wright, cette topographie pouvait être perçue comme une surface sur laquelle la population se "déplace", jusqu'à atteindre un maximum. Une telle topographie, qui dépend de l'état génique de la population, est une fonction impliquant les valeurs sélectives, le coefficient de consanguinité F et les valeurs reproductives de chacun des sexes pour une population différenciée selon le sexe. Sans différences eu égard au sexe, la topographie proposée est égale à la somme de deux composantes: d'une part, la valeur sélective moyenne des individus consanguins multipliée par F et d'autre part, la valeur sélective moyenne des individus non consanguins multipliée par $(1 - F)/2$. Le changement dans la fréquence d'un gène est obtenu en dérivant cette topographie par rapport à la fréquence du gène. De plus, l'hypothèse de sélection faible simplifiait grandement le calcul de F, puisqu'il était obtenu en supposant la neutralité des gènes.

En ce qui concerne le modèle d'autofécondation partielle avec sélection faible, Nagylaki (1992, 1997) a démontré que la topographie adaptative de Wright était valide pour prédire le changement dans la fréquence d'un gène, mais en autant que suffisamment de générations se soient écoulées depuis l'introduction du gène dans la population et que la population soit suffisamment loin de son état d'équilibre. Dans le modèle avec accouplement frère-sœur partiel dans une population diploïde, Pollak (1995) a souligné l'inexactitude, du moins quantitative, de la formule de Wright, lorsque le gène demeure rare dans la population après un nombre de générations suffisamment élevé. Plus précisément, la formule décrivant le changement dans la fréquence du gène doit être multipliée par une quantité faisant intervenir le coefficient de corrélation entre les fréquences de ce gène dans un couple reproducteur. Toutefois, puisque cette quantité est toujours positive, la formule de Wright reste qualitativement valide pour prédire l'augmentation ou la diminution du gène entre deux générations successives. Dans le Chapitre 2, on montre que la formule de Wright n'est plus valide, quantitativement et même qualitativement, dans le modèle avec accouplement frère-sœur partiel dans une population haplo-diploïde.

En résumé, le changement dans la fréquence d'un gène rare dans une population avec consanguinité partielle et soumise à des pressions sélectives, même faibles, ne peut être correctement décrit par la formule de Wright. Dans le Chapitre 2 est développée une approximation du changement dans la fréquence d'un gène mutant rare, lorsqu'introduit en petite quantité dans une population originalement à l'état de fixation. Cette approximation (voir Résultats 2.1 et 2.2 du Chapitre 2), basée sur le module de la plus grande valeur propre $\rho(s)$ de la matrice des approximations linéaires $\mathbf{M}(s)$ des équations de récurrence décrivant le passage d'une génération à la suivante, permet de déterminer des conditions d'invasion ou d'extinction du gène et d'interpréter les effets de la consanguinité sur l'évolution d'un gène mutant (le paramètre $s \geq 0$ mesure l'intensité de la sélection). Cette méthodologie s'inspire d'un article de Taylor (1985), bien qu'appliquée dans un contexte très différent, et fournit un nouvel outil dans l'analyse locale d'un point de fixation.

L'approximation proposée repose en grande partie sur l'applicabilité du théorème de Perron-Frobenius (voir l'énoncé du théorème dans l'appendice B) à la matrice des approximations linéaires $\mathbf{M}(s)$. On suppose que, près de la fixation de l'allèle commun, la population est représentée par un vecteur contenant les fréquences des types (génotypes, couples reproducteurs, etc.) porteurs d'au moins un allèle mutant et que la matrice des approximations linéaires $\mathbf{M}(s)$ décrit correctement le changement local dans les fréquences de ces types mutants. À cet égard, l'hypothèse de sélection faible devient cruciale, puisqu'elle garantit que la matrice $\mathbf{M}(s)$ est non négative et primitive, tout en permettant d'ignorer du même coup les termes quadratiques et d'ordre supérieur en s. Un autre avantage appréciable de l'hypothèse de la sélection faible réside dans le fait qu'on peut utiliser le coefficient de consanguinité et le coefficient d'apparentement calculés en absence totale de sélection, comme l'avait suggéré Wright dans sa topographie adaptative. Finalement, dans le but d'obtenir une approximation assez juste, il est nécessaire qu'un nombre suffisant de générations se soient écoulées depuis l'introduction de l'allèle mutant dans la population. Le Résultat 2.2 énonce les conditions requises (voir preuve dans l'Appendice B) pour y arriver et complète de façon rigoureuse les résultats de Taylor (1989). Cependant, dans le cas où un allèle mutant envahit la population, le nombre de générations ne doit pas devenir trop élevé car la matrice des approximations linéaires ne suffit plus à décrire le comportement local près du point de fixation de l'allèle commun.

À l'aide de cette approximation du changement dans la fréquence d'un allèle mutant rare, une étude des effets combinés de la sélection et de la consanguinité sur l'évolution de cet allèle a été entreprise dans les modèles avec consanguinité partielle. Plusieurs variantes de ces modèles sont examinées en détail au Chapitre 2, notamment concernant la consanguinité induite par l'autofécondation ou par l'accouplement frère-sœur, en supposant des différences de viabilité selon le sexe, et en considérant le cas d'une population diploïde et le cas d'une population haplo-diploïde. De l'analyse de ces modèles a émergé une interprétation basée sur la sélection de parentèle, même si aucune interaction entre individus apparentés était

définie au départ. Un constat étonnant surgit alors: un modèle classique avec différences de viabilité peut être interprété selon une approche, plus équivoque en présence de consanguinité, empruntée à la théorie de la sélection de parentèle. Cette approche mérite une investigation d'autant plus poussée qu'elle semble nouvelle et prometteuse.

Au Chapitre 2, on utilise le coefficient d'apparentement $R_{I\to J}$ entre les individus I et J formant un couple reproducteur afin d'expliquer l'invalidité de la formule de Wright dans le modèle avec accouplement frère-sœur partiel. Avec sélection faible, ce coefficient d'apparentement se réduit à un indice basé sur le pedigree de I et J (voir Appendice D). On explique l'apparition de ce coefficient par des effets dus à la consanguinité, induite par les interactions frère-sœur, se produisant lors de l'accouplement, causant ainsi une deuxième augmentation dans la fréquence de l'allèle mutant (Pollak, 1995).

Pour étudier plus avant les effets de telles interactions, un régime de sélection caractérisé par le choix entre deux stratégies possibles est proposé au Chapitre 3. Sous l'hypothèse de petites différences dans les stratégies, un examen attentif du changement dans la fréquence d'un allèle mutant rare révèle l'implication de coefficients d'apparentement. En outre, les conditions de protection de cet allèle, obtenues par l'application directe du Résultat 2.1, présentent de nombreuses similarités avec les conditions d'invasion initiale d'un allèle mutant rare dans les modèles de sélection de parentèle avec consanguinité partielle et valeurs sélectives additives (Uyenoyama, 1984). En réalité, ces ressemblances ne sont pas fortuites puisqu'on peut vérifier que la valeur sélective d'un individu, dans le cas de petites différences dans les stratégies, peut s'écrire comme une valeur sélective dans un modèle additif de sélection de parentèle, c'est-à-dire où on additionne le "coût" et le "bénéfice" du comportement adopté par l'individu. Dans un contexte particulier de comportement altruiste, des conditions explicites pour la protection d'un allèle mutant rare sont données en termes de rapport coût-bénéfice, suivant une approche adoptée, entre autres, par Karlin & Matessi (1983). On montre alors que la sélection de

parentèle ne favorise pas nécessairement l'altruisme, en accord avec les observations faites par Uyenoyama (1984). On fournit, par la même occasion, des exemples où une consanguinité accrue peut nuire à l'évolution d'un comportement altruiste.

Une deuxième hypothèse de sélection faible est considérée, soit l'hypothèse de petites différences dans les viabilités. Dans ce cas, l'application du Résultat 2.1 donne bel et bien une condition explicite pour la protection d'un allèle mutant rare, mais il semble qu'aucune interprétation basée sur les modèles de sélection de parentèle ne soit possible, à moins de considérer une hypothèse supplémentaire d'additivité sur les viabilités, ce qui apparaît très restrictif en regard de tous les effets possibles produits par des interactions entre individus apparentés.

Populations structurées

Les modèles avec consanguinité partielle étudiés dans cette thèse font partie d'une classe de modèles plus étendue, dite de populations structurées. En fait, on peut affirmer que la structure des modèles avec autofécondation ou accouplement frère-sœur est de type familial. Une généralisation directe de ces modèles consiste à étudier une population infinie, mais subdivisée en un grand nombre de sous-populations ou groupes. Dans chacun de ces groupes, seulement N femelles inséminées se reproduisent pour former la génération suivante. Chaque femelle peut, avec une certaine probabilité, migrer dans un autre groupe. Dans cette optique, le cas particulier $N = 1$ peut être perçu comme un modèle d'accouplement frère-sœur. Étant donné le nombre limité N de femelles dans un groupe, ce type de modèle produit aussi de la consanguinité.

L'Appendice E renferme une étude exploratoire sur les coefficients d'apparentement susceptibles d'être impliqués dans le changement de fréquence d'un allèle rare sous sélection faible dans une population structurée et où la dispersion des individus est permise. La formulation de ces modèles, dits de dispersion, fait suite à des articles de Bulmer (1986) et de Taylor (1988b). Le traitement analytique de ces

modèles devient rapidement compliqué même lorsque les valeurs de N sont petites. En effet, il faut considérer la composition génotypique des N femelles appartenant à un groupe, ce qui mène à un très grand nombre de compositions possibles lorsque N est grand. Pour obtenir une approximation assez précise du changement dans la fréquence d'un allèle mutant rare, il faudrait être en mesure d'utiliser un coefficient d'apparentement qui ne dépend ni des fréquences alléliques dans la population, ni des valeurs génotypiques.

Il a été fait mention plus tôt dans cette Introduction que les coefficients d'apparentement dans les modèles avec autofécondation partielle ou accouplement frère-sœur partiel se réduisaient à des indices basés sur le pedigree (voir Remarque 2 dans l'Appendice D). Une condition nécessaire permettant cette simplification (Lessard, 1992) est de vérifier les égalités (approximatives) suivantes:

$$\frac{f_{IJ}}{f_{II}} \cong \frac{\delta_{IJ}}{\delta_{II}} \cong \frac{\gamma_{IJ}}{\gamma_{II}},$$

de sorte qu'on pourrait utiliser le coefficient d'apparentement $R_{I\to J} \cong f_{IJ}/f_{II}$, ce dernier rapport de probabilités étant généralement beaucoup plus simple à calculer que les deux autres rapports. Quelques résultats analytiques et numériques présentés dans l'Appendice E suggèrent qu'on pourrait effectivement utiliser ce rapport de probabilités comme coefficient d'apparentement dans les modèles de dispersion. Toutefois, ces quelques analyses sont préliminaires et en ce sens, forment l'ébauche d'une éventuelle étude plus exhaustive des effets de la consanguinité sur l'évolution d'un allèle mutant introduit en petite quantité dans une population structurée.

Contributions respectives des auteurs aux articles contenus dans cette thèse

L'auteur de la présente thèse, Ghislain Rocheleau, a rédigé les manuscrits originaux des trois (3) articles composant le corps principal de celle-ci, ainsi que tous

les appendices. Le directeur de thèse, Sabin Lessard, a supervisé la recherche et contribué significativement aux aspects les plus mathématiques de celle-ci.

Le Chapitre 1 contient le manuscrit de l'article (publié) de Rocheleau, G., Lessard, S. (2000). *Stability analysis of the partial selfing selection model*, *Journal of Mathematical Biology* **40**: 541-574. Le coauteur Sabin Lessard est notamment à l'origine des résultats de convergence globale. Les résultats de stabilité locale qui ont permis d'établir la structure d'équilibre dans tous les cas sont dus à l'auteur principal, Ghislain Rocheleau.

Le Chapitre 2 contient le manuscrit de l'article de Lessard, S., Rocheleau G. (2002). *Change in frequency of a rare mutant allele: A general formula and applications to partial inbreeding models*, accepté pour publication dans *Journal of Mathematical Biology*. L'article est cependant disponible sur le site Internet de la revue. En tant qu'auteur principal, Sabin Lessard est le grand responsable des arguments mathématiques les plus pointus dans les preuves des Résultats 2.1 et 2.2. L'application de ces Résultats aux modèles avec consanguinité partielle a été développée par le coauteur, Ghislain Rocheleau.

Le Chapitre 3 contient le manuscrit de l'article de Rocheleau G., Lessard, S. *New insights into kin selection theory in family-structured populations with inbreeding*, soumis pour publication dans *Theoretical Population Biology*. À la suggestion de Sabin Lessard, Ghislain Rocheleau, l'auteur principal, a considéré l'évolution dans le cas de valeurs sélectives basées sur des stratégies individuelles à l'intérieur de familles et développé des interprétations particulières, fondées sur la sélection de parentèle, qui font intervenir coûts, bénéfices et coefficients d'apparentement.

Les Appendices D et E ont été entièrement conçus par l'auteur de cette thèse. Mon directeur de thèse a toutefois dirigé mon intérêt vers les modèles de dispersion, décrits dans l'Appendice E, et corrigé certaines équations.

Chapitre 1: Stability analysis of the partial selfing selection model

Abstract

We undertake a detailed study of the one-locus two-allele partial selfing selection model. We show that a polymorphic equilibrium can exist only in the cases of overdominance and underdominance and only for a certain range of selfing rates. Furthermore, when it exists, we show that the polymorphic equilibrium is unique. The local stability of the polymorphic equilibrium is investigated and exact analytical conditions are presented. We also carry out an analysis of local stability of the fixation states and then conclude that only overdominance can maintain polymorphism in the population. When the linear local analysis is inconclusive, a quadratic analysis is performed. For some sets of selective values, we demonstrate global convergence. Finally, we compare and discuss results under the partial selfing model and the random mating model.

1.1 Introduction

Previous studies on the partial selfing model with selection provided conditions for the existence of a polymorphic equilibrium, without any real consideration about its stability (local or global). For example, Workman and Jain (1966) determined the values, at equilibrium, of the allelic frequencies and Wright's fixation index, for a locus with two alleles. Jain and Workman (1967) later defined a set of partial fixation indices in order to find the equilibrium genotypic frequencies for a locus with multiple alleles. Weir (1970) introduced a matrix method, based on the mean fitness of the population, that produces numerical values of these fixation indices and genotypic frequencies at equilibrium. He also determined a necessary condition for the existence of a polymorphic equilibrium. The stability of such an equilibrium was briefly considered.

Kimura and Ohta (1971) first treated the stability of the polymorphic equilibrium in the case of overdominant alleles for a locus with two alleles. They obtained a necessary condition on the parameters of the model for the existence of this equilibrium point and showed the uniqueness of this point when it exists. Next, assuming the existence of the polymorphic equilibrium, they examined its stability by investigating the local stability of both fixation states. But no local study of the polymorphic equilibrium itself, by considering changes in genotypic frequencies in the neighborhood of this point, was done.

Recently, Overath and Asmussen (1998) obtained some results when considering a more general model that includes apomixis which occurs with probability a (production of seeds without meiosis). Letting $a = 0$ in their equations leads to the conclusion that "... *at most one polymorphic equilibrium can exist for a given set of fitnesses and mating system parameters and that such equilibria exist only for overdominant and underdominant selection.*" Also, they provided some analytical conditions for local stability of the polymorphic equilibrium, but were not able to assert the stability of this equilibrium point. They instead examined the local stability of the fixation states and the conditions that allow a protected polymorphism

(PP), that is, when both fixation states are unstable. They established that "... *for overdominance a PP exists if and only if a valid internal equilibrium also exists ... for underdominance both of the boundary equilibria will always be stable whenever a polymorphic equilibrium exists and, therefore, a PP never exists under these conditions. Since two adjacent equilibria are unlikely to be both stable or both unstable, these results also suggest that (in the absence of cycling) overdominant polymorphic equilibria will be stable whenever they exist, while underdominant polymorphic equilibria will always be unstable.*" In Section 1.4, we confirm their intuition by rigorously proving this last statement.

Assuming weak selection in the partial selfing model, Nagylaki (1997) presented a complete dynamical analysis for two alleles. Since weak selection represents a limit case of selection, we show in the Discussion section that the dynamical structure in this case can be deduced from that of the general model.

In this paper, we present the most complete analysis, up to now, on the one-locus two-allele partial selfing selection model. In Sections 1.2 and 1.3, we examine all possible combinations of selective values and point out some exact conditions on the selfing rate under which a polymorphic equilibrium exists. Furthermore, we show that at most one polymorphic equilibrium exists in each case. In Section 1.4, we look at the local stability of this polymorphic equilibrium when it exists and then derive new results. In Section 1.5, we study local stability of both fixation states and thus complete earlier works done by Kimura and Ohta (1971). In particular, when the linear local analysis of the fixation state is inconclusive, we deduce new results by performing a quadratic analysis. In Section 1.6, some special cases are treated and global stability is proved. Finally, in Section 1.7, we summarize the results obtained in the preceding sections and compare them with those known under random mating. In this manner, we can describe the effects of selfing on a population that was previously practicing random mating. This can be the case for instance of a population subject to isolation. Table 1.2 of Section 1.7 is particularly useful in that, for a given set of selective values, one can completely determine the ultimate structure of the population for any value of the selfing rate.

1.2 Model

Consider a single locus with two alleles, say A_1 and A_2, in an infinite diploid population with non-overlapping generations. Each individual of the population can reproduce, either by selfing with constant probability β ($0 < \beta < 1$), or by random outcrossing with the complementary probability $1 - \beta$. Let P_{11}, P_{12} and P_{22} denote the frequencies of the genotypes A_1A_1, A_1A_2 and A_2A_2, respectively, in the population. Then, the frequencies of the alleles A_1 and A_2 are

$$p = P_{11} + \tfrac{1}{2} P_{12} \quad \text{and} \quad q = P_{22} + \tfrac{1}{2} P_{12}.$$

Moreover, let the genotypes A_1A_1, A_1A_2, A_2A_2 have the corresponding selective values w_{11}, w_{12}, $w_{22} \geq 0$. Here, zygotic selection is applied through viability differences, that is, the genotypic selective parameters are proportional to the probabilities of survival from conception to maturity. It is assumed that the selective values are not all equal. Otherwise there will not be any selection. The case of a lethal homozygote ($w_{11} = 0$ or $w_{22} = 0$) and the case of a lethal heterozygote ($w_{12} = 0$) will be treated separately in Section 1.6. In the case of a non-lethal heterozygote ($w_{12} > 0$), we shall assume, without loss of generality, $w_{12} = 1$. Then, to simplify further the notation, it will be convenient to use the coefficients

$$a = 1 - w_{11} \quad \text{and} \quad b = 1 - w_{22}, \tag{1.1}$$

which cannot be both equal to 0 by assumption. There will be overdominance when $a, b > 0$, underdominance when $a, b < 0$, complete dominance when $a = 0$ or $b = 0$, and directional selection when $a > 0$ and $b < 0$ or $a < 0$ and $b > 0$. Symmetric selection will correspond to $a = b$. Note that we always have $a, b \leq 1$. The case $a = 1$ or $b = 1$ corresponds to the case of a lethal homozygote, which will be treated separately.

If P_{11}, P_{12} and P_{22} designate the genotypic frequencies among the zygotes in the current generation at the time of conception, then the genotypic frequencies among the adults in the current generation, after selection but before mating, are

$$P_{11}^{*} = \frac{w_{11} P_{11}}{w_{11} P_{11} + P_{12} + w_{22} P_{22}}, \qquad P_{12}^{*} = \frac{P_{12}}{w_{11} P_{11} + P_{12} + w_{22} P_{22}}, \qquad P_{22}^{*} = \frac{w_{22} P_{22}}{w_{11} P_{11} + P_{12} + w_{22} P_{22}}. \tag{1.2}$$

After mating and reproduction, the genotypic frequencies among the zygotes in the next generation are given by the equations

$$\begin{aligned} P_{11}' &= \beta\,[\,P_{11}^{*} + \tfrac{1}{4}P_{12}^{*}\,] + (1-\beta)[\,P_{11}^{*} + \tfrac{1}{2}P_{12}^{*}\,]^2, \\ P_{12}' &= \beta\,[\,\tfrac{1}{2}P_{12}^{*}\,] + 2\,(1-\beta)[\,P_{11}^{*} + \tfrac{1}{2}P_{12}^{*}\,][\,P_{22}^{*} + \tfrac{1}{2}P_{12}^{*}\,], \\ P_{22}' &= \beta\,[\,P_{22}^{*} + \tfrac{1}{4}P_{12}^{*}\,] + (1-\beta)[\,P_{22}^{*} + \tfrac{1}{2}P_{12}^{*}\,]^2. \end{aligned} \tag{1.3}$$

Here, we assume no fertility differences between the mating types, Mendelian segregation of genes and no gametic selection. It is useful to note that, under these assumptions, mating and reproduction do not change the allelic frequencies, that is,

$$p' = P_{11}' + \tfrac{1}{2}P_{12}' = P_{11}^{*} + \tfrac{1}{2}P_{12}^{*} = p^{*},$$

and then

$$q' = 1 - p' = 1 - p^{*} = q^{*}.$$

Figure 1.1 below summarizes the life cycle of the population and the notation used for the genotypic and allelic frequencies.

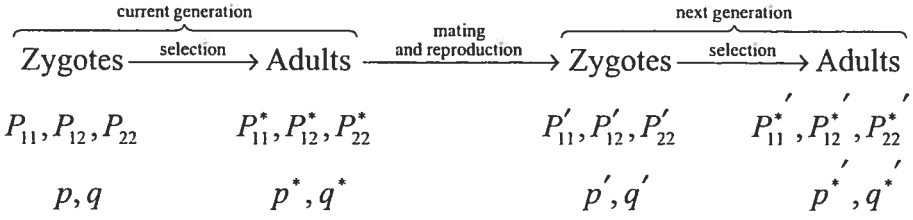

Figure 1.1 Life cycle and notation.

At each stage of the life cycle, the genotypic and allelic frequencies sum up to 1.

1.3 Equilibrium conditions

Apart from the fixation states ($P_{11} = 1$ and $P_{22} = 1$, which correspond to $q = 0$ and $p = 0$, respectively), there may exist polymorphic equilibria (at which $p, q \neq 0$). In order to determine the conditions for such equilibria, we use the fixation index F (Wright, 1951). The genotypic frequencies are written in the form

$$P_{11} = p^2 + pqF, \qquad P_{12} = 2pq(1-F), \qquad P_{22} = q^2 + pqF, \tag{1.4}$$

where $-1 \leq F \leq 1$. The value of F varies from one generation to the next. Under the assumption $p, q \neq 0$, and using the equations (1.1) to (1.4), we have in the next generation

$$\begin{aligned} F' &= 1 - \frac{P'_{12}}{2p'q'} \\ &= \beta\left\{1 - \frac{(1-F)\left[1 - a\left(p^2 + pqF\right) - b\left(q^2 + pqF\right)\right]}{2[1 - a(p + qF)][1 - b(q + pF)]}\right\}. \end{aligned} \tag{1.5}$$

At equilibrium, we must have $p' = p$. But, we have already noted that $p' = p^*$. Therefore, we have $p' = p$ if and only if

$$p^* = \frac{w_{11}P_{11} + \frac{1}{2}P_{12}}{w_{11}P_{11} + P_{12} + w_{22}P_{22}} = p,$$

which is equivalent, after algebraic manipulations using (1.4) and the assumption $p \neq 0, 1$, to

$$[a - (a+b)p]F = b - (a+b)p. \tag{1.6}$$

If

$$a - (a+b)p = 0,$$

then $p' = p \neq 0, 1$ if and only if

$$b - (a+b)p = 0,$$

which is compatible with the above condition if and only if $a = b$. On the other hand, if $a = b$, then we would have $F = 1$ at every polymorphic equilibrium where $p \neq \frac{1}{2}$. But then, owing to (1.5), we would have $F' = \beta < 1$, which contradicts equilibrium. Therefore, $\frac{1}{2}$ is the only admissible value for p at a polymorphic equilibrium in the case $a = b$. We have proved the following.

Result 1.1 $\dfrac{a}{a+b}$ *is an admissible value for p at a polymorphic equilibrium if and only if a = b. In this case,* $\frac{1}{2}$ *is the only admissible value for p at a polymorphic equilibrium.*

Let us assume $a \neq b$, and therefore

$$a-(a+b)p \neq 0 \quad \text{and} \quad F = \frac{b-(a+b)p}{a-(a+b)p}$$

at a polymorphic equilibrium. Then the equilibrium condition $F' = F$ with F' given by (1.5) becomes

$$G(p) = 0,$$

where

$$\begin{aligned} G(p) = {} & 2(a+b)(1-\beta)\left[a(1-b)+b(1-a)\right]p^2 \\ & +\left\{\left[a(1-b)+b(1-a)\right]\left[(3a+b)\beta-2b\right]-2a(a+b)(1-b)\right\}p \\ & +2ab(1-b)-\beta\, a\left[a(1-b)+b(1-a)\right]. \end{aligned} \tag{1.7}$$

The polynomial $G(p)$ is of the quadratic form $Ap^2 + Bp + C$ and admits two roots:

$$\hat{p}_- = \frac{-B-\sqrt{B^2-4AC}}{2A} \qquad \text{and} \qquad \hat{p}_+ = \frac{-B+\sqrt{B^2-4AC}}{2A},$$

where

$$\begin{aligned} A &= 2(a+b)(1-\beta)K, \\ B &= K\left[(3a+b)\beta - 2b\right] - 2a(a+b)(1-b), \\ C &= 2ab(1-b) - \beta aK, \end{aligned} \tag{1.8}$$

with

$$K = a(1-b) + b(1-a).$$

A priori, these two roots may correspond to polymorphic equilibria. But in order to be admissible, they must satisfy some constraints. Of course, the first one is $0 < \hat{p} < 1$, where $\hat{p}$ is a root of $G(p)$ and represents the frequency of allele A_1 at equilibrium. Then the frequency of allele A_2 at equilibrium satisfies $0 < \hat{q} = 1 - \hat{p} < 1$. The other constraints are

$$\hat{P}_{11} = \hat{p}^2 + \hat{p}\hat{q}\hat{F} \geq 0, \quad \hat{P}_{12} = 2\hat{p}\hat{q}\left(1 - \hat{F}\right) \geq 0, \quad \hat{P}_{22} = \hat{q}^2 + \hat{p}\hat{q}\hat{F} \geq 0,$$

where

$$\hat{F} = \frac{b - (a+b)\hat{p}}{a - (a+b)\hat{p}}, \tag{1.9}$$

which guarantee that the equilibrium genotypic frequencies are all non-negative, and then all less than or equal to one, since they sum up to one. This will be the case if and only if

$$-1 \leq \max\left(\frac{-\hat{p}}{\hat{q}}, \frac{-\hat{q}}{\hat{p}}\right) \leq \hat{F} \leq 1.$$

Therefore, $0 < \hat{p} < \frac{1}{2}$ will be admissible if and only if

$$-\frac{\hat{p}}{1-\hat{p}} \leq \frac{b - (a+b)\hat{p}}{a - (a+b)\hat{p}} \leq 1. \tag{1.10}$$

Workman and Jain (1966) have determined two conditions that must hold at equilibrium. It can be shown that equations (1.7) and (1.9) are in fact equivalent to these conditions.

Now, assuming

$$a-(a+b)\hat{p}>0, \tag{1.11}$$

the right-hand side inequality in (1.10) will hold if and only if $a \geq b$, while we will have the left-hand side inequality in (1.10) if and only if $b(1-2\hat{p}) \geq 0$, that is, $b \geq 0$. Conversely, if $a \geq b \geq 0$, then $a+b>0$, since by assumption a and b cannot be both equal to 0, and

$$\frac{a}{a+b} \geq \frac{1}{2},$$

which implies the inequality (1.11) under the constraint $\hat{p}<\frac{1}{2}$. Similarly, assuming

$$a-(a+b)\hat{p}<0, \tag{1.12}$$

both inequalities in (1.10) are true if and only if $a \leq b \leq 0$, and this condition implies (1.12) under the constraint $\hat{p}<\frac{1}{2}$. The conditions for $\frac{1}{2}<\hat{p}<1$ to be admissible are, by symmetry, $b \geq a \geq 0$ or $b \leq a \leq 0$. Finally, note that $\hat{p}=\frac{1}{2}$ would be admissible if and only if $a \geq b$ and $b \geq a$, that is, $a=b$. Therefore we have necessarily $\hat{p} \neq \frac{1}{2}$ in the case $a \neq b$. We conclude as follows.

Result 1.2 *A polymorphic equilibrium can exist only when a and b are of the same sign* ($a, b \geq 0$ *or* $a, b \leq 0$) *and the more frequent allele at a polymorphic equilibrium, when it exists, is necessarily the one associated with the parameter a or b closer to 0, that is, the one associated with the homozygote having the fitness closest to the heterozygote fitness. Equality of allelic frequencies at a polymorphic equilibrium is possible only in the case where the homozygotes have the same fitness* ($a=b$).

Note that this result on admissible allelic frequencies at a polymorphic equilibrium depends only on the fitness parameters. The proportion of selfing β is not involved.

Moreover, this result excludes the possibility of a polymorphic equilibrium in the case of directional selection (a and b of opposite signs).

Now, let us look at the existence of a polymorphic equilibrium. Under the condition that a and b are of the same sign ($a,\ b \geq 0$ or $a,\ b \leq 0$) and not both equal to 0, the quadratic polynomial $G(p)$ is convex with respect to p, since the coefficient of p^2 (coefficient A in (1.18)) is then positive. Moreover, evaluating $G(p)$ at $p = \frac{1}{2}$ yields

$$G(\tfrac{1}{2}) = -\frac{(a-b)^2}{2} \leq 0,$$

with a strict inequality in the case $a \neq b$. Therefore the roots $\hat{p}_-$ and $\hat{p}_+$ of $G(p)$ are real and satisfy

$$\hat{p}_- \leq \tfrac{1}{2} \quad \text{and} \quad \hat{p}_+ \geq \tfrac{1}{2},$$

with strict inequalities in the case $a \neq b$. Finally, we have $\hat{p}_- > 0$ if and only if

$$G(0) = 2ab(1-b) - \beta aK > 0,$$

and $\hat{p}_+ < 1$ if and only if

$$G(1) = 2ab(1-a) - \beta bK > 0.$$

Let us look at all the cases.

- **Case of complete dominance ($a = 0$ or $b = 0$).** We have $G(0) \leq 0$ and $G(1) \leq 0$. Therefore we have $\hat{p}_- \leq 0$ and $\hat{p}_+ \geq 1$, which eliminates the possibility of a polymorphic equilibrium.

- **Case of overdominance or underdominance without symmetry.** Without loss of generality, relabelling the alleles if necessary, we may assume that the homozygote having the fitness closest to the heterozygote fitness is A_2A_2. Then we are in the case $0 < b < a$ or $a < b < 0$. In this case, we have $G(0) > 0$ if and only if

$$\beta < \frac{2b(1-b)}{a(1-b)+b(1-a)} = \beta_0.$$

This is the condition to have $0 < \hat{p}_- < \frac{1}{2}$, and therefore the existence of a polymorphic equilibrium, which is unique, with the frequency of allele A_1 given by $\hat{p}_-$ and the fixation index at equilibrium by equation (1.9). Note that the above condition is always satisfied when $\frac{1}{2} \le b < a \le 1$, since then $\beta_0 \ge 1$.

- **Case of symmetry ($a = b$).** At a polymorphic equilibrium, we must have $p = \frac{1}{2}$ (Result 1.1) and then the equilibrium condition $F' = F$ with F' given by (1.5) becomes

$$aF^2 - [2 - a - \beta(1-a)]F + \beta(1-a) = 0,$$

which admits a unique root F in the interval $(-1, 1)$ for $a \le 1$ and $0 < \beta < 1$. This determines an admissible polymorphic equilibrium, which is unique. Note that $\beta_0 = 1$ in the case $a = b$.

In conclusion, we have:

Result 1.3 *There exists a polymorphic equilibrium only in the case of overdominance* $(a,\ b > 0)$ *or underdominance* $(a,\ b < 0)$ *when*

$$\beta < \frac{2b(1-b)}{a(1-b)+b(1-a)}, \qquad \text{if } a \le b < 0 \text{ or } 0 < b \le a,$$

or

$$\beta < \frac{2a(1-a)}{a(1-b)+b(1-a)}, \qquad \text{if } b \le a < 0 \text{ or } 0 < a \le b.$$

Moreover, a polymorphic equilibrium is unique when it exists.

Result 1.3 has been deduced recently by Overath and Asmussen (1998) in a model that also includes apomixis. Hence, we simply confirm the result obtained in their so-called "*standard mixed mating model without apomixis*".

Table 1.1 summarizes the conditions for a unique polymorphic equilibrium to exist. In the case of symmetric selection ($a = b$), the allelic frequencies at the polymorphic equilibrium are always the same and equal to $\frac{1}{2}$ for $0 < \beta < 1$. It remains to study the change in the allelic frequencies at the polymorphic equilibrium, when it exists, in non-symmetric cases ($a \neq b$) with respect to a change in the proportion of selfing β.

Table 1.1 Conditions for a (unique) polymorphic equilibrium to exist.

Selective values			
$a = b \neq 0$	$a < b < 0$ or $0 < b < a$	$b < a < 0$ or $0 < a < b$	all other cases
$\hat{p} = \frac{1}{2}$	$0 < \hat{p} < \frac{1}{2}$	$\frac{1}{2} < \hat{p} < 1$	*no polymorphic equilibrium*
$0 < \beta < 1$	$0 < \beta < \dfrac{2b(1-b)}{a(1-b)+b(1-a)}$ ($0 < \beta < 1$ *in the particular case* $\frac{1}{2} \leq b < a$)	$0 < \beta < \dfrac{2a(1-a)}{a(1-b)+b(1-a)}$ ($0 < \beta < 1$ *in the particular case* $\frac{1}{2} \leq a < b$)	$0 < \beta < 1$

At such an equilibrium, the frequency of allele A_1, denoted by $\hat{p}$, satisfies $G(\hat{p}) = 0$, where $G(p)$ is the polynomial given in (1.7). Taking the derivative with respect to β yields

$$\frac{\mathrm{d}}{\mathrm{d}\beta}G(\hat{p}) = -2(a+b)K\hat{p}^2 + 4(a+b)(1-\beta)K\hat{p}\left(\frac{\mathrm{d}\hat{p}}{\mathrm{d}\beta}\right) + (3a+b)K\hat{p} + B\left(\frac{\mathrm{d}\hat{p}}{\mathrm{d}\beta}\right) - aK = 0.$$

This leads to the equation

$$\frac{\mathrm{d}\hat{p}}{\mathrm{d}\beta} = \frac{-K(1-2\hat{p})[a-(a+b)\hat{p}]}{\sqrt{B^2 - 4AC}}.$$

This derivative of $\hat{p}$ with respect to β is negative when $a < b < 0$ or $0 < b < a$ and, by symmetry, positive when $b < a < 0$ or $0 < a < b$. Therefore we have proved the following result.

Result 1.4 *The frequency of the allele associated with the fittest homozygote, at the polymorphic equilibrium, when it exists, increases as β increases in the case of overdominance but decreases as β increases in the case of underdominance.*

In order to study the stability of the polymorphic equilibrium, we will consider first the cases of overdominance and underdominance without symmetry in Section 1.4. The special cases of dominance and symmetric selection will be studied apart in Section 1.6.

1.4 Stability of polymorphic equilibria

In the preceding section, we have derived conditions for a polymorphic equilibrium to exist. In the present section, we look at conditions for local stability of such an equilibrium. In particular, Results 1.5 and 1.6 present results that, to our knowledge, had never been derived before. Suppose that a polymorphic equilibrium with $p = \hat{p}$ and $F = \hat{F}$ exists. As proposed by Weir (1970), we apply small perturbations on the values of p and F at equilibrium so that

$$p = \hat{p} + \xi,$$
$$F = \hat{F} + \eta,$$

where ξ and η are small. In the next generation, using equations (1.2) and (1.4), we get

$$p' = (\hat{p}+\xi)\left\{\frac{1-a\left[\hat{p}+\xi+(\hat{q}-\xi)(\hat{F}+\eta)\right]}{1-a(\hat{p}+\xi)\left[\hat{p}+\xi+(\hat{q}-\xi)(\hat{F}+\eta)\right]-b(\hat{q}-\xi)\left[\hat{q}-\xi+(\hat{p}+\xi)(\hat{F}+\eta)\right]}\right\}.$$

Neglecting terms in ξ^2, η^2 and $\xi\eta$, and using the identity $b\hat{q}+b\hat{p}\hat{F} = a\hat{p}+a\hat{q}\hat{F}$, derived from (1.6), lead to the linear approximation

$$p' \cong \hat{p} + \left[1 - \frac{\hat{p}\hat{q}(a+b)(1-\hat{F})}{1-a(\hat{p}+\hat{q}\hat{F})}\right]\xi + \left[\frac{b\hat{p}^2\hat{q} - a\hat{p}\hat{q}^2}{1-a(\hat{p}+\hat{q}\hat{F})}\right]\eta.$$

Similarly, from equation (1.5), we get after many simplifications the linear approximation

$$F' \cong \hat{F} + \beta\left\{\frac{(1-\hat{F})^2(b\hat{p}-a\hat{q})}{2\left[1-a(\hat{p}+\hat{q}\hat{F})\right]^2}\right\}\xi + \beta\left\{\frac{1-a(\hat{p}+\hat{q}\hat{F})-(a\hat{q}^2+b\hat{p}^2)(1-\hat{F})}{2\left[1-a(\hat{p}+\hat{q}\hat{F})\right]^2}\right\}\eta.$$

Using again (1.6), we obtain the linear approximation

$$\begin{bmatrix} p' \\ F' \end{bmatrix} \cong \begin{bmatrix} \hat{p} \\ \hat{F} \end{bmatrix} + \mathbf{M} \begin{bmatrix} \xi \\ \eta \end{bmatrix},$$

where the entries of the matrix **M** take the form

$$\begin{aligned} m_{11} &= \frac{\hat{u}\left[1-b-(a-b)\hat{p}\right]}{\hat{v}}, & m_{12} &= \frac{-\hat{p}(1-\hat{p})\hat{u}^2}{\hat{v}}, \\ m_{21} &= -\frac{\beta(a-b)^2\hat{u}}{2\hat{v}^2}, & m_{22} &= \frac{\beta}{2}\left(\frac{\hat{u}}{\hat{v}}\right)^2\left[1-a+(a-b)\hat{p}\right], \end{aligned} \tag{1.13}$$

with

$$\hat{u} = a-(a+b)\hat{p} \quad \text{and} \quad \hat{v} = a(1-b) - K\hat{p}.$$

It remains to analyse the eigenvalues of **M**. We will consider separately the cases of overdominance and underdominance, without symmetry. The case of symmetric selection will be treated in a subsequent section.

1.4.1 Case of overdominance without symmetry

Let us assume, without loss of generality, $0 < b < a \leq 1$. In this case, a polymorphic equilibrium (with $0 < \hat{p} < \frac{1}{2}$) exists if and only if $0 < \beta < \min(\beta_0, 1)$, where

$$\beta_0 = \frac{2b(1-b)}{a(1-b)+b(1-a)}.$$

Let us first determine the signs of the entries m_{ij} of the matrix **M**. To achieve this, we must find the signs of $\hat{u}$ and $\hat{v}$. We already know that $\hat{u} > 0$ in the case at hand (see (1.11) and Table 1.1). On the other hand, $\hat{v} > 0$ if and only if

$$\hat{p} < \frac{1}{1+\dfrac{b(1-a)}{a(1-b)}}.$$

But, in the case at hand, this holds since

$$\hat{p} < \frac{1}{2} \quad \text{and} \quad 0 < \frac{b(1-a)}{a(1-b)} < 1.$$

Moreover, we have

$$1-b-(a-b)\hat{p} \geq (a-b)\left(1-\hat{p}\right) > 0$$

and

$$1-a+(a-b)\hat{p} \geq (a-b)\hat{p} > 0.$$

Therefore, we have

$$m_{11} > 0, \quad m_{12} < 0, \quad m_{21} < 0, \quad m_{22} > 0.$$

Now, let us examine the eigenvalues of the matrix **M**. The characteristic polynomial of **M** is

$$m(\lambda) = |\lambda \mathbf{I} - \mathbf{M}| = \lambda^2 - \left(m_{11} + m_{22}\right)\lambda + m_{11}m_{22} - m_{12}m_{21}.$$

The polynomial $m(\lambda)$ is a convex parabola in λ, whose roots are distinct and real, since the discriminant $\Delta(m(\lambda))$ satisfies

$$\Delta\left(m(\lambda)\right) = \left(m_{11} - m_{22}\right)^2 + 4m_{12}m_{21} > 0. \tag{1.14}$$

Note that these two roots are continuous with respect to β, and equal to 0 and $m_{11} > 0$ for $\beta = 0$. Moreover, $m_{11} < 1$ if and only if

$$\left(a^2 - b^2\right)\hat{p}\left(1-\hat{p}\right) > 0,$$

which holds in the case at hand. Therefore, to show that the greatest eigenvalue of **M** in modulus is smaller than 1 in modulus, and consequently that the polymorphic equilibrium is locally stable, it suffices to show that $m(0) > 0$ and $m(1) > 0$, for $0 < \beta < \min(\beta_0, 1)$. In effect, by continuity of the roots of $m(\lambda)$, this condition implies that both roots lie in the interval (0, 1). Actually, we have

$$m(0) = \frac{\beta}{2}\left(\frac{\hat{u}}{\hat{v}}\right)^3 (1-a)(1-b) > 0,$$

and

$$m(1) = \frac{(a-b)\hat{p}(1-\hat{p})}{\hat{v}} H(\beta, \hat{p}), \tag{1.15}$$

where

$$H(\beta, p) = (a+b) - \frac{\beta K}{2}\left[\frac{a-(a+b)p}{a(1-b)-Kp}\right]^2.$$

It is shown in the Appendix that $H(\beta, \hat{p}) > 0$, and therefore that $m(1) > 0$, for $0 < \beta < \min(\beta_0, 1)$. Consequently, we have the following result.

Result 1.5 *In the case of overdominance without symmetry* ($0 < a < b$ *or* $0 < b < a$), *the polymorphic equilibrium is locally stable when it exists.*

1.4.2 Case of underdominance without symmetry

We assume, without loss of generality, $a < b < 0$. As before, we first look at the signs of the elements m_{ij} of the matrix **M**. To do so, we must determine the signs of $\hat{u}$ and $\hat{v}$. But $\hat{u} < 0$ owing to (1.12) and Table 1.1, while $\hat{v} < 0$ if and only if

$$\hat{p} < \frac{a(1-b)}{K},$$

where $K < 0$. But it is trivial to verify that

$$\frac{a(1-b)}{K} > \frac{1}{2}.$$

Since $\hat{p} < \frac{1}{2}$, we obtain that $\hat{v} < 0$. From that, it is easy to see that the elements m_{ij} of the matrix **M** satisfy

$$m_{11} > 0, \quad m_{12} > 0, \quad m_{21} > 0, \quad m_{22} > 0.$$

Moreover, we have as before $m_{11} < 1$.

Then, we look at the characteristic polynomial $m(\lambda)$ of **M**. Because equation (1.14) still holds in the case $a < b < 0$, we conclude that $m(\lambda)$ is a convex parabola whose roots are distinct and real. It is easy to check that (see Appendix for details)

$$m(0) > 0 \quad \text{and} \quad m(1) < 0.$$

For $0 < \beta < \min(\beta_0, 1)$, we deduce that the greatest root of $m(\lambda)$ in modulus, which corresponds to the greatest eigenvalue of **M** in modulus, is greater than 1 in modulus. Therefore, we have

Result 1.6 *In the case of underdominance without symmetry* ($a < b < 0$ *or* $b < a < 0$), *the polymorphic equilibrium is locally unstable when it exists.*

Note that Results 1.5 and 1.6 confirm what Overath and Asmussen (1998) had previously deduced intuitively in their study of a protected polymorphism.

1.5 Stability of the fixation states

We have determined so far the stability of the polymorphic equilibrium, when it exists, in the vicinity of this equilibrium point. However, outside the neighborhood of this point, this stable structure might not be preserved. Consequently, we must examine the stability of the two fixation states: if both fixation states are locally unstable, then the two alleles will be preserved in the population through subsequent generations, therefore maintaining the polymorphism in this population. To study the stability of the fixation states, we will use the same technique as for the stability analysis of the polymorphic equilibrium. We will evaluate the matrix of the linear approximations of the recursive equations (1.3) in the neighborhood of each fixation state. Then, we will determine if the modulus of the greatest eigenvalue of this matrix is greater or smaller than 1. In the following, we consider two cases: overdominance without symmetry and underdominance without symmetry. In Section 1.5.1, we confirm and complete the study previously performed by Kimura and Ohta (1971) and Overath and Asmussen (1998). Section 1.5.2 however provides new results, since Overath and Asmussen (1998) did not study local stability of the fixation states when no polymorphic equilibrium exists.

1.5.1 Case of overdominance without symmetry

We assume, without loss of generality, $0 < w_{11} < w_{22} < 1$. First, we develop the recursive equations near the fixation state of A_1, that is, when the genotypic frequencies are such that $P_{11} \cong 1$, $P_{12} \cong 0$ and $P_{22} \cong 0$. Using (1.2) and (1.3), one can easily obtain the linear approximation

$$\begin{bmatrix} P'_{12} \\ P'_{22} \end{bmatrix} \cong \begin{bmatrix} \dfrac{2-\beta}{2w_{11}} & \dfrac{2(1-\beta)w_{22}}{w_{11}} \\ \dfrac{\beta}{4w_{11}} & \dfrac{\beta\, w_{22}}{w_{11}} \end{bmatrix} \begin{bmatrix} P_{12} \\ P_{22} \end{bmatrix}.$$

The matrix above will be denoted by $\mathbf{L}_1$. For $0 < \beta < 1$, it is clear that all the entries of $\mathbf{L}_1$ are strictly positive. The characteristic polynomial of $\mathbf{L}_1$ is

$$m_1(\lambda) = |\lambda \mathbf{I} - \mathbf{L}_1| = \lambda^2 - \left(\frac{2\beta w_{22} + 2 - \beta}{2w_{11}}\right)\lambda + \frac{\beta w_{22}}{2w_{11}^2}. \tag{1.15}$$

This polynomial is a convex parabola in λ, which admits two distinct real roots since its discriminant satisfies

$$\Delta\big(m_1(\lambda)\big) = \frac{1}{4w_{11}^2}\left\{\left[2\beta w_{22} - (2-\beta)\right]^2 + 8\beta(1-\beta)w_{22}\right\} > 0. \tag{1.16}$$

To determine whether the greatest eigenvalue of $\mathbf{L}_1$ in absolute value is smaller or greater than 1 in absolute value, we evaluate $m_1(\lambda)$ and the derivative of $m_1(\lambda)$, which is

$$\dot{m}_1(\lambda) = \frac{\mathrm{d}}{\mathrm{d}\lambda} m_1(\lambda) = 2\lambda - \left(\frac{2\beta w_{22} + 2 - \beta}{2w_{11}}\right),$$

at $\lambda = 0$ and $\lambda = 1$. One can trivially verify that

$$m_1(0) = \frac{\beta w_{22}}{2w_{11}^2} > 0 \quad \text{and} \quad \dot{m}_1(0) = -\frac{2\beta w_{22} + 2 - \beta}{2w_{11}} < 0. \tag{1.17}$$

By convexity of $m_1(\lambda)$, we deduce that both eigenvalues of $\mathbf{L}_1$ are strictly positive. We also have

$$m_1(1) = \frac{1}{2w_{11}^2}\left\{-2w_{11}(1-w_{11}) + \beta\left[w_{11}(1-w_{22}) + w_{22}(1-w_{11})\right]\right\} \tag{1.18}$$

and

$$\dot{m}_1(1) = \frac{1}{2w_{11}}\left[\beta(1-2w_{22}) - 2(1-2w_{11})\right]. \tag{1.19}$$

For further investigation, we subdivide the general case $0 < w_{11} < w_{22} < 1$ into two cases: $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$ and $\frac{1}{2} \le w_{11} < w_{22} < 1$. In both cases however, we will show that the greatest eigenvalue of $\mathbf{L}_1$ is greater than 1.

First, in both cases, it is clear that $m_1(1) < 0$ if and only if

$$\beta < \frac{2w_{11}(1-w_{11})}{w_{11}(1-w_{22}) + w_{22}(1-w_{11})} = \beta_1. \tag{1.20}$$

Note that $\beta_1 > 0$, and $\beta_1 < 1$ if and only if $w_{11} < \frac{1}{2}$. Hence, in the case $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$, we have $0 < \beta_1 < 1$ whereas, in the case $\frac{1}{2} \le w_{11} < w_{22} < 1$, we have that $\beta_1 \ge 1$ and consequently $m_1(1) < 0$. In the latter case, regardless of the sign of $\dot{m}_1(1)$, this suffices to assert that the greatest eigenvalue of $\mathbf{L}_1$ is greater than 1. In the former case however, we must examine the sign of $\dot{m}_1(1)$.

In the case $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$, when $\min(\frac{1}{2}, w_{22}) = w_{22}$, it is readily seen by (1.19) that $\dot{m}_1(1) < 0$ if and only if

$$\beta < \frac{2(1-2w_{11})}{1-2w_{22}} = \beta_2. \tag{1.21}$$

But, in this restricted case, it is easy to observe that $\beta_2 > 2$, thus leading to the conclusion that $\dot{m}_1(1) < 0$. When $w_{22} = \frac{1}{2}$ or $\min(\frac{1}{2}, w_{22}) = \frac{1}{2}$, we reach the same conclusion directly from (1.19). Therefore, whatever the sign of $m_1(1)$ is, we deduce that the greatest eigenvalue of $\mathbf{L}_1$ is greater than 1 in the case $0 < w_{11} < \min(\frac{1}{2}, w_{22}) < 1$.

Result 1.7 *In the case of overdominance without symmetry, the fixation of the less fit homozygote is locally unstable, for all* $0 < \beta < 1$.

Next, we examine the recursive equations near the fixation state of A_2, that is, when the genotypic frequencies are such that $P_{11} \cong 0$, $P_{12} \cong 0$ and $P_{22} \cong 1$. By the symmetry of equations (1.3), the following linear approximation is easily obtained:

$$\begin{bmatrix} P'_{11} \\ P'_{12} \end{bmatrix} \cong \begin{bmatrix} \dfrac{\beta w_{11}}{w_{22}} & \dfrac{\beta}{4w_{22}} \\ \dfrac{2(1-\beta)w_{11}}{w_{22}} & \dfrac{2-\beta}{2w_{22}} \end{bmatrix} \begin{bmatrix} P_{11} \\ P_{12} \end{bmatrix}.$$

The matrix $\mathbf{L}_2$ of linear approximation is formed of strictly positive entries for $0 < \beta < 1$. By interchanging w_{11} and w_{22} in (1.15), we find that the characteristic polynomial of $\mathbf{L}_2$ is

$$m_2(\lambda) = \lambda^2 - \left(\frac{2\beta w_{11} + 2 - \beta}{2w_{22}} \right) \lambda + \frac{\beta w_{11}}{2w_{22}^2}. \tag{1.22}$$

Again, the polynomial $m_2(\lambda)$ is a convex parabola in λ, which admits two distinct real roots since its discriminant is strictly positive. In a direct manner, one can verify that

$$m_2(0) > 0 \quad \text{and} \quad \dot{m}_2(0) < 0,$$

and therefore deduce, by convexity of $m_2(\lambda)$, that both eigenvalues of $\mathbf{L}_2$ are strictly positive. Also, we easily compute that

$$m_2(1) = \frac{1}{2w_{22}^2} \left\{ -2w_{22}(1 - w_{22}) + \beta \left[w_{11}(1 - w_{22}) + w_{22}(1 - w_{11}) \right] \right\} \tag{1.23}$$

and

$$\dot{m}_2(1) = \frac{1}{2w_{22}} \left[\beta(1 - 2w_{11}) - 2(1 - 2w_{22}) \right] \tag{1.24}$$

At this point, we subdivide the general case $0 < w_{11} < w_{22} < 1$ into two cases: $0 < w_{11} < w_{22} \leq \frac{1}{2}$ and $0 < \max(\frac{1}{2}, w_{11}) < w_{22} < 1$, since they provide different results.

From equation (1.23), it is trivial to verify that $m_2(1) < 0$ if and only if

$$\beta < \frac{2w_{22}(1-w_{22})}{w_{11}(1-w_{22}) + w_{22}(1-w_{11})} = \beta_0. \tag{1.25}$$

In Section 1.3, we have outlined that $0 < \beta_2 < 1$ if and only if $w_{22} > \frac{1}{2}$. Hence, in the case $0 < w_{11} < w_{22} \leq \frac{1}{2}$, we have $\beta_2 \geq 1$ and consequently $m_2(1) < 0$. Regardless of the sign of $\dot{m}_2(1)$, this suffices to ensure that the greatest eigenvalue of $\mathbf{L}_2$ is greater than 1 in this case. Note that a polymorphic equilibrium always exists in this case (see Table 1.1).

In the case $0 < \max(\frac{1}{2}, w_{11}) < w_{22} < 1$, it becomes necessary to look at the value of $\dot{m}_2(1)$. From equation (1.24), when $\max(\frac{1}{2}, w_{11}) = w_{11}$, we obtain that $\dot{m}_2(1) > 0$ if and only if

$$\beta < \frac{2(1-2w_{22})}{1-2w_{11}} = \beta_3. \tag{1.26}$$

But one can easily show that $\beta_3 > 2$, and then conclude that $\dot{m}_2(1) > 0$ in this specific case. When $w_{11} = \frac{1}{2}$ or $\max(\frac{1}{2}, w_{11}) = \frac{1}{2}$, the same conclusion arises directly from (1.24). Therefore, in the case $0 < \max(\frac{1}{2}, w_{11}) < w_{22} < 1$, three situations may occur with respect to condition (1.25):

(i) if $\beta < \beta_0$, then $m_2(1) < 0$ and consequently the greatest eigenvalue of $\mathbf{L}_2$ is greater than 1.

(ii) if $\beta > \beta_0$, then $m_2(1) > 0$ and consequently the greatest eigenvalue of $\mathbf{L}_2$ is smaller than 1.

(iii) if $\beta = \beta_0$, then $m_2(1) = 0$ and consequently the greatest eigenvalue of $\mathbf{L}_2$ is equal to 1. This situation requires a more refined analysis of the recursive equations (1.3). This analysis is performed in the Appendix.

Note that a polymorphic equilibrium exists if and only if $\beta < \beta_0$ (see Table 1.1). We summarize our conclusions in the result below.

Result 1.8 *In the case of overdominance without symmetry, the fixation of the fittest homozygote is locally unstable when a polymorphic equilibrium exists and locally stable otherwise, even in a degenerate case corresponding to a critical value for* β.

1.5.2. Case of underdominance without symmetry

We assume, without loss of generality, $1 < w_{22} < w_{11}$. The analysis of this case proceeds almost the same way as in the case $0 < w_{11} < w_{22} < 1$. Near the fixation state of A_1, we have deduced earlier the matrix of linear approximation $\mathbf{L}_1$ and its characteristic polynomial $m_1(\lambda)$ given by equation (1.15). Since (1.16) and (1.17) still hold, we infer that both eigenvalues of $\mathbf{L}_1$ are strictly positive. Next, by (1.18), we have that $m_1(1) > 0$ if and only if the inequality in (1.20) is verified, i.e. when $\beta < \beta_1$. Similarly to the case $0 < w_{11} < w_{22} < 1$, it is trivial to show that $\beta_1 > 1$, and therefore to conclude that $m_1(1) > 0$. In addition, by (1.19), we have that $\dot{m}_1(1) > 0$ if and only if the inequality in (1.21) is verified, i.e. when $\beta < \beta_2$. But, it is readily seen that $\beta_2 > 2$, which allows us to conclude that $\dot{m}_1(1) > 0$. Hence, we can assert that the greatest eigenvalue of $\mathbf{L}_1$ is smaller than 1. This leads to the result below.

Result 1.9 *In the case of underdominance without symmetry, the fixation of the fittest homozygote is locally stable, for all* $0 < \beta < 1$.

We finish this section by examining the recursive equations near the fixation state of A_2. We have previously determined the matrix of the linear approximation $\mathbf{L}_2$ and its characteristic polynomial $m_2(\lambda)$ given by (1.22). One can deduce that both eigenvalues of $\mathbf{L}_2$ are strictly positive. Next, by (1.23), we have that $m_2(1) > 0$ if and only if the inequality in (1.25) is verified, i.e. when $\beta < \beta_0$. In the case $w_{11} > w_{22} > 1$, we have shown that $0 < \beta_0 < 1$. Also, by (1.24), we have that $\dot{m}_2(1) > 0$ if and only

if the inequality in (1.26) is verified, i.e. when $\beta < \beta_3$. Therefore, three situations may occur:

(i) if $\beta < \beta_0$, then $m_2(1) > 0$. Besides, it is easy to show that $\beta_0 < \beta_3$. Hence, we have that $\dot{m}_2(1) > 0$ and consequently that the greatest eigenvalue of $\mathbf{L}_2$ is smaller than 1.

(ii) if $\beta > \beta_0$, then $m_2(1) < 0$. Consequently, whatever the sign of $\dot{m}_2(1)$ is, the greatest eigenvalue of $\mathbf{L}_2$ is always greater than 1.

(iii) if $\beta = \beta_0$, then $m_2(1) = 0$. Consequently, the greatest eigenvalue of $\mathbf{L}_2$ is equal to 1. This represents a degenerate case which requires a more refined analysis (see Appendix).

Result 1.10 *In the case of underdominance without symmetry, the fixation of the less fit homozygote is locally stable when a polymorphic equilibrium exists and locally unstable otherwise, even in a degenerate case corresponding to a critical value for* β.

1.6 Special cases

We conclude this exhaustive study of the partial selfing selection model by considering special combinations of selective values, for which the treatment will differ from those used in the preceding sections. In fact, for some special cases, global convergence can be obtained, thus providing new interesting results.

1.6.1 Case of directional selection

We assume, without loss of generality, $0 < w_{11} < 1 < w_{22}$. We have shown in Section 1.3 that there exists no polymorphic equilibrium in this case. The only remaining equilibria are the fixation states of A_1 and A_2, respectively $p = 1$ and $p = 0$. We will show that there is global convergence to the fixation of A_2, if both alleles are initially present in the population.

We have derived earlier that $p' = p^*$. Using equations (1.2), it is readily verified that $p' \leq p$ if and only if

$$\left(w_{11}P_{11} + \tfrac{1}{2}P_{12}\right)\left(\tfrac{1}{2}P_{12} + P_{22}\right) \leq \left(P_{11} + \tfrac{1}{2}P_{12}\right)\left(\tfrac{1}{2}P_{12} + w_{22}P_{22}\right),$$

for $w_{11} < 1$ and $1 < w_{22}$. Moreover, if $P_{11} + \frac{1}{2}P_{12} = p \neq 0$ and $\frac{1}{2}P_{12} + P_{22} = 1 - p \neq 0$, then we have equality above if and only if $w_{11}P_{11} + \frac{1}{2}P_{12} = P_{11} + \frac{1}{2}P_{12}$ and $\frac{1}{2}P_{12} + P_{22} = \frac{1}{2}P_{12} + w_{22}P_{22}$, that is, if and only if $P_{12} = 1$, which implies that $p = \frac{1}{2}$. But, as shown in the Appendix, the state $P_{12} = 1$ cannot be an accumulation point of the iterates of the recursive equations (1.3) and furthermore cannot be maintained from one generation to the next. Therefore, p decreases to 0 from every state for which $p \neq 1$. We refer the reader to the Appendix for a rigourous proof.

Result 1.11 *In the case of directional selection, there is global convergence to the fixation of the fittest homozygote, for all* $0 < \beta < 1$.

1.6.2 Case of complete dominance

As a special case of directional selection, we consider complete dominance. We assume, without loss of generality, $w_{11} = w_{12} = 1$. After some manipulations, one can get

$$\Delta p = p' - p = \left[\frac{(1 - w_{22})(1 - P_{11} - P_{12})}{(1 - w_{22})(P_{11} + P_{12}) + w_{22}} \right] p .$$

At equilibrium, we must have $\Delta p = 0$. This equality is satisfied if and only if $p = 0$ or $P_{11} + P_{12} = 1$. The first solution corresponds to the fixation of A_2 whereas the second solution cannot be a set of accumulation points of the iterates of the recursive equations (1.3) except for $P_{11} = 1$, which corresponds to the fixation of A_1. The latter assertion is proved in the Appendix.

The sign of Δp is completely determined by the sign of the function

$$g(x) = \frac{(1 - w_{22})(1 - x)}{(1 - w_{22})x + w_{22}},$$

where $x = P_{11} + P_{12}$. To analyse this function, we evaluate its derivative, which is

$$\dot{g}(x) = \frac{-(1 - w_{22})}{[(1 - w_{22})x + w_{22}]^2} .$$

In the following, we distinguish two cases:

- **Case of a deleterious recessive allele ($w_{22} < 1$).** First, we have that $g(0) = (1 - w_{22})/w_{22} > 0$ and $g(1) = 0$. For $0 < x < 1$, the derivative of $g(x)$ is strictly negative and then $g(x)$ is strictly decreasing on this interval. This implies that Δp is strictly positive, so p increases from one generation to the next. In fact,

unless $p = 0$ or $p = 1$, p increases to 1, that is, the system globally converges to the fixation of A_1.

- **Case of a deleterious dominant allele ($w_{22} > 1$).** In this case, we have that $g(0) < 0$ and $g(1) = 0$. For $0 < x < 1$, the derivative of $g(x)$ is strictly positive and then $g(x)$ is strictly increasing on this interval. This implies that Δp is strictly negative, so p decreases from one generation to the next. Unless $p = 0$ or $p = 1$, p decreases to 0, that is, the system globally converges to the fixation of A_2.

Result 1.12 *In the case of complete dominance, there is global convergence to the fixation of the fittest homozygote, for all* $0 < \beta < 1$.

1.6.3 Case of symmetric selection

We assume $w_{11} = w_{22} = w \neq 0, 1$. In this symmetric case, we have shown that there exists a unique polymorphic equilibrium with $\hat{p} = \hat{q} = \frac{1}{2}$. Using equations (1.3), it is easy to show that $P'_{11} - P'_{22} = P^*_{11} - P^*_{22}$. Therefore, we have

$$\left|P'_{11} - P'_{22}\right| = \left[\frac{w}{(w-1)(P_{11} + P_{22}) + 1}\right]\left|P_{11} - P_{22}\right|.$$

To obtain $\left|P'_{11} - P'_{22}\right| = \left|P_{11} - P_{22}\right|$, either $P_{11} = P_{22}$ or $P_{11} \neq P_{22}$, and then

$$\frac{w}{(w-1)(P_{11} + P_{22}) + 1} = 1,$$

which is possible if and only if $P_{11} + P_{22} = 1$. But this last equality can be maintained only at the fixation states ($P_{11} = 1$ for the fixation of A_1 and $P_{22} = 1$ for the fixation of A_2). Elsewhere, the states for which $P_{11} + P_{22} = 1$ cannot represent a set of accumulation points of the iterates of the recursive equations (1.3). This can be ascertained from Result A.1 provided in the Appendix.

Next we examine the function

$$f(x) = \frac{w}{(w-1)x+1},$$

where $x = P_{11} + P_{22}$, in order to exhibit the general behavior of the system at hand. We need the derivative of $f(x)$ with respect to x, which is simply

$$\dot{f}(x) = -\frac{w(w-1)}{[(w-1)x+1]^2}.$$

In the following, we must consider the two cases $w < 1$ and $w > 1$ separately.

- **Case of symmetric overdominance ($w < 1$).** In this case, $\dot{f}(x) > 0$ for every x on the interval [0, 1], thus ensuring that the function $f(x)$ is strictly increasing on this interval. We also have that $0 < w = f(0) < f(x) < f(1) = 1$ for $0 < x < 1$. Hence, we conclude that $|P_{11} - P_{22}|$ decreases to 0, unless $P_{11} = 1$ or $P_{22} = 1$, and consequently that there is convergence to the manifold $P_{11} = P_{22}$.

  Next, we verify that there is convergence to the polymorphic equilibrium on the manifold $P_{11} = P_{22}$. To this end, we shall employ the transformation equation, from one generation to the next, for the frequency of the genotype A_1A_1. Letting $P_{11} = P_{22}$ in equations (1.3), one obtains

$$P'_{11} = \frac{1}{4} + \frac{\beta}{2}\left(\frac{wP_{11}}{1-2(1-w)P_{11}}\right).$$

  We note that $P'_{11} = \frac{1}{4}$, when $P_{11} = 0$, and $P'_{11} = \frac{1}{4} + \frac{\beta}{4}$, when $P_{11} = \frac{1}{2}$. The derivative of P'_{11} with respect to P_{11} is such that

$$\frac{\mathrm{d}}{\mathrm{d}P_{11}} P_{11}' = \frac{\beta}{2}\left\{\frac{w}{[1-2(1-w)P_{11}]^2}\right\} > 0,$$

for $0 \le P_{11} \le \frac{1}{2}$. The second derivative of P_{11}' being also strictly positive, we deduce that P_{11}' is strictly increasing and convex, for $0 \le P_{11} \le \frac{1}{2}$. Therefore, the frequency P_{11} converges to the value $\hat{P}_{11}$, which satisfies $\hat{P}_{11}' = \hat{P}_{11}$ and $0 < \hat{P}_{11} < \frac{1}{2}$, and is given by

$$\hat{P}_{11} = \frac{3 - w(1+\beta) - \sqrt{[3-w(1+\beta)]^2 - 8(1-w)}}{8(1-w)},$$

that is, there is convergence to the polymorphic equilibrium on the manifold $P_{11} = P_{22}$. A more rigorous proof of global convergence is presented in the Appendix.

Result 1.13 *In the case of symmetric overdominance, there is global convergence to the polymorphic equilibrium, for all* $0 < \beta < 1$.

- **Case of symmetric underdominance ($w > 1$).** In this case, $f'(x) < 0$ for every x on the interval [0, 1], thus ensuring that the function $f(x)$ is strictly decreasing on this interval. We also have that $w = f(0) > f(x) > f(1) = 1$, for $0 < x < 1$. Hence, we conclude that $|P_{11} - P_{22}|$ increases to 1, if $P_{11} \neq P_{22}$ initially. This implies convergence to one of the fixation states, $P_{11} = 1$ or $P_{22} = 1$. If $P_{11} > P_{22}$ initially, then the system will converge to the fixation of A_1 whereas, if $P_{11} < P_{22}$ initially, then the system will converge to the fixation of A_2, since these inequalities are always preserved afterwards. Consequently, the polymorphic equilibrium is unstable. However, there will be convergence to the polymorphic equilibrium on the manifold $P_{11} = P_{22}$, because the results previously outlined in the case $w < 1$ remain valid except that the function P_{11}' is now concave, for $0 \le P_{11} \le \frac{1}{2}$.

Result 1.14 *In the case of symmetric underdominance, the polymorphic equilibrium is unstable and both fixation states are stable, for all* $0 < \beta < 1$.

1.6.4 Case of a lethal homozygote

We assume, without loss of generality, $w_{11} = 0$. The gene A_1 is lethal when homozygote, that is, an individual who carries the genotype A_1A_1 does not survive prior to mating and reproduction, and thus does not contribute any zygote to the next generation. We shall consider the genotype frequencies of the adults from one generation to the next (for better understanding, see equations (1.2), (1.3) and Figure 1.1):

$$P_{11}^{*\prime} = \frac{w_{11}P_{11}'}{w_{11}P_{11}' + P_{12}' + w_{22}P_{22}'} = 0,$$

$$P_{12}^{*\prime} = \frac{P_{12}'}{w_{11}P_{11}' + P_{12}' + w_{22}P_{22}'} = \frac{P_{12}'}{P_{12}' + w_{22}P_{22}'},$$

$$P_{22}^{*\prime} = \frac{w_{22}P_{22}'}{w_{11}P_{11}' + P_{12}' + w_{22}P_{22}'} = \frac{w_{22}P_{22}'}{P_{12}' + w_{22}P_{22}'}.$$

Observing that $P_{12}^* = 1 - P_{22}^*$ after the very first generation, one obtains that

$$P_{22}^{*\prime} = \frac{w_{22}\left[1+(2+\beta)P_{22}^* + (1-\beta)P_{22}^{*2}\right]}{2(1-P_{22}^*)\left[1+(1-\beta)P_{22}^*\right] + w_{22}\left[1+(2+\beta)P_{22}^* + (1-\beta)P_{22}^{*2}\right]}. \qquad (1.27)$$

Letting $P_{22}^{*\prime} = P_{22}^*$ in (1.27) provides a non-trivial value for P_{22}^* at equilibrium, which is given by

$$\hat{P}_{22}^* = \frac{-\left[2(1-w_{22}) - \beta w_{22}\right] + \sqrt{\left[2(1-w_{22}) - \beta w_{22}\right]^2 + 4w_{22}(2-w_{22})(1-\beta)}}{2(2-w_{22})(1-\beta)}.$$

This value enables us to determine the value of p at the polymorphic equilibrium (when it exists), which is simply

$$\hat{p} = \hat{P}_{11}^{*} + \tfrac{1}{2}\hat{P}_{12}^{*} = \tfrac{1}{2}\left(1 - \hat{P}_{22}^{*}\right).$$

One can verify that, when $w_{22} \leq \frac{1}{2}$, there exists a polymorphic equilibrium for all $0 < \beta < 1$, whereas when $\frac{1}{2} < w_{22} < 1$, there exists a polymorphic equilibrium if and only if $\beta < 2\left(1 - w_{22}\right) = \beta_0$. This is effectively the value of β_0 encountered previously, whose term w_{11} equals 0. Note that these results are consistent with Result 1.3.

To study the stability of the equilibrium points, we will utilize the recursive equation of P_{22}^{*}, as given in (1.27). Generally, the derivative of this equation, calculated at these equilibrium points, suffices to indicate the stability of such points. If the derivative is smaller than 1 in absolute value, then the equilibrium point is stable whereas if it is greater than 1, then the equilibrium point is unstable. If the derivative is equal to 1 in absolute value, we must look at the second derivative of the recursive equation at this point.

After some tedious algebraic manipulations, we find that the first derivative of equation (1.27) is given by

$$\frac{\mathrm{d}}{\mathrm{d}P_{22}^{*}} P_{22}^{*\prime} = \frac{4w_{22}\left[1 + \beta + 2(1-\beta)P_{22}^{*} + (1-\beta)P_{22}^{*2}\right]}{\left\{2\left(1 - P_{22}^{*}\right)\left[1 + (1-\beta)P_{22}^{*}\right] + w_{22}\left[1 + (2+\beta)P_{22}^{*} + (1-\beta)P_{22}^{*2}\right]\right\}^{2}} > 0,$$

for $0 \leq P_{22}^{*} \leq 1$ and $0 < \beta < 1$. Thus, $P_{22}^{*\prime}$ is strictly increasing as a function of P_{22}^{*} on the interval [0, 1]. Moreover, one can easily compute

$$\left.\frac{\mathrm{d}}{\mathrm{d}P_{22}^{*}} P_{22}^{*\prime}\right|_{P_{22}^{*}=0} = \frac{4w_{22}(1+\beta)}{\left(2 + w_{22}\right)^{2}} \quad \text{and} \quad \left.\frac{\mathrm{d}}{\mathrm{d}P_{22}^{*}} P_{22}^{*\prime}\right|_{P_{22}^{*}=1} = \frac{2-\beta}{2w_{22}}.$$

It is easy to show that the derivative at $P_{22}^* = 0$ is always smaller than 1, whereas the derivative at $P_{22}^* = 1$ is smaller than 1 if and only if $\beta > 2(1 - w_{22}) = \beta_0$.

When $w_{22} > 1$, no polymorphic equilibrium exists. In addition, we observe that $P_{22}^{*\prime} = w_{22}/(2 + w_{22}) > 0$ at $P_{22}^* = 0$. Since the derivative of $P_{22}^{*\prime}$ evaluated at $P_{22}^* = 1$ is smaller than 1 for $w_{22} > 1$, we deduce that, unless $P_{22}^* = 1$, there is global convergence to $P_{22}^* = 1$ or equivalently, to the fixation of A_2. The same arguments remain valid when $w_{22} = 1$ and also when $w_{22} < 1$, but only if $\beta \geq \beta_0$, since no polymorphic equilibrium exists for these specific values of β.

However, when $\beta < \beta_0$, a polymorphic equilibrium exists. Because the derivative of $P_{22}^{*\prime}$ at $P_{22}^* = 1$ is greater than 1, the fixation of A_2 is now unstable. Also, since $P_{22}^{*\prime} = w_{22}/(2 + w_{22}) > 0$ at $P_{22}^* = 0$ and $P_{22}^{*\prime}$ is strictly increasing on [0, 1], the derivative of $P_{22}^{*\prime}$ calculated at $P_{22}^* = \hat{P}_{22}^*$ must be assumed smaller than 1. This enables us to assert global convergence to the polymorphic equilibrium in this case.

Result 1.15 *In the case of a lethal homozygote, there is global convergence to the polymorphic equilibrium, when it exists, or to the fixation of the other homozygote, when no polymorphic equilibrium exists.*

1.6.5 Case of a lethal heterozygote

This time, an individual who carries the heterozygote genotype A_1A_2 does not survive prior to mating and reproduction. Note that this case is a special case of underdominance. We assume, without loss of generality, $w_{12} = 0 < w_{22} < w_{11}$. Similarly to the previous case, we consider the genotype frequencies of the adults from one generation to the next. These frequencies are expressed as:

$$P_{11}^{*\prime} = \frac{w_{11}P_{11}'}{w_{11}P_{11}' + w_{22}P_{22}'}, \qquad P_{12}^{*\prime} = 0, \qquad P_{22}^{*\prime} = \frac{w_{22}P_{22}'}{w_{11}P_{11}' + w_{22}P_{22}'}.$$

Noting that $P_{22}^* = 1 - P_{11}^*$ after the first generation, one can write

$$P_{11}^{*\prime} = \frac{w_{11}P_{11}^*\left[\beta + (1-\beta)P_{11}^*\right]}{w_{11}P_{11}^*\left[\beta + (1-\beta)P_{11}^*\right] + w_{22}(1-P_{11}^*)\left[\beta + (1-\beta)(1-P_{11}^*)\right]}. \qquad (1.28)$$

Letting $P_{11}^{*\prime} = P_{11}^*$ in (1.28) provides a non-trivial solution for the polymorphic equilibrium, that is, with $0 < P_{11}^* < 1$, if and only if $\beta < \beta_0 = w_{22}/w_{11}$. Thus, at the polymorphic equilibrium, we have

$$\hat{P}_{11}^* = \frac{w_{22} - \beta w_{11}}{(1-\beta)(w_{11} + w_{22})},$$

and the frequency of A_1 is given by

$$\hat{p} = \hat{P}_{11}^* + \tfrac{1}{2}\hat{P}_{12}^* = \hat{P}_{11}^* = \frac{w_{22} - \beta w_{11}}{(1-\beta)(w_{11} + w_{22})}.$$

To study the stability of the equilibrium points, we evaluate the derivative of the recursive equation of P_{11}^*, as expressed in (1.28). Simple calculations yield

$$\frac{\mathrm{d}}{\mathrm{d}P_{11}^*}P_{11}^{*\prime} = \frac{w_{11}w_{22}\left[\beta + 2(1-\beta)P_{11}^*(1-P_{11}^*)\right]}{\left\{w_{11}P_{11}^*\left[\beta + (1-\beta)P_{11}^*\right] + w_{22}(1-P_{11}^*)\left[\beta + (1-\beta)(1-P_{11}^*)\right]\right\}^2} > 0,$$

for $0 \le P_{11}^* \le 1$ and $0 < \beta < 1$. Hence, the recursive equation (1.28) is strictly increasing for P_{11}^* on the interval [0, 1]. We easily compute

$$\left.\frac{\mathrm{d}}{\mathrm{d}P_{11}^*}P_{11}^{*\prime}\right|_{P_{11}^*=0} = \frac{\beta w_{11}}{w_{22}} \quad \text{and} \quad \left.\frac{\mathrm{d}}{\mathrm{d}P_{11}^*}P_{11}^{*\prime}\right|_{P_{11}^*=1} = \frac{\beta w_{22}}{w_{11}}.$$

The derivative at $P_{11}^* = 0$ is smaller than 1 if and only if $\beta < \beta_0$, whereas the derivative at $P_{11}^* = 1$ is always smaller than 1. Therefore, the fixation of A_1 is always stable.

When $\beta < \beta_0$, a polymorphic equilibrium exists and, since the derivative of $P_{11}^{*\prime}$ at $P_{11}^* = 0$ is smaller than 1, the fixation of A_2 is stable. Because the fixation of A_1 is always stable and $P_{11}^{*\prime}$ is strictly increasing on [0, 1], the derivative of $P_{11}^{*\prime}$ at $P_{11}^* = \hat{P}_{11}^*$ must be greater than 1 and consequently the polymorphic equilibrium is unstable. If $P_{11}^* > \hat{P}_{11}^*$ initially, then the system converges to the fixation of A_1, unless $P_{11}^* = 1$. If $P_{11}^* < \hat{P}_{11}^*$ initially, then the system converges to the fixation of A_2, unless $P_{11}^* = 0$.

When $\beta \geq \beta_0$, no polymorphic equilibrium exists. In addition, since the derivative of $P_{11}^{*\prime}$ at $P_{11}^* = 0$ is greater than or equal to 1 in this case, the fixation of A_2 is now unstable. Also, from the fact that $P_{11}^{*\prime}$ is strictly increasing on [0, 1] and that the fixation of A_1 is stable, we deduce that there must be global convergence to the fixation of A_1, unless $P_{11}^* = 0$ or $P_{11}^* = 1$.

Finally, when $w_{11} = w_{22}$, the value of $\hat{P}_{11}^*$ at the polymorphic equilibrium equals $\frac{1}{2}$. The derivative of $P_{11}^{*\prime}$ evaluated respectively at $P_{11}^* = 0$ and $P_{11}^* = 1$ equals β, thus ensuring that it is smaller than 1. Consequently, the fixation states are stable and the polymorphic equilibrium unstable, for $0 < \beta < 1$.

Result 1.16 *In the case of a lethal heterozygote, the polymorphic equilibrium is unstable, when it exists, and both fixation states are stable; otherwise, when no polymorphic equilibrium exists, there is global convergence to the fittest homozygote.*

1.7 Discussion

Table 1.2 summarizes the results derived in the present paper as well as the results for the panmictic model ($\beta = 0$), in order to perform a comparison with the partial selfing model. In this table, we assume that

$$\beta_0 = \frac{2w_{22}(w_{12} - w_{22})}{w_{22}(w_{12} - w_{11}) + w_{11}(w_{12} - w_{22})}, \tag{1.31}$$

$p^{(0)}$ designates the initial frequency of allele A_1 in the population, and $(\hat{p}_R, \hat{q}_R)$ designates the respective frequencies of allele A_1 and A_2 at the polymorphic equilibrium under the panmictic model, where

$$\hat{p}_R = \frac{w_{22} - w_{12}}{w_{11} - 2w_{12} + w_{22}} \quad \text{and} \quad \hat{q}_R = 1 - \hat{p}_R = \frac{w_{11} - w_{12}}{w_{11} - 2w_{12} + w_{22}}.$$

Under the partial selfing model, $(\hat{p}_{PS}, \hat{q}_{PS})$ designates the respective frequencies of allele A_1 and A_2 at the polymorphic equilibrium

$$\hat{p}_{PS} = \frac{-B - \sqrt{B^2 - 4AC}}{2A} \quad \text{and} \quad \hat{q}_{PS} = 1 - \hat{p}_{PS} = \frac{2A + B + \sqrt{B^2 - 4AC}}{2A},$$

where

$$A = 2(1-\beta)(2w_{12} - w_{11} - w_{22})[w_{22}(w_{12} - w_{11}) + w_{11}(w_{12} - w_{22})],$$

$$B = [w_{22}(w_{12} - w_{11}) + w_{11}(w_{12} - w_{22})][(2-\beta)(w_{22} - w_{12}) - 3\beta(w_{11} - w_{12})] - 2w_{22}(w_{12} - w_{11})(2w_{12} - w_{11} - w_{22}),$$

$$C = 2w_{22}(w_{12} - w_{11})(w_{12} - w_{22}) - \beta(w_{12} - w_{11})[w_{22}(w_{12} - w_{11}) + w_{11}(w_{12} - w_{22})].$$

Table 1.2 Comparative results under the panmictic model and the partial selfing model.

Selective values	Panmixia ($\beta = 0$)	Partial selfing
OVERDOMINANCE		$\underline{0 < \beta < 1}$
$0 < w_{11} < w_{22} \leq \frac{w_{12}}{2}$	Global convergence to polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$	Polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$ locally stable
	Fixation of A_1 unstable	Fixation of A_1 locally unstable
	Fixation of A_2 unstable	Fixation of A_2 locally unstable
		$\underline{0 < \beta < 1}$
$0 = w_{11} < w_{22} \leq \frac{w_{12}}{2}$	Global convergence to polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$	Global convergence to polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$
	Fixation of A_1 unstable	Fixation of A_1 unstable
	Fixation of A_2 unstable	Fixation of A_2 unstable
		$\underline{0 < \beta < \beta_0}$
$0 < \max\left(w_{11}, \frac{w_{12}}{2}\right) < w_{22} < w_{12}$	Global convergence to polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$	Polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$ locally stable
	Fixation of A_1 unstable	Fixation of A_1 locally unstable
	Fixation of A_2 unstable	Fixation of A_2 locally unstable
		$\underline{\beta_0 \leq \beta < 1}$
		No polymorphic equilibrium
		Fixation of A_1 locally unstable
		Fixation of A_2 locally stable
		$\underline{0 < \beta < \beta_0}$
$0 = w_{11} < \frac{w_{12}}{2} < w_{22} < w_{12}$	Global convergence to polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$	Global convergence to polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$
	Fixation of A_1 unstable	Fixation of A_1 unstable
	Fixation of A_2 unstable	Fixation of A_2 unstable
		$\underline{\beta_0 \leq \beta < 1}$
		No polymorphic equilibrium
		Fixation of A_1 unstable
		Global convergence to fixation of A_2

		$0 < \beta < 1$
$0 < w_{11} = w_{22} < w_{12}$	Global convergence to polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$ Fixation of A_1 unstable Fixation of A_2 unstable	Global convergence to polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$ Fixation of A_1 unstable Fixation of A_2 unstable
UNDERDOMINANCE		$0 < \beta < \beta_0$
$0 < w_{12} < w_{22} < w_{11}$	Polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$ unstable If $p^{(0)} > \hat{p}_R$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_R$, then convergence to fixation of A_2	Polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$ locally unstable Fixation of A_1 locally stable Fixation of A_2 locally stable
		$\beta_0 \leq \beta < 1$
		No polymorphic equilibrium Fixation of A_1 locally stable Fixation of A_2 locally unstable
		$0 < \beta < \beta_0$
$0 = w_{12} < w_{22} < w_{11}$	Polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$ unstable If $p^{(0)} > \hat{p}_R$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_R$, then convergence to fixation of A_2	Polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$ unstable If $p^{(0)} > \hat{p}_{PS}$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_{PS}$, then convergence to fixation of A_2
		$\beta_0 \leq \beta < 1$
		No polymorphic equilibrium Global convergence to fixation of A_1 Fixation of A_2 unstable

		$0 < \beta < 1$
$0 \leq w_{12} < w_{11} = w_{22}$	Polymorphic equilibrium $(\hat{p}_R, \hat{q}_R)$ unstable If $p^{(0)} > \hat{p}_R$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_R$, then convergence to fixation of A_2	Polymorphic equilibrium $(\hat{p}_{PS}, \hat{q}_{PS})$ unstable If $p^{(0)} > \hat{p}_{PS}$, then convergence to fixation of A_1 If $p^{(0)} < \hat{p}_{PS}$, then convergence to fixation of A_2
DIRECTIONAL		$0 < \beta < 1$
$0 < w_{11} \leq w_{12} < w_{22}$ or $0 < w_{11} < w_{12} \leq w_{22}$ or $0 = w_{11} < w_{12} \leq w_{22}$	No polymorphic equilibrium Fixation of A_1 unstable Global convergence to fixation of A_2	No polymorphic equilibrium Fixation of A_1 unstable Global convergence to fixation of A_2

The comparison between the panmictic model and the partial selfing model has some interesting implications. In effect, a population under random mating at a given locus that suddenly practices partial selfing in some proportion β would undergo important changes in its genic structure and its genetic variability. This explains why our main attention will purposely be turned to those cases that guarantee the preservation of both genes A_1 and A_2 in the population.

A first look at Table 1.2 suggests but does not prove that polymorphism in the population can be maintained only in the overdominant case, and this in both models. For the panmictic model, there is global convergence to the polymorphic equilibrium. For the partial selfing model, however, we know only that a protected polymorphism exists, with both fixation states unstable, whenever a stable polymorphic equilibrium exists and vice versa.

On the one hand, when the heterozygote is strongly favored compared with the homozygotes ($0 < w_{11} < w_{22} \leq w_{12}/2$), referred by Overath and Asmussen (1998)

as "*double overdominance*", introduction of selfing does not modify the polymorphic structure of the population even if one of the genes is lethal for a homozygote. On the other hand, when the selective values of the homozygotes tend to be closer to that of the heterozygote ($0 < \max(w_{11}, w_{12}/2) < w_{22} < w_{12}$), referred by Overath and Asmussen (1998) as "*simple overdominance*", the polymorphism is preserved under the sole condition that the proportion β of selfing is not too large ($\beta < \beta_0$). A larger proportion will break the polymorphic structure of the population. Table 1.2 then shows what Overath and Asmussen (1998) hypothesized as " ... *when any self-fertilization occurs, simple overdominant selection may not be sufficient to maintain both alleles in the population.*" In case of equality of the selective values of the homozygotes, there is global convergence to the polymorphic equilibrium, regardless of the value of β. This seems intuitively sound because of the symmetry of the recursive equations in this case.

In every other sets of selective values but the overdominant case, it appears impossible for a polymorphism to be maintained in the population. For instance, when one of the genes is completely dominant ($0 < w_{11} = w_{12} < w_{22}$ or $0 < w_{22} < w_{11} = w_{12}$), selection will determine the ultimate structure of the population. In the former case, there will be eventual extinction of the gene A_1, whereas in the latter case, there will be eventual extinction of the gene A_2. These results remain valid in both models. These features were "predictable", since the case of a gene completely dominant is a particular case of directional selection.

As deduced by Overath and Asmussen (1998), the partial selfing model has the same general equilibrium structure as the random mating model. They conclude as follows: " ... *(1) at most one polymorphic equilibrium exists; (2) a polymorphic equilibrium exists only with overdominance or underdominance; (3) a stable polymorphic equilibrium exists only when selection is overdominant; and (4) a protected polymorphism, with both fixation states unstable, exists whenever a stable internal equilibrium exists and vice versa.*" We rigorously proved all four results above. Furthermore, we have deduced some important qualitative features of the

partial selfing model. In most cases, when the proportion β is not too large, it is essentially selection that will determine the ultimate genetic structure and, if it is possible, the preservation of the polymorphism in the population. When this proportion gets larger, no polymorphic equilibrium exists. Selfing is thus mostly responsible for compromising a possible polymorphism in the population. In fact, the partial selfing model with selection produces a struggle between two forces, selection on the one hand and selfing on the other.

Finally, it should be noted that Nagylaki (1997) has provided a complete analysis of the partial selfing model with weak selection. As expected, our results on the dynamical structure of the strong-selection model agree with those obtained under weak selection. However, Nagylaki's treatment differs greatly from ours, since his differential equation is "... *the weak-selection limit of the discrete selection model with constant inbreeding coefficient* ...". Thus, the dynamical analysis of the model is reduced to the study of a one-dimensional differential equation for the allelic frequencies. Following his notation, substituting $w_{ij} = 1 + \lambda u_{ij}$ in β_0 given in equation (1.31) and then letting λ tend to 0, one can show that

$$\tilde{\beta} = \frac{2(w_{12} - w_{22})}{(w_{12} - w_{11}) + (w_{12} - w_{22})}$$

is the limit, as λ goes to 0, of β_0. The value $\tilde{\beta}$ can be obtained from a detailed analysis of the four cases described in Nagylaki (1997). In the case of overdominance, it can be shown that β_0 monotonically decreases to $\tilde{\beta}$. This implies that strong selection is more favorable than weak selection for the preservation of a polymorphism. This can be explained by the fact that strong selection can produce a wider range of selective values than weak selection. Further, note that neither underdominance nor directional weak selection can maintain polymorphism in the population.

1.8 Summary

We have shown that a polymorphic equilibrium can exist only in the case of overdominance or underdominance and for a certain range of selfing rates (see Table 1.1). The existence of a polymorphic equilibrium in the case of directional selection is thus precluded. Moreover, a polymorphic equilibrium is unique when it exists. The results above have been first outlined by Kimura and Ohta (1971) in the case of overdominance only, and by Overath and Asmussen (1998) in their study of the partial selfing selection model with apomixis, and have been rigorously proved in the present paper. Also, the most frequent allele at a polymorphic equilibrium is the one associated with the homozygote that has the fitness closest to that of the heterozygote. Equal allelic frequencies at a polymorphic equilibrium appear only when the homozygotes have the same fitness. These new results have also been mathematically proved in this paper.

An analysis of local stability at the polymorphic equilibrium has also been conducted in this paper and has produced new results. In the case of overdominance, the polymorphic equilibrium is locally stable when it exists. In the case of underdominance, it is locally unstable when it exists. An analysis of local stability at the fixation states has confirmed results already known for the partial selfing model (Kimura and Ohta, 1971, Overath and Asmussen, 1998). We took this analysis a step further by carrying out a quadratic analysis in the degenerate case, that is, when the leading eigenvalue of the matrix of the linear approximation is equal to one, by applying a criterion due to Lessard and Karlin (1982). The local analysis outlined the fact that a protected polymorphism can only exist in the case of overdominance.

Finally, we have considered some special sets of selective values for which we can prove global convergence. In the case of directional selection and in the case of dominance, we showed that there is global convergence to the fixation of the fitter homozygote. In the case of symmetric overdominance, there is global convergence to the polymorphic equilibrium, whereas in the case of symmetric underdominance,

both fixation states are stable and the polymorphic equilibrium is unstable. In the case of a lethal homozygote, there is global convergence to the polymorphic equilibrium when it exists, or to the fixation of the other homozygote when no polymorphic equilibrium exists. In the case of a lethal heterozygote, the polymorphic equilibrium is unstable when it exists and both fixation states are stable. Otherwise, when no polymorphic equilibrium exists, there is global convergence to the fixation of the fittest homozygote. These new results of global convergence represent one of our major contributions to the study of the partial selfing selection model. Some of these results about the dynamical structure of the model have also been derived by Nagylaki (1997) for weak selection. However, since weak selection is a limiting case of selection, our results on strong selection provide a wider applicability.

Acknowledgements

This research started from a discussion with Drs. Bernard Godelle and Pierre-Henri Gouyon, from the Université de Paris-Sud. We thank Dr Thomas Nagylaki and two anonymous reviewers for very helpful comments on an earlier draft of this paper.

Chapitre 2: Change in frequency of a rare mutant allele: A general formula and applications to partial inbreeding models

Abstract

We deduce and prove a general formula to approximate the change in frequency of a mutant allele under weak selection, when this allele is introduced in small frequency into a population which was previously at a fixation state. We apply the formula to autosomal genes in partial selfing models and to autosomal as well as sex-linked genes in partial sib-mating models. It is shown that the fate of a rare mutant allele depends not only on the selection parameters, the inbreeding coefficient and the reproductive values of the sexes in sex-differentiated populations, but also on coefficients of relatedness between mates. This is interpreted as a kin selection effect caused by inbreeding per se.

2.1 Introduction

An approximate adaptive topography for partially inbred populations evolving under weak selection was proposed some time ago by Wright (1942). This topography is a function of the population state which involves, apart from the selection parameters, Wright's fixation index, F, also called the inbreeding coefficient, and the reproductive values of the sexes in the case of a sex-differentiated population. Without sex differences, the adaptive topography proposed is F times the mean fitness of inbred individuals plus $(1 - F)/2$ times the mean fitness of outbred individuals. Such an adaptive topography was first designed to predict the change in the frequency of any given gene, this change being given by the derivative of this topography with respect to an increase in the frequency of this gene alone. This will be referred to as *Wright's formula*.

In the case of a partial selfing population undergoing weak selection, it has been shown (Nagylaki, 1992, 1997) that, at least after enough generations have passed and as long as the population is far enough from equilibrium, the population evolves so that to go upward the adaptive topography proposed by Wright. In the case of a partial sib-mating population without sex differences, the change in the frequency of a mutant allele, after enough generations have passed and as long as the mutant allele is rare, does not completely agree with Wright's formula, as pointed out by Pollak (1995). Actually, in this case, Wright's adaptive topography has to be multiplied by $(1 + r)$, where r is the coefficient of correlation between the frequencies of the mutant allele in two mates, in order to yield a correct approximation for the change in frequency of the mutant allele in the population. Nevertheless, since the missing multiplicative factor is always positive, Wright's formula still correctly predicts the increase or decrease of gene frequencies, as long as the terms neglected in the approximation remain smaller. Therefore, in this case, we can say that Wright's formula is *qualitatively valid*, although it is not *quantitatively valid*.

In Pollak's (1995) paper, there are claims that are made without formal proofs. Moreover, it is of interest to know whether or not Wright's formula remains generally valid to predict the increase or decrease of gene frequencies in populations with inbreeding, that is, qualitatively valid. Finally, there is a need to interpret the effect of inbreeding on the change of gene frequencies that makes quantitatively invalid Wright's formula.

In this paper, we deduce and prove a general formula to approximate the change in frequency of a mutant allele under weak selection, when introduced in small frequency into a population which was previously at a fixation state. This can be used to study the fate of the mutant allele when rare and get conditions for its invasion or extinction. It is assumed that the population state can be described by a n-dimensional vector whose entries represent the frequencies of group types (actually, genotypes or mating types) carrying the mutant allele and that the linear approximation for the transformation of this vector near the origin from one generation to the next is given by a non-negative matrix which is smooth enough with respect to the intensity of selection and whose at least some power is positive. The formula is applied to autosomal genes in a partial selfing model and autosomal as well as sex-linked genes in a partial sib-mating model. Exact conditions for invasion of a rare mutant allele are deduced. We address the question of the quantitative and qualitative validity of Wright's formula in such models and we discuss the effect of inbreeding from a kin selection perspective.

2.2 Framework and basic results

We are interested in the fate of a mutant allele under weak selection, when introduced in small frequency into an infinite population at fixation. Let $\mathbf{x} = (x_1, x_2, \ldots, x_n)$ be a frequency vector describing the population state such that $\mathbf{x} = \mathbf{0}$, that is, the state with zero everywhere, corresponds to the fixation of a particular gene. Actually, x_1, x_2, ..., x_n will represent frequencies of types, genotypes or mating types, carrying the mutant allele. Let T be the transformation for the population state from one generation to the next, assuming discrete non-overlapping generations, such that $\mathbf{x}' = T(\mathbf{x})$ denotes the frequency vector in the next generation, given that it is $\mathbf{x}$ in the current generation. Assume that T is smooth enough with respect to $\mathbf{x}$ in the neighborhood of the fixation state $\mathbf{x} = \mathbf{0}$. Let $\mathbf{M}(s)$ be the matrix of linear approximation of the recurrence equations defined by T near the fixation state, so that

$$\mathbf{x}' = \mathbf{M}(s)\mathbf{x} + O(\|\mathbf{x}\|^2), \tag{2.1}$$

where $\|\mathbf{x}\|$ represents some norm of the vector $\mathbf{x}$, s measures the intensity of selection and $O(\|\mathbf{x}\|^2)$ denotes a function in $\mathbf{x}$ such that $\|O(\|\mathbf{x}\|^2)\|/\|\mathbf{x}\|^2$ remains bounded as $\|\mathbf{x}\|^2$ goes to 0. We will assume that the parameter s is positive and small, which models weak selection, the limiting case $s = 0$ corresponding to neutrality. The matrix $\mathbf{M}(s)$ is necessarily non-negative and the leading eigenvalue of this matrix will determine the fate of the mutant allele in the population if s is small enough and as long as the mutant allele remains rare enough.

Suppose that the non-negative matrix $\mathbf{M}(s)$ is such that there exists some integer k for which the matrix $\mathbf{M}^k(s)$ displays only positive entries for every $s \geq 0$, that is, $\mathbf{M}(s)$ is primitive for every $s \geq 0$. By the Perron-Frobenius theory (see, e.g., Gantmacher, 1959, Seneta, 1981), the greatest eigenvalue in modulus, denoted by $\rho(s)$, is simple, positive and strictly dominates the other eigenvalues in modulus.

Furthermore, there exist left and right eigenvectors associated to $\rho(s)$, denoted by $\xi(s)$ and $\eta(s)$ respectively, which exhibit only positive entries, and such positive eigenvectors are necessarily associated to the leading eigenvalue $\rho(s)$.

In absence of selection ($s = 0$), the Hardy-Weinberg law (see, e.g., Crow and Kimura, 1970) will guarantee that the frequency of the mutant allele will be invariant from one generation to the next. This frequency, denoted by p, will be given by $\mathbf{f}^{\mathrm{T}}\mathbf{x} = \sum_i f_i x_i$ (T for transpose), where f_i represents the frequency of the mutant allele in the mutant type i, for $i = 1, \ldots, n$ and $\mathbf{f} = (f_1, \ldots, f_n)$. Therefore $\mathbf{f}$ will be a positive left eigenvector for the eigenvalue 1, which entails $\rho(0) = 1$ with $\xi(0) = \mathbf{f}$. For s small, let $\dot{\rho}(s)$ and $\dot{\mathbf{M}}(s)$ denote the derivatives of $\rho(s)$ and $\mathbf{M}(s)$ with respect to s. These derivatives exist if $\mathbf{M}(s)$ is smooth enough with respect to s, which will be assumed. We are now ready to state a first result under the above assumptions (proof in Appendix).

Result 2.1 *The leading eigenvalue of* $\mathbf{M}(s)$ *for s small is approximated by*

$$\rho(s) = 1 + \dot{\rho}(0)s + O(s^2),$$

where

$$\dot{\rho}(0) = \frac{\xi(0)^{\mathrm{T}}\dot{\mathbf{M}}(0)\eta(0)}{\xi(0)^{\mathrm{T}}\eta(0)},$$

$\xi(0)$ *and* $\eta(0)$ *being positive left and right eigenvectors of* $\mathbf{M}(0)$ *for the eigenvalue* 1.

Actually, we can even go further and approximate the change in frequency of the mutant allele when rare from one generation to the next (proof in Appendix).

Result 2.2 *Let* $p^{(k)}$ *be the frequency of a rare mutant allele at generation k in a population previously at fixation. Under weak selection (s small enough) and for k*

sufficiently large, but not too large in the case $\dot{\rho}(0) > 0$, *the change in frequency of the rare mutant allele is approximated by*

$$\Delta p^{(k)} = p^{(k+1)} - p^{(k)} = \dot{\rho}(0)\, p^{(k)}\, s + \textit{smaller terms.}$$

Invasion or extinction of the mutant allele when rare will thus depend upon the sign of $\dot{\rho}(0)$. In effect, if $\dot{\rho}(0) < 0$, then $\rho(s) < 1$, for s sufficiently small, and the mutant allele will eventually disappear in the population if its initial frequency is small enough. Conversely, if $\dot{\rho}(0) > 0$, then $\rho(s) > 1$, for s sufficiently small, and extinction is precluded, which means protection of the mutant allele in the population (see, e.g., Lessard and Karlin, 1982, and references therein). The case $\dot{\rho}(0) = 0$ is a degenerate case that would require a quadratic approximation for $\rho(s)$.

In the next sections, we apply Results 2.1 and 2.2 to genetic models with partial inbreeding, namely partial selfing and partial sib-mating, and deduce conditions for the spread of a rare mutant allele.

2.3 Partial selfing model

Consider a single locus with two alleles, say A_1 and A_2, in an infinite diploid population undergoing discrete non-overlapping generations. Assume that every individual of the population can reproduce, either by selfing with probability α $(0 < \alpha < 1)$, or by random outcrossing with the complementary probability $1 - \alpha$. Let P_{11}, P_{12} and P_{22} denote the frequencies of the genotypes A_1A_1, A_1A_2 and A_2A_2, respectively, in the population. Then, the frequencies of the alleles A_1 and A_2 are

$$p_1 = P_{11} + \tfrac{1}{2}P_{12} \quad \text{and} \quad p_2 = P_{22} + \tfrac{1}{2}P_{12}.$$

Moreover, let the genotypes A_1A_1, A_1A_2, A_2A_2 have the respective selective values $w_{11} = 1 + h_{11}\,s$, $w_{12} = 1 + h_{12}\,s$, $w_{22} = 1 + h_{22}\,s$. Here, zygotic selection is applied through viability differences, that is, the genotypic selective values are proportional to the probabilities of survival from conception to maturity. It is assumed that the selective values are not all equal. Let us recall that s is assumed to be positive and small.

If P_{11}, P_{12} and P_{22} designate the genotypic frequencies among the zygotes in the current generation at the time of conception, then the genotypic frequencies among the adults in the current generation, after selection but before mating, are

$$P_{11}^* = \frac{w_{11}\,P_{11}}{w_{11}\,P_{11} + w_{12}P_{12} + w_{22}\,P_{22}}, \qquad P_{12}^* = \frac{w_{12}P_{12}}{w_{11}\,P_{11} + w_{12}P_{12} + w_{22}\,P_{22}},$$

$$P_{22}^* = \frac{w_{22}\,P_{22}}{w_{11}\,P_{11} + w_{12}P_{12} + w_{22}\,P_{22}}.$$

After mating and reproduction, the genotypic frequencies among the zygotes in the next generation are given by the equations

$$P'_{11} = \alpha\,[\,P^*_{11} + \tfrac{1}{4}P^*_{12}\,] + (1-\alpha)[\,P^*_{11} + \tfrac{1}{2}P^*_{12}\,]^2,$$

$$P'_{12} = \alpha\,[\,\tfrac{1}{2}P^*_{12}\,] + 2\,(1-\alpha)[\,P^*_{11} + \tfrac{1}{2}P^*_{12}\,][\,P^*_{22} + \tfrac{1}{2}P^*_{12}\,],$$

$$P'_{22} = \alpha\,[\,P^*_{22} + \tfrac{1}{4}P^*_{12}\,] + (1-\alpha)[\,P^*_{22} + \tfrac{1}{2}P^*_{12}\,]^2.$$

Here, we assume Mendelian segregation of genes, no fertility differences between the mating types and no gametic selection. It is useful to note that under these assumptions, mating and reproduction do not change the allelic frequencies, that is,

$$p'_1 = P'_{11} + \tfrac{1}{2}P'_{12} = P^*_{11} + \tfrac{1}{2}P^*_{12} = p^*_1,$$

and

$$p'_2 = 1 - p'_1 = 1 - p^*_1 = p^*_2.$$

Figure 2.1 below summarizes the life cycle in the population and the notation used for the genotypic and allelic frequencies. Of course, at each stage of the life cycle, the genotypic and allelic frequencies sum up to 1.

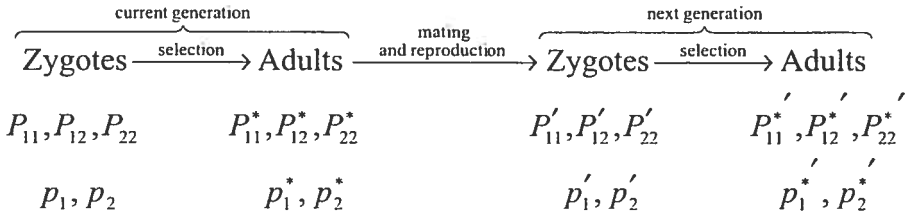

Figure 2.1 Life cycle and notation for genotypic and allelic frequencies in the partial selfing model.

Let us suppose that the allele A_1 is rare in the population. Developing the recurrence equations for P_{11}, P_{12} near the fixation of A_2 (P_{11}, $P_{12} \cong 0$) yields the matrix of linear approximation

$$\mathbf{M}(s)=\begin{bmatrix} \alpha(1+d_{11}s) & \frac{\alpha}{4}(1+d_{12}s) \\ 2(1-\alpha)(1+d_{11}s) & \left(1-\frac{\alpha}{2}\right)(1+d_{12}s) \end{bmatrix}+O(s^2),$$

where $d_{1j} = h_{1j} - h_{22}$, for $j = 1, 2$. One can easily deduce $\mathbf{M}(0)$ and calculate its eigenvalues, which are

$$\lambda_1 = 1,\ \lambda_2 = \frac{\alpha}{2}.$$

As expected, we have $\rho(0) = 1$. Left and right positive eigenvectors associated to this eigenvalue 1 are given respectively by

$$\xi(0)^{\mathrm{T}} = (2,\ 1) \quad \text{and} \quad \eta(0)^{\mathrm{T}} = \left(\alpha,\ 4(1-\alpha)\right).$$

Now, using Result 2.1, we find that

$$\dot{\rho}(0) = Fd_{11} + (1-F)d_{12}, \tag{2.2}$$

where

$$F = \frac{\alpha}{2-\alpha}.$$

Here, F is the inbreeding coefficient at equilibrium in the partial selfing model when there is no selection, that is, when $s = 0$ (Wright, 1921). Nagylaki (1997) confirmed that the above value of F can be used as an approximation in the case of weak selection (see also Pollak and Sabran, 1992).

Equation (2.2) allows us to obtain necessary and sufficient conditions for non extinction of A_1 when it is rare and selection is weak. Recall that $d_{1j} = h_{1j} - h_{22}$, for $j = 1, 2$. Therefore, $d_{1j} > 0$ means that A_1A_j is fitter than A_2A_2 for $j = 1, 2$.

Result 2.3 *If selection is weak enough in the partial selfing model, allele* A_1 *is preserved from extinction if and only if*

(*i*) $d_{12} > 0$, $d_{11} \leq 0$ *and* $\alpha < \dfrac{2d_{12}}{2d_{12} - d_{11}} = \alpha_0$, *or*

(*ii*) $d_{12} < 0$, $d_{11} > 0$ *and* $\alpha > \alpha_0$, *or*

(*iii*) $d_{12} \geq 0$ *and* $d_{11} > 0$.

This result agrees with those obtained by Nagylaki (1997) who achieved a complete dynamical analysis of the partial selfing model under weak selection. For studies of the partial selfing model under arbitrary selection parameters, see, e.g., Kimura and Ohta (1971) and Rocheleau and Lessard (2000).

2.4. Partial sib-mating model

The complete study of the partial sib-mating model with selection bears some difficulties due to the non-linearity of the transformation equations which must be expressed in terms of the mating types. Again, consider a single autosomal locus with two alleles, A_1 and A_2, in an infinite diploid population undergoing discrete non-overlapping generations. Let p_1, p_2 and q_1, q_2 be the allelic frequencies in males and females respectively. The frequencies of the genotypes A_1A_1, A_1A_2, A_2A_2 are denoted by P_{11}, P_{12}, P_{22} in males and Q_{11}, Q_{12}, Q_{22} in females. Every individual is given a fixed probability β of sib-mating and the complementary probability $1 - \beta$ of random mating ($0 < \beta < 1$). As a generalized version of the common non sex-differentiated selection model, we shall assign different viability values depending upon the sexes. These values for A_1A_1, A_1A_2, A_2A_2 will be $f_{11} = 1 + u_{11}s$, $f_{12} = 1 + u_{12}s$, $f_{22} = 1 + u_{22}s$ in females and $m_{11} = 1 + v_{11}s$, $m_{12} = 1 + v_{12}s$, $m_{22} = 1 + v_{22}s$ in males. It is assumed that the selective values are not all equal in at least one of the sexes. Figure 2.2 below schematizes the life cycle from one generation to the next.

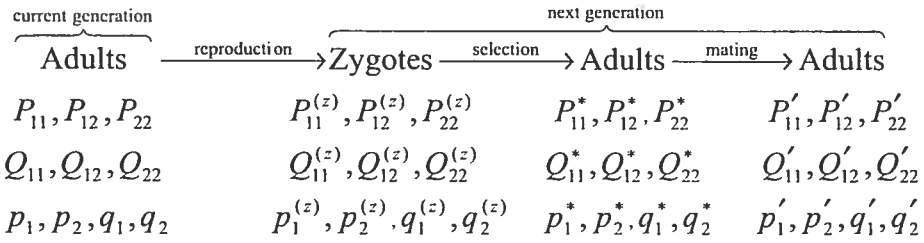

Figure 2.2 Life cycle and notation for frequencies in males and females in the partial sib-mating model.

Clearly, at each stage of the life cycle, the frequencies of the genotypes and alleles in males and females must sum up to 1. In a mated couple, we have to distinguish the sex of each member. Let x_1, ..., x_9 designate the frequencies of the mating types in the population, as illustrated in Table 2.1.

Table 2.1 Male × female mating types in the current generation and male × female couples of sibs produced in the next generation.

Male × female mating type	Frequency	Zygotes	Male × female couples of sibs
$(A_1A_1 \times A_1A_1)$	x_1	A_1A_1	$(A_1A_1 \times A_1A_1)$
$(A_1A_1 \times A_1A_2)$	x_2	$\frac{1}{2}A_1A_1{:}\frac{1}{2}A_1A_2$	$\frac{1}{4}(A_1A_1 \times A_1A_1){:}\frac{1}{4}(A_1A_1 \times A_1A_2)$
			$\frac{1}{4}(A_1A_2 \times A_1A_1){:}\frac{1}{4}(A_1A_2 \times A_1A_2)$
$(A_1A_2 \times A_1A_1)$	x_3	$\frac{1}{2}A_1A_1{:}\frac{1}{2}A_1A_2$	$\frac{1}{4}(A_1A_1 \times A_1A_1){:}\frac{1}{4}(A_1A_1 \times A_1A_2)$
			$\frac{1}{4}(A_1A_2 \times A_1A_1){:}\frac{1}{4}(A_1A_2 \times A_1A_2)$
$(A_1A_1 \times A_2A_2)$	x_4	A_1A_2	$(A_1A_2 \times A_1A_2)$
$(A_2A_2 \times A_1A_1)$	x_5	A_1A_2	$(A_1A_2 \times A_1A_2)$
$(A_1A_2 \times A_1A_2)$	x_6	$\frac{1}{4}A_1A_1{:}\frac{1}{2}A_1A_2{:}\frac{1}{4}A_2A_2$	$\frac{1}{16}(A_1A_1 \times A_1A_1){:}\frac{1}{8}(A_1A_1 \times A_1A_2)$
			$\frac{1}{8}(A_1A_2 \times A_1A_1){:}\frac{1}{16}(A_1A_1 \times A_2A_2)$
			$\frac{1}{16}(A_2A_2 \times A_1A_1){:}\frac{1}{4}(A_1A_2 \times A_1A_2)$
			$\frac{1}{8}(A_1A_2 \times A_2A_2){:}\frac{1}{8}(A_2A_2 \times A_1A_2)$
			$\frac{1}{16}(A_2A_2 \times A_2A_2)$
$(A_1A_2 \times A_2A_2)$	x_7	$\frac{1}{2}A_1A_2{:}\frac{1}{2}A_2A_2$	$\frac{1}{4}(A_1A_2 \times A_1A_2){:}\frac{1}{4}(A_1A_2 \times A_2A_2)$
			$\frac{1}{4}(A_2A_2 \times A_1A_2){:}\frac{1}{4}(A_2A_2 \times A_2A_2)$
$(A_2A_2 \times A_1A_2)$	x_8	$\frac{1}{2}A_1A_2{:}\frac{1}{2}A_2A_2$	$\frac{1}{4}(A_1A_2 \times A_1A_2){:}\frac{1}{4}(A_1A_2 \times A_2A_2)$
			$\frac{1}{4}(A_2A_2 \times A_1A_2){:}\frac{1}{4}(A_2A_2 \times A_2A_2)$
$(A_2A_2 \times A_2A_2)$	x_9	A_2A_2	$(A_2A_2 \times A_2A_2)$

We shall now derive the recurrence equations for the frequencies of the mating types from one generation to the next. The genotypic frequencies in the male and female adults, respectively, of the current generation in terms of the frequencies of the mating types are

$$P_{11} = x_1 + x_2 + x_4, \quad P_{12} = x_3 + x_6 + x_7, \quad P_{22} = x_5 + x_8 + x_9,$$

and

$$Q_{11} = x_1 + x_3 + x_5, \quad Q_{12} = x_2 + x_6 + x_8, \quad Q_{22} = x_4 + x_7 + x_9,$$

with $P_{11} + P_{12} + P_{22} = 1$ and $Q_{11} + Q_{12} + Q_{22} = 1$. The frequency of allele A_1, in the male and female adults, respectively, is

$$p_1 = P_{11} + \tfrac{1}{2} P_{12} = x_1 + x_2 + x_4 + \tfrac{1}{2}\left(x_3 + x_6 + x_7\right)$$

and

$$q_1 = Q_{11} + \tfrac{1}{2} Q_{12} = x_1 + x_3 + x_5 + \tfrac{1}{2}\left(x_2 + x_6 + x_8\right).$$

The adults of the current generation reproduce and the zygotes of the next generation are in the proportions indicated in Table 2.1. The genotypic frequencies of the zygotes just after conception are

$$P_{11}^{(z)} = Q_{11}^{(z)} = x_1 + \tfrac{1}{2} x_2 + \tfrac{1}{2} x_3 + \tfrac{1}{4} x_6,$$
$$P_{12}^{(z)} = Q_{12}^{(z)} = \tfrac{1}{2} x_2 + \tfrac{1}{2} x_3 + x_4 + x_5 + \tfrac{1}{2} x_6 + \tfrac{1}{2} x_7 + \tfrac{1}{2} x_8,$$
$$P_{22}^{(z)} = Q_{22}^{(z)} = \tfrac{1}{4} x_6 + \tfrac{1}{2} x_7 + \tfrac{1}{2} x_8 + x_9.$$

After selection, the genotypic frequencies among the zygotes in the population are modified so that, before mating, they are given by

$$P_{11}^{*}=\frac{m_{11}P_{11}^{(z)}}{T_{\mathrm{M}}},\quad P_{12}^{*}=\frac{m_{12}P_{12}^{(z)}}{T_{\mathrm{M}}},\quad P_{22}^{*}=\frac{m_{22}P_{22}^{(z)}}{T_{\mathrm{M}}},$$
$$Q_{11}^{*}=\frac{f_{11}Q_{11}^{(z)}}{T_{\mathrm{F}}},\quad Q_{12}^{*}=\frac{f_{12}Q_{12}^{(z)}}{T_{\mathrm{F}}},\quad Q_{22}^{*}=\frac{f_{22}Q_{22}^{(z)}}{T_{\mathrm{F}}},$$

where

$$\begin{aligned}T_{\mathrm{M}}&=m_{11}\left(x_1+\tfrac{1}{2}x_2+\tfrac{1}{2}x_3+\tfrac{1}{4}x_6\right)+m_{12}\left(\tfrac{1}{2}x_2+\tfrac{1}{2}x_3+x_4+x_5+\tfrac{1}{2}x_6+\tfrac{1}{2}x_7+\tfrac{1}{2}x_8\right)\\&\quad+m_{22}\left(\tfrac{1}{4}x_6+\tfrac{1}{2}x_7+\tfrac{1}{2}x_8+x_9\right),\\T_{\mathrm{F}}&=f_{11}\left(x_1+\tfrac{1}{2}x_2+\tfrac{1}{2}x_3+\tfrac{1}{4}x_6\right)+f_{12}\left(\tfrac{1}{2}x_2+\tfrac{1}{2}x_3+x_4+x_5+\tfrac{1}{2}x_6+\tfrac{1}{2}x_7+\tfrac{1}{2}x_8\right)\\&\quad+f_{22}\left(\tfrac{1}{4}x_6+\tfrac{1}{2}x_7+\tfrac{1}{2}x_8+x_9\right).\end{aligned}$$

Finally, the recurrence equations for the frequencies of the mating types from one generation to the next, taking into account that a proportion β of matings are between sibs (see Table 2.1) and a proportion $1-\beta$ occur at random, are

$$\begin{aligned}x_1'&=(1-\beta)P_{11}^{*}Q_{11}^{*}+\beta\, f_{11}m_{11}\left(x_1+\tfrac{1}{4}x_2+\tfrac{1}{4}x_3+\tfrac{1}{16}x_6\right)/T_{\mathrm{FS}},\\x_2'&=(1-\beta)P_{11}^{*}Q_{12}^{*}+\beta\, f_{12}m_{11}\left(\tfrac{1}{4}x_2+\tfrac{1}{4}x_3+\tfrac{1}{8}x_6\right)/T_{\mathrm{FS}},\\x_3'&=(1-\beta)P_{12}^{*}Q_{11}^{*}+\beta\, f_{11}m_{12}\left(\tfrac{1}{4}x_2+\tfrac{1}{4}x_3+\tfrac{1}{8}x_6\right)/T_{\mathrm{FS}},\\x_4'&=(1-\beta)P_{11}^{*}Q_{22}^{*}+\beta\, f_{22}m_{11}\left(\tfrac{1}{16}x_6\right)/T_{\mathrm{FS}},\\x_5'&=(1-\beta)P_{22}^{*}Q_{11}^{*}+\beta\, f_{11}m_{22}\left(\tfrac{1}{16}x_6\right)/T_{\mathrm{FS}},\\x_6'&=(1-\beta)P_{12}^{*}Q_{12}^{*}+\beta\, f_{12}m_{12}\left(\tfrac{1}{4}x_2+\tfrac{1}{4}x_3+x_4+x_5+\tfrac{1}{4}x_6+\tfrac{1}{4}x_7+\tfrac{1}{4}x_8\right)/T_{\mathrm{FS}},\\x_7'&=(1-\beta)P_{12}^{*}Q_{22}^{*}+\beta\, f_{22}m_{12}\left(\tfrac{1}{8}x_6+\tfrac{1}{4}x_7+\tfrac{1}{4}x_8\right)/T_{\mathrm{FS}},\\x_8'&=(1-\beta)P_{22}^{*}Q_{12}^{*}+\beta\, f_{12}m_{22}\left(\tfrac{1}{8}x_6+\tfrac{1}{4}x_7+\tfrac{1}{4}x_8\right)/T_{\mathrm{FS}},\\x_9'&=(1-\beta)P_{22}^{*}Q_{22}^{*}+\beta\, f_{22}m_{22}\left(\tfrac{1}{16}x_6+\tfrac{1}{4}x_7+\tfrac{1}{4}x_8+x_9\right)/T_{\mathrm{FS}},\end{aligned}\tag{2.3}$$

where

$$\begin{aligned}T_{\mathrm{FS}}&=f_{11}m_{11}\left(x_1+\tfrac{1}{4}x_2+\tfrac{1}{4}x_3+\tfrac{1}{16}x_6\right)+\left(f_{12}m_{11}+f_{11}m_{12}\right)\left(\tfrac{1}{4}x_2+\tfrac{1}{4}x_3+\tfrac{1}{8}x_6\right)\\&\quad+\left(f_{22}m_{11}+f_{11}m_{22}\right)\left(\tfrac{1}{16}x_6\right)+f_{12}m_{12}\left(\tfrac{1}{4}x_2+\tfrac{1}{4}x_3+x_4+x_5+\tfrac{1}{4}x_6+\tfrac{1}{4}x_7+\tfrac{1}{4}x_8\right)\\&\quad+\left(f_{22}m_{12}+f_{12}m_{22}\right)\left(\tfrac{1}{8}x_6+\tfrac{1}{4}x_7+\tfrac{1}{4}x_8\right)+f_{22}m_{22}\left(\tfrac{1}{16}x_6+\tfrac{1}{4}x_7+\tfrac{1}{4}x_8+x_9\right).\end{aligned}$$

Now, assuming that allele A_1 is rare in the population (x_1, x_2, ..., $x_8 \equiv 0$), the recurrence equations (2.3) yield the matrix of linear approximation $\mathbf{M}(s)$ (provided in the Appendix), up to terms of order s and with the notation

$$d_{1j}^{\mathrm{f}} = u_{1j} - u_{22} \quad \text{and} \quad d_{1j}^{\mathrm{m}} = v_{1j} - v_{22},$$

for $j = 1, 2$. The matrix $\mathbf{M}(0)$ is easily obtained and its eigenvalues in decreasing order (calculated by Mathematica) are all positive and given by

$$\lambda_1 = 1,\ \lambda_2 = \frac{2\beta + \sqrt{4\beta^2 + 16\beta}}{8},\ \lambda_3 = \frac{\beta}{2},\ \lambda_4 = \frac{\beta}{4},$$

$$\lambda_5 = \frac{2\beta - \sqrt{4\beta^2 + 16\beta}}{8},\ \lambda_6 = \lambda_7 = \lambda_8 = 0.$$

Positive left and right eigenvectors, respectively, associated to the eigenvalue 1 are

$$\xi(0)^{\mathrm{T}} = (4,\ 3,\ 3,\ 2,\ 2,\ 2,\ 1,\ 1)$$

and

$$\eta(0)^{\mathrm{T}} = \left(\frac{\beta(2+\beta)}{16(2-\beta)(1-\beta)}, \frac{\beta}{4(2-\beta)}, \frac{\beta}{4(2-\beta)}, \frac{1}{4}, \frac{1}{4}, 1, \frac{5\beta^2 - 20\beta + 16}{4\beta(2-\beta)}, \frac{5\beta^2 - 20\beta + 16}{4\beta(2-\beta)}\right).$$

Result 2.1 permits us to obtain

$$\dot{\rho}(0) = (1+r)\left[F\left(\frac{d_{11}^{\mathrm{f}} + d_{11}^{\mathrm{m}}}{2}\right) + (1-F)\left(\frac{d_{12}^{\mathrm{f}} + d_{12}^{\mathrm{m}}}{2}\right)\right], \tag{2.4}$$

where

$$F = \frac{\beta}{4 - 3\beta} \quad \text{and} \quad r = \frac{\beta}{2-\beta} = \frac{2F}{1+F}.$$

The coefficient F is the inbreeding coefficient at equilibrium in the partial sib-mating model without selection as shown by Ghai (1969). The coefficient r is known as the coefficient of relationship (Wright, 1922) and it represents the coefficient of correlation between two mated individuals relative to their frequencies of A_1 at the specified locus (see, e.g., Li, 1976). Since $F > 0$ and $r > 0$, the sign of $\dot{\rho}(0)$ is completely determined by those of d_{11}^{f}, d_{11}^{m}, d_{12}^{f} and d_{12}^{m}.

If we assume equal selective values for the sexes ($u_{11} = v_{11}$, $u_{12} = v_{12}$ and $u_{22} = v_{22}$) and define $d_{1j} = d_{1j}^{f} = d_{1j}^{m}$ for $i, j = 1, 2$, equation (2.4) reduces to

$$\dot{\rho}(0) = (1+r)\left[Fd_{11} + (1-F)d_{12}\right]. \tag{2.5}$$

It should be noted that equation (2.5) agrees with one derived less rigorously by Pollak (1995) for the same model.

A detailed analysis of equation (2.4) also allows us to determine necessary and sufficient conditions under which invasion of allele A_1 will occur under weak selection when it is rare in the population. We define

$$h_{ij} = \frac{u_{ij} + v_{ij}}{2} \quad \text{and} \quad d_{1j} = h_{1j} - h_{22},$$

for $i, j = 1, 2$. Therefore, as in the partial selfing model, $d_{1j} > 0$ means that A_1A_j is fitter than A_2A_2, for $j = 1, 2$, if the fitness of a genotype is defined as the average fitness of that genotype in females and males, giving the same weight to the fitnesses in each of the sexes.

Result 2.4 *If selection is weak enough in the partial sib-mating model for autosomal genes, allele* A_1 *is preserved from extinction if and only if*

(*i*) $d_{12} > 0$, $d_{11} \leq 0$ *and* $\beta < \dfrac{4d_{12}}{4d_{12} - d_{11}} = \beta_0$, *or*

(*ii*) $d_{12} < 0$, $d_{11} > 0$ *and* $\beta > \beta_0$, *or*

(*iii*) $d_{12} \geq 0$ *and* $d_{11} > 0$.

2.5 Partial sib-mating model for sex-linked genes

In this model, we suppose that females possess two genes at the concerned locus while males have only one. Thus, the female population is diploid at this locus whereas the male population is haploid. Given two alleles, A_1 and A_2, we assign selective values $f_{11} = 1 + u_{11}s, f_{12} = 1 + u_{12}s, f_{22} = 1 + u_{22}s$ to the female genotypes A_1A_1, A_1A_2, A_2A_2 and the selective values $m_1 = 1 + v_1s$, $m_2 = 1 + v_2s$ to the male genotypes A_1, A_2. These selective values are not all equal in at least one of the sexes. All possible mating types and their frequencies are depicted in Table 2.2. The genotypic frequencies in the male and female adults, respectively, in the current generation are given by

$$P_1 = x_1 + x_2 + x_3, \quad P_2 = x_4 + x_5 + x_6,$$

and

$$Q_{11} = x_1 + x_4, \quad Q_{12} = x_2 + x_5, \quad Q_{22} = x_3 + x_6,$$

Table 2.2 Mating types in the current generation and couples of sibs produced in the next generation for a sex-linked locus.

Mating type	Frequency	Zygotes		Couples of sibs
		female	male	
$(A_1A_1 \times A_1)$	x_1	A_1A_1	A_1	$(A_1A_1 \times A_1)$
$(A_1A_2 \times A_1)$	x_2	$\frac{1}{2}A_1A_1{:}\frac{1}{2}A_1A_2$	$\frac{1}{2}A_1{:}\frac{1}{2}A_2$	$\frac{1}{4}(A_1A_1 \times A_1){:}\frac{1}{4}(A_1A_1 \times A_2)$
				$\frac{1}{4}(A_1A_2 \times A_1){:}\frac{1}{4}(A_1A_2 \times A_2)$
$(A_2A_2 \times A_1)$	x_3	A_1A_2	A_2	$(A_1A_2 \times A_2)$
$(A_1A_1 \times A_2)$	x_4	A_1A_2	A_1	$(A_1A_2 \times A_1)$
$(A_1A_2 \times A_2)$	x_5	$\frac{1}{2}A_1A_2{:}\frac{1}{2}A_2A_2$	$\frac{1}{2}A_1{:}\frac{1}{2}A_2$	$\frac{1}{4}(A_1A_2 \times A_1){:}\frac{1}{4}(A_1A_2 \times A_2)$
				$\frac{1}{4}(A_2A_2 \times A_1){:}\frac{1}{4}(A_2A_2 \times A_2)$
$(A_2A_2 \times A_2)$	x_6	A_2A_2	A_2	$(A_2A_2 \times A_2)$

with $P_1 + P_2 = 1$ and $Q_{11} + Q_{12} + Q_{22} = 1$. Then, the frequency of allele A_1 in the male and female adults, respectively, is

$$p_1 = P_1 = x_1 + x_2 + x_3 \quad \text{and} \quad q_1 = Q_{11} + \tfrac{1}{2}Q_{12} = x_1 + x_4 + \tfrac{1}{2}(x_2 + x_5).$$

After mating and reproduction of the adults in the current generation, the genotypic frequencies in male and female zygotes, respectively, in the next generation are

$$P_1^{(z)} = x_1 + \tfrac{1}{2}x_2 + x_4 + \tfrac{1}{2}x_5, \quad P_2^{(z)} = \tfrac{1}{2}x_2 + x_3 + \tfrac{1}{2}x_5 + x_6,$$

and

$$Q_{11}^{(z)} = x_1 + \tfrac{1}{2}x_2, \quad Q_{12}^{(z)} = \tfrac{1}{2}x_2 + x_3 + x_4 + \tfrac{1}{2}x_5, \quad Q_{22}^{(z)} = \tfrac{1}{2}x_5 + x_6.$$

After selection among the zygotes, these genotypic frequencies become

$$P_1^* = \frac{m_1 P_1^{(z)}}{T_M}, \quad P_2^* = \frac{m_2 P_2^{(z)}}{T_M},$$
$$Q_{11}^* = \frac{f_{11} Q_{11}^{(z)}}{T_F}, \quad Q_{12}^* = \frac{f_{12} Q_{12}^{(z)}}{T_F}, \quad Q_{22}^* = \frac{f_{22} Q_{22}^{(z)}}{T_F},$$

where

$$T_M = m_1(x_1 + \tfrac{1}{2}x_2 + x_4 + \tfrac{1}{2}x_5) + m_2(\tfrac{1}{2}x_2 + x_3 + \tfrac{1}{2}x_5 + x_6),$$
$$T_F = f_{11}(x_1 + \tfrac{1}{2}x_2) + f_{12}(\tfrac{1}{2}x_2 + x_3 + x_4 + \tfrac{1}{2}x_5) + f_{22}(\tfrac{1}{2}x_5 + x_6).$$

Assuming a probability β of sib-mating and $1 - \beta$ of random mating ($0 < \beta < 1$), the recurrence equations for the frequencies of the mating types from one generation to the next are

$$x_1' = (1-\beta)Q_{11}^* P_1^* + \beta f_{11} m_1 (x_1 + \tfrac{1}{4}x_2)/T_{FS},$$
$$x_2' = (1-\beta)Q_{12}^* P_1^* + \beta f_{12} m_1 (\tfrac{1}{4}x_2 + x_4 + \tfrac{1}{4}x_5)/T_{FS},$$
$$x_3' = (1-\beta)Q_{22}^* P_1^* + \beta f_{22} m_1 (\tfrac{1}{4}x_5)/T_{FS},$$
$$x_4' = (1-\beta)Q_{11}^* P_2^* + \beta f_{11} m_2 (\tfrac{1}{4}x_2)/T_{FS},$$
$$x_5' = (1-\beta)Q_{12}^* P_2^* + \beta f_{12} m_2 (\tfrac{1}{4}x_2 + x_3 + \tfrac{1}{4}x_5)/T_{FS},$$
$$x_6' = (1-\beta)Q_{22}^* P_2^* + \beta f_{22} m_2 (\tfrac{1}{4}x_5 + x_6)/T_{FS},$$

where

$$T_{FS} = f_{11}m_1x_1 + \tfrac{1}{4}(f_{11}+f_{12})(m_1+m_2)x_2 + f_{12}m_2x_3 + f_{12}m_1x_4 + \tfrac{1}{4}(f_{12}+f_{22})(m_1+m_2)x_5 + f_{22}m_2x_6.$$

Near the fixation state of allele A_2, the matrix of linear approximation $\mathbf{M}(s)$, ignoring terms of order s^2 or smaller and using the notation $d_1^{\mathrm{m}} = v_1 - v_2$ and $d_{1j}^{\mathrm{f}} = u_{1j} - u_{22}$, for $j = 1, 2$, reads as

$$\begin{bmatrix}
\beta(1+d_{11}^{\mathrm{f}}s+d_1^{\mathrm{m}}s) & \frac{\beta}{4}(1+d_{11}^{\mathrm{f}}s+d_1^{\mathrm{m}}s) & 0 & 0 & 0 \\
0 & \frac{\beta}{4}(1+d_{12}^{\mathrm{f}}s+d_1^{\mathrm{m}}s) & 0 & \beta(1+d_{12}^{\mathrm{f}}s+d_1^{\mathrm{m}}s) & \frac{\beta}{4}(1+d_{12}^{\mathrm{f}}s+d_1^{\mathrm{m}}s) \\
(1-\beta)(1+d_1^{\mathrm{m}}s) & \left(\frac{1-\beta}{2}\right)(1+d_1^{\mathrm{m}}s) & 0 & (1-\beta)(1+d_1^{\mathrm{m}}s) & \left(\frac{2-\beta}{4}\right)(1+d_1^{\mathrm{m}}s) \\
(1-\beta)(1+d_{11}^{\mathrm{f}}s) & \left(\frac{2-\beta}{4}\right)(1+d_{11}^{\mathrm{f}}s) & 0 & 0 & 0 \\
0 & \left(\frac{2-\beta}{4}\right)(1+d_{12}^{\mathrm{f}}s) & 1+d_{12}^{\mathrm{f}}s & (1-\beta)(1+d_{12}^{\mathrm{f}}s) & \left(\frac{2-\beta}{4}\right)(1+d_{12}^{\mathrm{f}}s)
\end{bmatrix}$$

The matrix $\mathbf{M}(0)$ is easily deduced and its eigenvalues (calculated by Mathematica), in decreasing order, are

$$\lambda_1 = 1,\ \lambda_2 = \frac{2\beta + \sqrt{4\beta^2+16\beta}}{8},\ \lambda_3 = \frac{\beta}{2},\ \lambda_4 = \frac{2\beta - \sqrt{4\beta^2+16\beta}}{8},\ \lambda_5 = -\frac{1}{2}.$$

Positive left and right eigenvectors of $\mathbf{M}(0)$ associated to the eigenvalue 1 are given by

$$\xi(0)^{\mathsf{T}} = (3,2,1,2,1) \quad \text{and} \quad \eta(0)^{\mathsf{T}} = \left(\frac{\beta}{4(1-\beta)}, 1, \frac{4-3\beta}{2\beta}, \frac{1}{2}, \frac{4-3\beta}{\beta}\right).$$

Result 2.1 yields

$$\dot{\rho}(0)=\left(\frac{2}{3}+\frac{1}{3}r_{Y\to X}\right)\left[Fd_{11}^{\mathrm{f}}+(1-F)d_{12}^{\mathrm{f}}\right]+\left(\frac{1}{3}+\frac{2}{3}r_{X\to Y}\right)d_{1}^{\mathrm{m}} \tag{2.6}$$

where

$$F=\frac{\beta}{4-3\beta},\quad r_{Y\to X}=\frac{\beta}{2-\beta},\quad r_{X\to Y}=\frac{\beta}{4-3\beta}.$$

Again, F represents the inbreeding coefficient in females at equilibrium in absence of selection. The coefficient $r_{Y\to X}$ represents the coefficient of regression of the frequency of A_1 genes carried by the male of a mated couple (Y) on the frequency of A_1 genes carried by the female of this couple (X), when there is no selection and the population is at equilibrium. The coefficient $r_{X\to Y}$ is defined analogously. It must be noted that when females and males are both diploid at the given locus, then

$$r=r_{Y\to X}=r_{X\to Y}=\frac{\beta}{2-\beta}.$$

Proof of this assertion and derivation of the regression coefficients are found in the Appendix. One should observe that the dissymmetry of the recurrence equations is reflected into the expression of $\dot{\rho}(0)$. In effect, the contribution of each sex is weighted by its corresponding coefficient of regression. The fractions $\frac{2}{3}$ and $\frac{1}{3}$ correspond to reproductive values of females and males, respectively, and are proportional to the contributions of the two sexes at the sex-linked locus in question.

A detailed analysis of equation (2.6) gives the following result, where

$$d_{12}=\frac{2}{3}(u_{12}-u_{22})+\frac{1}{3}(v_1-v_2)\quad\text{and}\quad d_{11}=\frac{1}{2}(u_{11}-u_{22})+\frac{1}{2}(v_1-v_2).$$

Result 2.5 *If selection is weak enough in the partial sib-mating model for sex-linked genes, allele* A_1 *is preserved from extinction if and only if*

(*i*) $d_{12} > 0$, $d_{11} \leq 0$ *and* $\beta < \dfrac{3d_{12}}{3d_{12} - d_{11}} = \beta_1$, *or*

(*ii*) $d_{12} < 0$, $d_{11} > 0$ *and* $\beta > \beta_1$, *or*

(*iii*) $d_{12} \geq 0$ *and* $d_{11} > 0$.

2.6 Discussion

Result 2.1 provides a general criterion for determining the fate of a mutant allele introduced into a population at fixation when selection is weak enough and the mutant allele is rare enough. If the derivative with respect to the intensity of selection, denoted by s, of the leading eigenvalue $\rho(s)$ of the linearized transformation for the population state near fixation, represented by the matrix $\mathbf{M}(s)$, is positive at $s = 0$, then the mutant allele is preserved from extinction. On the contrary, if this derivative is negative, then the mutant allele goes extinct. In the degenerate case where this derivative would be 0, a quadratic analysis would be required (see, e.g., Lessard and Karlin, 1982). The expression given in Result 2.1 for this derivative evaluated at $s = 0$ can be traced back to Taylor (1985) in a context of sex allocation when a mutant strategy, say a sex ratio $m + s$, is confronted to a resident strategy, say a sex ratio m. In this context, a derivative equal to zero when $s = 0$ characterizes an evolutionary equilibrium strategy m. In general, when the matrix $\mathbf{M}(s)$ is non-negative and $\mathbf{M}^k(s)$ is positive for some integer k, this derivative is equal to 0 at s = 0 if and only if the derivative of the characteristic polynomial of $\mathbf{M}(s)$ at $s = 0$ is 0 (see, e.g., Taylor and Bulmer, 1980). Actually, the sign of the derivative of the leading eigenvalue is then the same as the sign of the derivative of the characteristic polynomial (Courteau and Lessard, 2000). In practice, this property facilitates the application of Result 2.1 to decide about the invasion or extinction of a rare mutant gene since the characteristic polynomial is generally easier to compute than the leading eigenvalue.

Result 2.2 on the change in frequency of a rare mutant allele from one generation to the next may seem obvious as outlined by Taylor (1989), but a careful analysis has to be performed. The main difficulty lies on the fact that the frequency of the mutant allele, p, is not generally the component of the population state in the direction of the leading left eigenvector for the matrix $\mathbf{M}(s)$ unless $s = 0$. We must also make sure that the terms of order different from ps in the change of the gene

frequency after enough generations have passed are smaller than ps (this excludes functions of order sp^2 or ps^2 for instance) and do not depend on the number of generations that have elapsed, as long as the mutant allele is rare enough and selection is weak enough. We have shown that this is the case under mild regularity conditions.

Results 2.1 and 2.2 have been deduced in a framework of an infinite population described by genotype frequencies or mating type frequencies, but this framework can be extended to a more general situation of a population structured into mating groups. Then, we would have to take into account the relative contributions of the groups and the relative contributions of the sexes in the expression of the gene frequencies.

Application of Results 2.1 and 2.2 to autosomal genes in partial selfing or partial sib-mating populations, confirms some previous results obtained in the case of weak selection (see, e.g., Pollak and Sabran, 1992, and Nagylaki, 1997, for the case of partial selfing, and Pollak, 1995, for the case of partial sib-mating). In random mating populations, a rare mutant allele at an autosomal locus invades a population at fixation if and only if the mutant heterozygote has a selective advantage over the resident homozygote ($d_{12} > 0$). With partial selfing or partial sib-mating, this condition may be neither sufficient, in the case where the mutant homozygote is less fit than the resident homozygote ($d_{11} < 0$), nor necessary, in the case where the mutant homozygote is fitter than the resident homozygote ($d_{11} > 0$), in both cases if the selfing or sib-mating rate is large enough. In that case, the threshold value is higher for the rate of sib-mating than for the rate of selfing, and this is so since sib-mating creates less inbreeding than selfing at the same rate. The effect of inbreeding on autosomal genes is to produce more homozygotes in the population and, as its level increases, it can overcome the fitness effect of overdominance or underdominance of the heterozygotes, but not the effect of directional selection, on the fate of a mutant allele. In the case of dominance of the resident allele ($d_{12} = 0$), a necessary and sufficient condition for invasion of a mutant allele is that the mutant homozygote is fitter than the resident homozygote ($d_{11} > 0$).

In sex-differentiated populations with partial sib-mating, all the above results apply with the fitness of a genotype being defined as an average of the fitnesses of that genotype in females and males. In the case of autosomal genes, this average gives the same weight to each of the sexes. In the case of sex-linked genes, the weighting of the fitnesses in females and males differs in the calculation of d_{12} and d_{11}. In the former, the fitnesses in females weigh twice the fitnesses in males, while in the latter, they weigh the same. The reason is that, in outbred individuals, each of the two genes in females counts as much as the gene in males, but in inbred individuals, both count as one since they are the same by descent.

The approximation for the change in frequency of a mutant allele when rare in a population undergoing weak selection does not always agree with Wright's (1942) formula. Although this formula proves to be quantitatively valid in the case of partial selfing, it turns out that it is only qualitatively valid in the case of autosomal genes in partial sib-mating populations. This confirms a finding of Pollak (1995). Actually, it is likely that Wright's formula is quantitatively valid only for a few particular cases like partial selfing. It is also likely that it is qualitatively valid only in symmetric cases as illustrated by our result on sex-linked genes in partial sib-mating populations. In this case, the formula is neither quantitatively nor qualitatively valid. This happens because, in sex-differentiated populations, the correct approximation under the assumption of weak selection involves not only the inbreeding coefficient and the reproductive values of the sexes, but also coefficients of regression of the frequency of the mutant allele in one mate on the frequency in the other, all calculated as if there were no selection.

In the case of autosomal genes, the coefficients of regression reduce to coefficients of correlation, which are symmetric, while the reproductive values of the sexes are equal to 1/2 since both sexes contribute equally to the future generations. Considering this case without sex differences in a partial sib-mating population and making the reasonable assumption, among others, that the inbreeding coefficient F

can be calculated ignoring selection if selection is weak enough as in a partial selfing population, Pollak (1995) gets a correct approximation for the change in frequency of a rare allele, denoted by A, and explains the presence of the coefficient of correlation between two mates relative to their frequencies of A, denoted by *m*, as follows: "*... because full sibs are more likely to have the same alleles than a random pair of individuals, a positive correlation between mates is induced in their frequencies of A. This results in a second increase within a generation in the frequency of A, which is m times as large as that from viability selection.*"

In the case of sex-linked genes, the reproductive values of the females and males are 2/3 and 1/3, respectively, since the contribution of females to future generations is twice that of the males. Moreover, an individual who carries a rare mutant allele and who survives to reproduce will contribute to the reproduction of its mate and this will cause a second change in the frequency of the mutant allele, weighted by the reproductive value of the sex of the mate times the coefficient of regression of the frequency of the mutant allele in the mate on the corresponding frequency in the individual. Assuming weak selection, this coefficient is approximated by the expected fraction of genes in the mate that are identical by descent to one or more genes in the individual. Such a coefficient, called a coefficient of relatedness, has been encountered in kin selection models (see, e.g., Hamilton, 1970, Lessard, 1992). What is interesting here is that a classical viability selection model without interactions between kin affecting viability can be put into the framework of kin selection theory, which is still controversial, when there is inbreeding. The reason is that there are interactions between kin that affect their reproductive success and these take place at mating.

Chapter 3: New insights into kin selection theory in family-structured populations with inbreeding

Abstract

The change of gene frequencies in large populations when there is partial inbreeding depends not only upon viability differences, the inbreeding coefficient and the reproductive values of the sexes in sex-differentiated models, but also upon coefficients of relatedness between mates. This can be interpreted as a kin selection effect caused by inbreeding even if there is no interaction between kin affecting individual fitness. In this paper, we consider family-specific fitnesses that depend on mixed strategies of two basic phenotypes or behaviours. Pairwise interactions are assumed, which is classical in ESS theory, but they are restricted here between offspring within the same sibship. To study the change in frequency of a rare mutant allele, we consider two different forms of weak selection, one applied through small differences in genotypic values determining individual mixed strategies, the other through small differences in viabilities according to the strategies chosen by interacting individuals. Under these two specific forms of weak selection, we deduce conditions for initial increase in frequency of a rare mutant allele for autosomal genes in the partial selfing model as well as autosomal and sex-linked genes in the partial sib-mating model. Assuming small differences in genotypic values, we show that conditions for protection of a mutant allele are tantamount to conditions for initial increase in frequency obtained in additive kin selection models. With particular reference to altruism versus selfishness, we provide explicit ranges of values for the selfing or sib-mating rate based on cost-benefit ratios that allow the spreading of a rare mutant allele into the population. Under the hypothesis of small differences in viabilities however, such ranges of values cannot be obtained unless stringent restrictions are imposed on viability parameters. Our analysis confirms that inbreeding does not necessarily promote altruism.

3.1 Introduction

In a previous paper (Lessard and Rocheleau, 2002), we studied the change in frequency of a rare mutant allele in partially inbred populations evolving under weak selection. In that paper, we proposed an approximate adaptive topography to predict the change in frequency of the mutant allele, which is quantitatively different from the one proposed by Wright (1942) in the case of partial sib-mating, and even qualitatively different in the case of a sex-linked model. Pollak (1995) had already noticed such a discrepancy with Wright's formula in the partial sib-mating model at an autosomal locus and provided an explanation based on the positive correlation between the frequencies of the mutant gene in two mates under this type of mating. We arrived at a similar conclusion in the partial sib-mating model at a sex-linked locus (or equivalently, haplo-diploid model). Because of the asymmetry induced by a sex-linked model however, a regression coefficient of the frequency of the mutant allele in one mate on the corresponding frequency in the other mate must be used instead of a correlation coefficient. Two regression coefficients have to be calculated depending on the sexes of the mates. At this point, we must recall that a weak selection hypothesis is essential for these regression coefficients to be calculated under selective neutrality of the genes at the considered locus. In that paper, we also sketched an explanation based on kin selection theory even if there was no interaction between kin which can possibly affect individual fitness.

Actually, our previous investigations led us to ascertain basic results which we shall use extensively in this paper. Originally, we wanted to deduce a general formula that approximates the change in frequency of a mutant allele under weak selection, when introduced in small frequency into a structured population which was previously at a fixation state. The weak selection hypothesis is rendered through a parameter s, called the intensity of selection. It is assumed that s is positive and small ($s = 0$ corresponding to selective neutrality). Also, we suppose that any population state can be described by a vector whose components represent the frequencies of

group types (in this paper, genotypes or mating types) carrying the mutant allele. Moreover, the linear approximation for the transformation of this vector near the origin from one generation to the next is given by a non-negative matrix $\mathbf{M}(s)$. This matrix $\mathbf{M}(s)$ is assumed to be smooth enough with respect to s and to have at least some power that exhibits only positive elements. Under these hypotheses, the leading eigenvalue of $\mathbf{M}(s)$, denoted by $\rho(s)$, will determine the fate of the mutant allele as long as this allele remains rare enough in the population. We reproduce below two basic results (see, e.g., Taylor, 1985, 1989, for similar statements, and Lessard and Rocheleau, 2002, for formal proofs).

Result 3.1 *For s small enough, the leading eigenvalue of* $\mathbf{M}(s)$ *is approximated by*

$$\rho(s) = 1 + \dot{\rho}(0)s + \textit{smaller terms},$$

where

$$\dot{\rho}(0) = \frac{\xi(0)^{\mathrm{T}} \dot{\mathbf{M}}(0) \eta(0)}{\xi(0)^{\mathrm{T}} \eta(0)},$$

with $\dot{\mathbf{M}}(0)$ *being the derivative of* $\mathbf{M}(s)$ *with respect to s evaluated at* $s = 0$, $\xi(0)$ *and* $\eta(0)$ *being respectively left and right (positive) eigenvectors of* $\mathbf{M}(0)$ *associated to the eigenvalue* 1 *and* T *denoting matrix transposition.*

The second result is more important since it provides a useful approximation for the change in frequency of a rare mutant allele from one generation to the next.

Result 3.2 *Let* $p^{(k)}$ *be the frequency of a rare mutant allele at generation k in a population initially at fixation. Under weak selection (s small enough) and for k sufficiently large, but not too large in the case* $\dot{\rho}(0) > 0$, *the change in frequency of the mutant allele from generation k to generation* $k + 1$ *is approximated by*

$$\Delta p^{(k)} = \dot{\rho}(0)\, p^{(k)}\, s + \textit{smaller terms}.$$

Therefore, the sign of the derivative of $\rho(s)$ evaluated at $s = 0$, denoted by $\dot{\rho}(0)$, will predict the fate of a rare mutant allele when introduced in small frequency into a population: $\dot{\rho}(0) < 0$ will entail extinction, while $\dot{\rho}(0) > 0$ will imply protection of the allele.

In this paper, we extend results obtained under three specific models of partial inbreeding, namely the partial selfing model, the partial sib-mating model at an autosomal locus and the partial sib-mating model at a sex-linked locus. To this end, we consider family-specific fitnesses based on mixed strategies. More precisely, an individual's fitness will depend upon the choice between two possible pure strategies (phenotypes or behaviours), which choice is a probability distribution determined by the individual's genotype, and by the corresponding choice of one of its sibs chosen at random and interacting with it. Pairwise interactions are classical in ESS theory (Maynard Smith and Price, 1973), but they are restricted here between offspring within the same sibship. The resulting fitnesses can be interpreted as a special case of family-specific fitnesses in the sense of Michod (1980), who considered the partial selfing model and the partial sib-mating model at an autosomal locus with two alleles, allowing the genotypic fitnesses to vary from one family type to another. However, due to the difficulty of getting exact analytical results for these models, the analysis was restricted, through numerical simulations, to the local dynamics near fixation of either allele in the particular context of additive or multiplicative allelic effects. Wade and Breden (1981) also studied the partial sib-mating model with additive genotypic fitnesses but from a group selection perspective.

Both Michod (1980) and Wade and Breden (1981) argued that inbreeding generally facilitates the evolution of an altruistic allele in kin selection models, although the first author gave an example of "extreme altruism" in the multiplicative model for which the initial increase in frequency of a rare altruistic allele is retarded. They inferred that inbreeding promotes altruism by enhancing the between-family genetic variance at the expense of the within-family genetic variance. However,

Uyenoyama (1984) showed that, even in additive models of kin selection, increased inbreeding may increase the within-family variance, resulting in more stringent conditions for the evolution of a rare altruistic allele. For many mixed mating models of kin selection with inbreeding being produced by selfing, parthenogenesis or sib-mating, Uyenoyama (1984) considered the case of additive genotypic fitnesses, but also assumed additional restrictions in the haplo-diploid partial sib-mating model in order to avoid multiplicative effects and to clearly isolate additive effects. Initial increase conditions for an altruistic allele were reported for all models but it was assumed that the heterozygote's propensity of performing altruism did not exhibit overdominance or underdominance.

In all papers mentioned above, no restrictions were imposed on the intensity levels of selection. To determine initial increase in frequency of a rare mutant allele in the population, their authors investigated, numerically or analytically, the dominant eigenvalue of the matrix of linear approximation near fixation of the common allele for various levels of selection. In this paper however, to apply Results 3.1 and 3.2 presented above, we must assume some kind of weak selection. Consequently, we have considered two different forms of weak selection: one applied through small differences in genotypic values determining individual mixed strategies and one through small differences in viabilities according to the strategies chosen by interacting individuals. Section 3.2 describes the effects of these hypotheses on genotypic fitnesses. Despite the fact that weak selection is crucial in our analysis, family-specific fitnesses based on strategies can provide for many different effects on genotypic fitnesses, not only additive or multiplicative. Therefore, apart from weak selection, we do not presuppose any hypothesis about the genotypic fitnesses and the propensity to adopt either pure strategies.

In Section 3.3, we introduce the notation used in the three models of partial inbreeding mentioned earlier and give the basic recurrence equations from one generation to the next. Section 3.4 is devoted to applications of Results 3.1 and 3.2 in

these partial inbreeding models under the two specific forms of weak selection. We then derive explicit expressions for $\dot{p}(0)$ upon which conditions for protection of a rare mutant allele are based. To contrast with the more classical approach of viability selection models, Section 3.5 sets out an alternative interpretation from a kin selection perspective. If one strategy makes for altruism behaviour towards kin, then simple conditions for protection of a rare mutant allele can be inferred from changes in strategies and cost-benefit ratios. Section 3.6 summarizes our results and compares them to results previously derived in kin selection theory.

3.2 Family-specific fitnesses based on strategies

We consider a special type of family-specific fitnesses (see, e.g., Michod, 1980, and references therein). Suppose that an individual can choose between two possible phenotypes or behaviours, called pure strategies. In the kin selection context for instance, it might be an altruistic versus a non-altruistic behaviour. In a diploid population with alleles A_1 and A_2 segregating at an autosomal locus, an individual of genotype A_iA_j either chooses strategy 1 with probability h_{ij} ($= h_{ji}$) or strategy 2 with complementary probability $1 - h_{ij}$. Then, the genotypic value h_{ij} corresponds to a mixed strategy. Furthermore, random pairwise interactions between individuals are assumed but only between offspring within the same sibship. As a mere consequence, this implies that an offspring's fitness will depend not only upon its own genotype but also upon the genotype of one of its sib chosen at random, which in turn depends upon the genotypes of the parents. More explicitly, the fitness of an A_iA_j offspring whose parents' genotypes are A_iA_k and A_jA_l is denoted by $f_{ij:(ik\times jl)}$ and takes the form

$$f_{ij:(ik\times jl)} = h_{ij}\left[g_{ik\times jl}m_{11} + \left(1 - g_{ik\times jl}\right)m_{12}\right] + \left(1 - h_{ij}\right)\left[g_{ik\times jl}m_{21} + \left(1 - g_{ik\times jl}\right)m_{22}\right], \tag{3.1}$$

where $g_{ik\times jl}$ designates the probability that a sib chosen at random adopts strategy 1 and $(1 - g_{ik\times jl})$ the probability that it chooses strategy 2, while $m_{uv} \geq 0$ (u, $v = 1, 2$) denotes the viability of an offspring adopting strategy u when in interaction with a sib adopting strategy v. In general, $m_{12} \neq m_{21}$ unless stated otherwise. Notice that we have the following equalities:

$$f_{11:(11\times12)} = f_{11:(12\times11)}, \quad f_{12:(11\times12)} = f_{12:(12\times11)}, \quad f_{12:(11\times22)} = f_{12:(22\times11)},$$
$$f_{12:(12\times22)} = f_{12:(22\times12)}, \quad f_{22:(12\times22)} = f_{22:(22\times12)},$$

and

$$g_{11\times11} = h_{11}, \quad g_{11\times12} = \tfrac{1}{2}h_{11} + \tfrac{1}{2}h_{12}, \quad g_{11\times22} = h_{12}, \quad g_{12\times12} = \tfrac{1}{4}h_{11} + \tfrac{1}{2}h_{12} + \tfrac{1}{4}h_{22},$$
$$g_{12\times22} = \tfrac{1}{2}h_{12} + \tfrac{1}{2}h_{22}, \quad g_{22\times22} = h_{22}.$$

Similar fitnesses can be defined in the context of a sex-linked locus (or equivalently, for a haplo-diploid population). Suppose that females are diploid and males haploid at the concerned locus. Then, the possible genotypes for females are given by A_1A_1, A_1A_2, A_2A_2 whereas for males, they are A_1 and A_2. A female of genotype A_iA_j either chooses strategy 1 with probability h_{ij} or strategy 2 with complementary probability $1 - h_{ij}$, while a male of genotype A_i either chooses strategy 1 with probability h_i or strategy 2 with complementary probability $1 - h_i$. By analogy with equation (3.1), the female and male fitnesses are expressed as

$$f_{ij:(ik\times j)} = h_{ij}\left[g_{ik\times j}m_{11} + (1 - g_{ik\times j})m_{12}\right] + (1 - h_{ij})\left[g_{ik\times j}m_{21} + (1 - g_{ik\times j})m_{22}\right] \tag{3.2a}$$

and

$$f_{i:(ik\times j)} = h_{i}\left[g_{ik\times j}m_{11} + (1 - g_{ik\times j})m_{12}\right] + (1 - h_{i})\left[g_{ik\times j}m_{21} + (1 - g_{ik\times j})m_{22}\right], \tag{3.2b}$$

respectively, where

$$g_{11\times 1} = \tfrac{1}{2}h_{11} + \tfrac{1}{2}h_1,\quad g_{12\times 1} = \tfrac{1}{4}h_{11} + \tfrac{1}{4}h_{12} + \tfrac{1}{4}h_1 + \tfrac{1}{4}h_2,\quad g_{22\times 1} = \tfrac{1}{2}h_{12} + \tfrac{1}{2}h_2,$$
$$g_{11\times 2} = \tfrac{1}{2}h_{12} + \tfrac{1}{2}h_1,\quad g_{12\times 2} = \tfrac{1}{4}h_{12} + \tfrac{1}{4}h_{22} + \tfrac{1}{4}h_1 + \tfrac{1}{4}h_2,\quad g_{22\times 2} = \tfrac{1}{2}h_{22} + \tfrac{1}{2}h_2.$$

For the sake of convenience, we let the allele designated by i in (3.2a) and (3.2b) be the one transmitted by the mother. A more precise but cumbersome notation might have been used to identify clearly the origin of the alleles, since the female fitness $f_{ij:(ik\times j)}$ is not generally equal to $f_{ij:(jk\times i)}$ (the same fact prevails for the male fitnesses).

To approximate the change in frequency of a mutant allele when rare in a population, we will assume weak selection in order to apply the aforementioned Results 3.1 and 3.2. The first form of weak selection considered in this paper is applied through the genotypic values, that is, *small differences in mixed strategies*. We then assume

$$h_{ij} = h + \delta_{ij} s \quad (h_i = h + \delta_i s \text{, for males at a sex-linked locus}), \tag{3.3}$$

where s measures the intensity of selection and $0 < h < 1$ is interpreted as a reference value. We recall that s shall be assumed small and positive. Moreover, we have $\delta_{ij} = \delta_{ji}$ for all i, j.

The second form of weak selection is applied through *small differences in viabilities*; we then assume

$$m_{uv} = 1 + a_{uv} s, \tag{3.4}$$

where s still measures the intensity of selection. It is also assumed that s is small and positive. In general, $a_{uv} \neq a_{vu}$ when $u \neq v$, unless stated otherwise.

3.3 Recurrence equations under regular systems of mating

3.3.1 Partial selfing model

Consider a single autosomal locus with two alleles A_1 and A_2 in an infinite diploid population undergoing discrete non-overlapping generations. Assume that every individual of the population can reproduce, either by selfing with probability α ($0 < \alpha < 1$), or by random outcrossing with the complementary probability $1 - \alpha$. Let P_{11}, P_{12} and P_{22} designate the frequencies of the genotypes A_1A_1, A_1A_2 and A_2A_2, respectively, in the population at the current generation. The frequencies of the alleles A_1 and A_2 are denoted by

$$p_1 = P_{11} + \tfrac{1}{2}P_{12} \quad \text{and} \quad p_2 = P_{22} + \tfrac{1}{2}P_{12},$$

respectively. Applying fitnesses as defined in equation (3.1) and after mating and reproduction, the genotypic frequencies in the population at the beginning of the next generation are given by

$$\begin{aligned}
P'_{11} &= \frac{\alpha}{T_S}\left[f_{11:(11\times11)}P_{11} + \tfrac{1}{4}f_{11:(12\times12)}P_{12}\right] \\
&\quad + \frac{(1-\alpha)}{T_R}\left[f_{11:(11\times11)}P_{11}^2 + f_{11:(11\times12)}P_{11}P_{12} + \tfrac{1}{4}f_{11:(12\times12)}P_{12}^2\right], \\
P'_{12} &= \frac{\alpha}{T_S}\left[\tfrac{1}{2}f_{12:(12\times12)}P_{12}\right] + \frac{(1-\alpha)}{T_R}\begin{bmatrix} f_{12:(11\times12)}P_{11}P_{12} + \tfrac{1}{2}f_{12:(12\times12)}P_{12}^2 \\ + 2f_{12:(11\times22)}P_{11}P_{22} + f_{12:(12\times22)}P_{12}P_{22} \end{bmatrix}, \qquad (3.5) \\
P'_{22} &= \frac{\alpha}{T_S}\left[f_{22:(22\times22)}P_{22} + \tfrac{1}{4}f_{22:(12\times12)}P_{12}\right] \\
&\quad + \frac{(1-\alpha)}{T_R}\left[f_{22:(22\times22)}P_{22}^2 + f_{22:(12\times22)}P_{12}P_{22} + \tfrac{1}{4}f_{22:(12\times12)}P_{12}^2\right],
\end{aligned}$$

where T_S and T_R are normalizing terms to ensure that all the multiplying factors of α and $1 - \alpha$, respectively, sum up to 1.

3.3.2 Partial sib-mating model: case of an autosomal locus

Again, consider a single autosomal locus with alleles A_1 and A_2 in an infinite diploid population undergoing discrete non-overlapping generations. Every individual has the choice to mate and reproduce with a sib with probability β or mate at random with the complementary probability $1 - \beta$ $(0 < \beta < 1)$. The genotypic frequencies P_{11}, P_{12}, P_{22} and allelic frequencies p_1, p_2 are similarly defined as in the partial selfing model. Nonetheless, the genotypic frequencies are no longer sufficient to describe the complete dynamics of the model from one generation to the next.

Let x_1, x_2, x_3, x_4, x_5, x_6 be the respective frequencies of the mating types $(A_1A_1 \times A_1A_1)$, $(A_1A_1 \times A_1A_2)$, $(A_1A_1 \times A_2A_2)$, $(A_1A_2 \times A_1A_2)$, $(A_1A_2 \times A_2A_2)$, $(A_2A_2 \times A_2A_2)$ among the adults of the current generation. Thus, the genotypic frequencies among the adults of the current generation can alternatively be written as

$$P_{11} = x_1 + \tfrac{1}{2}x_2 + \tfrac{1}{2}x_3, \qquad P_{12} = \tfrac{1}{2}x_2 + x_4 + \tfrac{1}{2}x_5, \qquad P_{22} = \tfrac{1}{2}x_3 + \tfrac{1}{2}x_5 + x_6.$$

Using fitnesses given by equation (3.1) and after mating and reproduction, the genotypic frequencies among the adults of the next generation become

$$P_{11}^* = \frac{f_{11:(11\times11)}x_1 + \frac{1}{2}f_{11:(11\times12)}x_2 + \frac{1}{4}f_{11:(12\times12)}x_4}{T_R},$$

$$P_{12}^* = \frac{\frac{1}{2}f_{12:(11\times12)}x_2 + f_{12:(11\times22)}x_3 + \frac{1}{2}f_{12:(12\times12)}x_4 + \frac{1}{2}f_{12:(12\times22)}x_5}{T_R},$$

$$P_{22}^* = \frac{\frac{1}{4}f_{22:(12\times12)}x_4 + \frac{1}{2}f_{22:(12\times22)}x_5 + f_{22:(22\times22)}x_6}{T_R},$$

where T_R is a normalizing term such that the genotypic frequencies sum up to 1. The frequencies of the mating types from one generation of adults to the next are then described by the following recurrence equations:

$$
\begin{aligned}
x_1' &= (1-\beta)P_{11}^{*2} + \frac{\beta}{T_{SM}}\left[f^2_{11:(11\times11)}x_1 + \tfrac{1}{4}f^2_{11:(11\times12)}x_2 + \tfrac{1}{16}f^2_{11:(12\times12)}x_4\right],\\
x_2' &= 2(1-\beta)P_{11}^{*}P_{12}^{*} + \frac{\beta}{T_{SM}}\left[\tfrac{1}{2}f_{11:(11\times12)}f_{12:(11\times12)}x_2 + \tfrac{1}{4}f_{11:(12\times12)}f_{12:(12\times12)}x_4\right],\\
x_3' &= 2(1-\beta)P_{11}^{*}P_{22}^{*} + \frac{\beta}{T_{SM}}\left[\tfrac{1}{8}f_{11:(12\times12)}f_{22:(12\times12)}x_4\right],\\
x_4' &= (1-\beta)P_{12}^{*2} + \frac{\beta}{T_{SM}}\left[\tfrac{1}{4}f^2_{12:(11\times12)}x_2 + f^2_{12:(11\times22)}x_3 + \tfrac{1}{4}f^2_{12:(12\times12)}x_4 + \tfrac{1}{4}f^2_{12:(12\times22)}x_5\right],\\
x_5' &= 2(1-\beta)P_{12}^{*}P_{22}^{*} + \frac{\beta}{T_{SM}}\left[\tfrac{1}{4}f_{12:(12\times12)}f_{22:(12\times12)}x_4 + \tfrac{1}{2}f_{12:(12\times22)}f_{22:(12\times22)}x_5\right],\\
x_6' &= (1-\beta)P_{22}^{*2} + \frac{\beta}{T_{SM}}\left[\tfrac{1}{16}f^2_{22:(12\times12)}x_4 + \tfrac{1}{4}f^2_{22:(12\times22)}x_5 + f^2_{22:(22\times22)}x_6\right],
\end{aligned}
\tag{3.6}
$$

where T_{SM} ensures that all the multiplying factors of β sum up to 1.

3.3.3 Partial sib-mating model: case of a sex-linked locus

Now, consider a sex-linked locus (or equivalently, a haplo-diploid population) for which females are diploid while males are haploid. The frequencies of genotypes A_1A_1, A_1A_2 and A_2A_2 among females are written Q_{11}, Q_{12}, Q_{22}, respectively, and the frequencies of genotypes A_1 and A_2 among males are written, respectively, as P_1 and P_2. Let x_1, x_2, x_3, x_4, x_5, x_6 be the respective frequencies of the mating types $(A_1A_1\times A_1)$, $(A_1A_2\times A_1)$, $(A_2A_2\times A_1)$, $(A_1A_1\times A_2)$, $(A_1A_2\times A_2)$, $(A_2A_2\times A_2)$ among the adults of the current generation. The respective frequencies of alleles A_1 and A_2 are

denoted by q_1 and q_2 among females and by p_1 and p_2 among males and can be expressed in terms of frequencies of mating types as

$$q_1 = Q_{11} + \tfrac{1}{2}Q_{12} = x_1 + x_4 + \tfrac{1}{2}(x_2 + x_5) \quad \text{and} \quad p_1 = P_1 = x_1 + x_2 + x_3 .$$

Using fitnesses in (3.2a) and (3.2b), the genotypic frequencies among females and among males of the next generation are respectively given by

$$Q_{11}^* = \frac{f_{11:(11\times1)}x_1 + \frac{1}{2}f_{11:(12\times1)}x_2}{T_F},$$

$$Q_{12}^* = \frac{\frac{1}{2}f_{12:(12\times1)}x_2 + f_{12:(22\times1)}x_3 + f_{12:(11\times2)}x_4 + \frac{1}{2}f_{12:(12\times2)}x_5}{T_F},$$

$$Q_{22}^* = \frac{\frac{1}{2}f_{22:(12\times2)}x_5 + f_{22:(22\times2)}x_6}{T_F},$$

and

$$P_1^* = \frac{f_{1:(11\times1)}x_1 + \frac{1}{2}f_{1:(12\times1)}x_2 + f_{1:(11\times2)}x_4 + \frac{1}{2}f_{1:(12\times2)}x_5}{T_M},$$

$$P_2^* = \frac{\frac{1}{2}f_{2:(12\times1)}x_2 + f_{2:(22\times1)}x_3 + \frac{1}{2}f_{2:(12\times2)}x_5 + f_{2:(22\times2)}x_6}{T_M},$$

where T_F and T_M are normalizing terms. The frequencies of the mating types from one generation of adults to the next are described by the following recursive equations:

$$x_1' = (1-\beta)Q_{11}^*P_1^* + \frac{\beta}{T_{SM}}\left[f_{11:(11\times1)}f_{1:(11\times1)}x_1 + \tfrac{1}{4}f_{11:(12\times1)}f_{1:(12\times1)}x_2\right],$$

$$x_2' = (1-\beta)Q_{12}^*P_1^* + \frac{\beta}{T_{SM}}\left[\tfrac{1}{4}f_{12:(12\times1)}f_{1:(12\times1)}x_2 + f_{12:(11\times2)}f_{1:(11\times2)}x_4 + \tfrac{1}{4}f_{12:(12\times2)}f_{1:(12\times2)}x_5\right],$$

$$x_3' = (1-\beta)Q_{22}^* P_1^* + \frac{\beta}{T_{SM}}\left[\tfrac{1}{4} f_{22:(12\times 2)} f_{1:(12\times 2)} x_5\right],$$

$$x_4' = (1-\beta)Q_{11}^* P_2^* + \frac{\beta}{T_{SM}}\left[\tfrac{1}{4} f_{11:(12\times 1)} f_{2:(12\times 1)} x_2\right], \tag{3.7}$$

$$x_5' = (1-\beta)Q_{12}^* P_2^* + \frac{\beta}{T_{SM}}\left[\tfrac{1}{4} f_{12:(12\times 1)} f_{2:(12\times 1)} x_2 + f_{12:(22\times 1)} f_{2:(22\times 1)} x_3 + \tfrac{1}{4} f_{12:(12\times 2)} f_{2:(12\times 2)} x_5\right],$$

$$x_6' = (1-\beta)Q_{22}^* P_2^* + \frac{\beta}{T_{SM}}\left[\tfrac{1}{4} f_{22:(12\times 2)} f_{2:(12\times 2)} x_5 + f_{22:(22\times 2)} f_{2:(22\times 2)} x_6\right],$$

where T_{SM} is such that all the multiplying factors of β sum up to 1.

3.4 Conditions for protection of a rare mutant allele under weak selection

3.4.1 Case of small differences in mixed strategies

Suppose that allele A_1 is rare and that weak selection is applied through the genotypic values. Using the fitnesses (3.1) with h_{ij} in the form (3.3) in the recurrence equation (3.5) for P_{11}, P_{12} near fixation of A_2 ($P_{11}, P_{12} \cong 0$) in the partial selfing model, one obtains the following matrix of linear approximation up to terms of order s:

$$\mathbf{M}(s) = \begin{bmatrix} \alpha\left\{1+\frac{d_{11}s}{K}\left(A(h)+B(h)\right)\right\} & \frac{\alpha}{4}\left\{1+\frac{s}{K}\left(d_{11}A(h)+(\tfrac{1}{4}d_{11}+\tfrac{1}{2}d_{12})B(h)\right)\right\} \\ 2(1-\alpha)\left\{1+\frac{d_{12}s}{K}\left(A(h)+B(h)\right)\right\} & \frac{\alpha}{2}\left\{1+\frac{s}{K}\left(d_{12}A(h)+(\tfrac{1}{4}d_{11}+\tfrac{1}{2}d_{12})B(h)\right)\right\} \\ & +(1-\alpha)\left\{1+\frac{d_{12}s}{K}\left(A(h)+\tfrac{1}{2}B(h)\right)\right\} \end{bmatrix},$$

where

$$\begin{aligned} K &= h^2 m_{11} + h(1-h)(m_{12}+m_{21}) + (1-h)^2 m_{22}, \\ A(h) &= h(m_{11}-m_{21}) + (1-h)(m_{12}-m_{22}), \\ B(h) &= h(m_{11}-m_{12}) + (1-h)(m_{21}-m_{22}), \end{aligned}$$

and $d_{1j} = \delta_{1j} - \delta_{22}$, for $j = 1, 2$. One can easily determine $\mathbf{M}(0)$ and calculate its eigenvalues, which are

$$\lambda_1 = 1, \quad \lambda_2 = \frac{\alpha}{2}.$$

We have $\rho(0) = 1$ and respective left and right positive eigenvectors associated to this eigenvalue 1 are given by

$$\xi(0)^{\mathrm{T}} = (1, \tfrac{1}{2}) \quad \text{and} \quad \eta(0)^{\mathrm{T}} = \left(\alpha, 4(1-\alpha)\right).$$

Now, applying Result 3.1 yields

$$\dot{\rho}(0) = \frac{1}{K}\left[A(h) + \left(\frac{1+\alpha}{2}\right)B(h) \right] \left[Fd_{11} + (1-F)d_{12} \right], \tag{3.8a}$$

where

$$F = \frac{\alpha}{2-\alpha}. \tag{3.8b}$$

Here, F is the inbreeding coefficient at equilibrium in the partial selfing model when there is no selection, that is, when $s = 0$ (Wright, 1921). Nagylaki (1997) confirmed that the above value of F can be used as an approximation in the case of weak selection.

In the partial sib-mating model at an autosomal locus, we need to develop the recurrence equations (3.6) near fixation of allele A_2 ($x_1, x_2, ..., x_5 \cong 0$). The matrix of linear approximation $\mathbf{M}(s)$ can easily be obtained (see Appendix). The eigenvalues of $\mathbf{M}(0)$, ranked in decreasing order, are all positive and given by

$$\lambda_1 = 1, \quad \lambda_2 = \frac{2\beta + \sqrt{4\beta^2 + 16\beta}}{8}, \quad \lambda_3 = \frac{\beta}{2}, \quad \lambda_4 = \frac{\beta}{4}, \quad \lambda_5 = \frac{2\beta - \sqrt{4\beta^2 + 16\beta}}{8}.$$

Respective left and right eigenvectors associated to the eigenvalue 1 are

$$\xi(0)^{\mathrm{T}} = (1, \tfrac{3}{4}, \tfrac{1}{2}, \tfrac{1}{2}, \tfrac{1}{4})$$

and

$$\eta(0)^{\mathrm{T}} = \left(\frac{\beta(2+\beta)}{16(2-\beta)(1-\beta)}, \frac{\beta}{2(2-\beta)}, \frac{1}{2}, 1, \frac{5\beta^2 - 20\beta + 16}{2\beta(2-\beta)} \right).$$

Result 3.1 allows us to calculate

$$\dot{\rho}(0) = \frac{1}{K}\left[A(h) + \left(\frac{1+\beta}{2}\right)B(h)\right](1+R)\left[Fd_{11} + (1-F)d_{12}\right], \tag{3.9a}$$

where

$$F = \frac{\beta}{4-3\beta} \quad \text{and} \quad R = \frac{\beta}{2-\beta}. \tag{3.9b}$$

The coefficient F is the inbreeding coefficient at equilibrium in the partial sib-mating model without selection (see, e.g., Karlin, 1968). The coefficient R is also known as the coefficient of relationship (Wright, 1922) and it represents the coefficient of correlation between two mated individuals relative to their frequencies of A_1 at the specified locus assuming no selection (see, e.g., Li, 1976).

In the partial sib-mating model for a sex-linked locus, equations in (3.7) are developed near fixation of A_2 and yield a matrix of linear approximation (see Appendix) in which the parameters $d_{1j} = \delta_{1j} - \delta_{22}$, for $j = 1, 2$ and $d_1 = \delta_1 - \delta_2$ come into play. The matrix $\mathbf{M}(0)$ is easily deduced and its eigenvalues, ranked in decreasing order, are

$$\lambda_1 = 1,\ \lambda_2 = \frac{2\beta + \sqrt{4\beta^2 + 16\beta}}{8},\ \lambda_3 = \frac{\beta}{2},\ \lambda_4 = \frac{2\beta - \sqrt{4\beta^2 + 16\beta}}{8},\ \lambda_5 = -\frac{1}{2}.$$

Positive left and right eigenvectors of $\mathbf{M}(0)$ associated to the eigenvalue 1 are given by

$$\xi(0)^{\mathsf{T}} = (1, \tfrac{2}{3}, \tfrac{1}{3}, \tfrac{2}{3}, \tfrac{1}{3}) \quad \text{and} \quad \eta(0)^{\mathsf{T}} = \left(\frac{\beta}{4(1-\beta)}, 1, \frac{4-3\beta}{2\beta}, \frac{1}{2}, \frac{4-3\beta}{\beta}\right).$$

Result 3.1 yields

$$\dot{\rho}(0) = \frac{1}{K}\left[A(h) + \left(\frac{1+\beta}{2}\right)B(h)\right] \times\left[\left(\frac{2}{3} + \frac{1}{3}R_{I\to M}\right)\left[Fd_{11} + (1-F)d_{12}\right] + \left(\frac{1}{3} + \frac{2}{3}R_{J\to M}\right)d_1\right], \tag{3.10a}$$

where

$$F = \frac{\beta}{4-3\beta}, \quad R_{I\to M} = \frac{\beta}{2-\beta} \quad \text{and} \quad R_{J\to M} = \frac{\beta}{4-3\beta}. \qquad (3.10b)$$

Again, F represents the inbreeding coefficient in diploid females at equilibrium in absence of selection. The coefficient $R_{I\to M}$ defines the coefficient of regression of the frequency of A_1 genes carried by the male of a mated couple on the frequency of A_1 genes carried by the female I of this couple, when there is no selection and the population is at equilibrium. The coefficient $R_{J\to M}$ is defined analogously for the female of a mated couple and the male J of this couple. In both regression coefficients, subscript M stands for mate. It must be noted that when females and males are both diploid at the given locus, then

$$R = R_{I\to M} = R_{J\to M} = \frac{\beta}{2-\beta}.$$

The asymmetry of the recurrence equations (3.7) is reflected into the expression of $\dot{\rho}(0)$. The fractions $\frac{2}{3}$ and $\frac{1}{3}$ correspond to reproductive values of females and males, respectively, and measure the genetic contributions of the two sexes at a sex-linked locus in absence of selection. Because the frequencies of genes in two mated individuals are correlated, the contribution of one sex (say, e.g., females) through the other sex must be weighted by a coefficient of regression (in this case, of males on their female mates).

3.4.2 Case of small differences in viabilities

This time, we shall use fitnesses (3.1) with m_{uv} in the form (3.4). In the partial selfing model, substituting these values into equations (3.5) and developing these further near the fixation of A_2 give the following matrix of linear approximation up to terms of order s:

$$\mathbf{M}(s)=\begin{bmatrix} \alpha\{1+sK^{*}_{11\times11}\} & \frac{\alpha}{4}\{1+s(\frac{1}{4}K^{*}_{11\times11}+\frac{1}{2}K^{*}_{11\times12}+\frac{1}{4}K^{*}_{11\times22})\} \\ 2(1-\alpha)\{1+sK^{*}_{12\times12}\} & \frac{\alpha}{2}\{1+s(\frac{1}{4}K^{*}_{12\times11}+\frac{1}{2}K^{*}_{12\times12}+\frac{1}{4}K^{*}_{12\times22})\} \\ & +(1-\alpha)\{1+s(\frac{1}{2}K^{*}_{12\times12}+\frac{1}{2}K^{*}_{12\times22})\} \end{bmatrix},$$

where

$$K^{*}_{ij\times kl}=K_{ij\times kl}-K_{22\times22}$$

and

$$K_{ij\times kl}=h_{ij}h_{kl}a_{11}+h_{ij}(1-h_{kl})a_{12}+(1-h_{ij})h_{kl}a_{21}+(1-h_{ij})(1-h_{kl})a_{22}\,.$$

Applying Result 3.1 yields

$$\begin{aligned}\dot{\rho}(0)=&\left[\alpha K^{*}_{11\times11}+(1-\alpha)K^{*}_{12\times12}\right]\hat{\eta}_1\\&+\begin{bmatrix}\frac{\alpha}{16}(K^{*}_{11\times11}+K^{*}_{11\times22}+K^{*}_{12\times11})+\frac{\alpha}{8}K^{*}_{11\times12}\\+\frac{(2-\alpha)}{8}K^{*}_{12\times12}+\frac{(4-3\alpha)}{16}K^{*}_{12\times22}\end{bmatrix}\hat{\eta}_2,\end{aligned}\tag{3.11a}$$

where

$$\hat{\eta}_1=\frac{\alpha}{2-\alpha}\quad\text{and}\quad\hat{\eta}_2=\frac{4(1-\alpha)}{2-\alpha}\tag{3.11b}$$

represent the *relative* frequencies of the mutant genotypes A_1A_1 and A_1A_2, respectively, in the long run near fixation of A_2, normalized such that the scalar product with the frequencies of the mutant allele in the different genotypes represented by $\xi(0)$ is equal to 1, that is, $\hat{\boldsymbol{\eta}}=\boldsymbol{\eta}(0)/(\xi(0)^{\mathrm{T}}\boldsymbol{\eta}(0))$.

We repeat the same procedure for the partial sib-mating model at an autosomal locus. The matrix of linear approximation can easily be obtained for this

model along with the matrix of linear approximation for the case of a sex-linked locus (see Appendix). Regarding the partial sib-mating model at an autosomal locus, equation (3.6) along with the matrix of linear approximation gives

$$\dot{\rho}(0)=(1+\beta)K^*_{1\times 11}\hat{\eta}_1+\left[\frac{1}{4}\left(1+\frac{3\beta}{4}\right)(K^*_{1\times 11}+K^*_{1\times 12})+\frac{1}{4}\left(\frac{1}{2}+\frac{3\beta}{4}\right)(K^*_{12\times 11}+K^*_{12\times 12})\right]\hat{\eta}_2$$

$$+\left(\frac{1}{2}+\frac{\beta}{2}\right)K^*_{12\times 12}\hat{\eta}_3+\begin{bmatrix}\frac{1}{16}\left(1+\frac{\beta}{2}\right)(K^*_{1\times 11}+2K^*_{1\times 12}+K^*_{1\times 22})\\ +\frac{1}{8}\left(\frac{1}{2}+\frac{\beta}{2}\right)(K^*_{12\times 11}+2K^*_{12\times 12}+K^*_{12\times 22})\\ +\frac{1}{16}\left(\frac{\beta}{2}\right)(K^*_{22\times 11}+2K^*_{22\times 12})\end{bmatrix}\hat{\eta}_4 \qquad (3.12a)$$

$$+\left[\frac{1}{4}\left(\frac{1}{2}+\frac{\beta}{4}\right)(K^*_{12\times 12}+K^*_{12\times 22})+\frac{1}{4}\left(\frac{\beta}{4}\right)K^*_{22\times 12}\right]\hat{\eta}_5,$$

where $K^*_{ij\times kl}$ is defined as previously and

$$\hat{\eta}_1=\frac{\beta^2(2+\beta)}{(2-\beta)(4-\beta)(4-3\beta)},\quad \hat{\eta}_2=\frac{8\beta^2(1-\beta)}{(2-\beta)(4-\beta)(4-3\beta)},$$

$$\hat{\eta}_3=\frac{8\beta(1-\beta)}{(4-\beta)(4-3\beta)},\quad \hat{\eta}_4=\frac{16\beta(1-\beta)}{(4-\beta)(4-3\beta)},\quad \hat{\eta}_5=\frac{8(1-\beta)(16-20\beta+5\beta^2)}{(2-\beta)(4-\beta)(4-3\beta)}, \qquad (3.12b)$$

are the *relative* frequencies of the mating couples carrying the mutant allele A_1 in the long run near fixation of A_2, normalized such that the scalar product with $\xi(0)$ equals 1. In the partial sib-mating model at a sex-linked locus, equation (3.7) produces

$$\dot{\rho}(0)=\left[\left(1+\frac{\beta}{2}\right)(K^*_{1\times11}+K^*_{1\times1})+\left(\frac{1}{2}+\beta\right)(K^*_{1\times11}+K^*_{1\times1})\right]\frac{\hat{\eta}_1}{3}$$

$$+\left[\begin{array}{l}\frac{1}{4}\left(1+\frac{\beta}{4}\right)(K^*_{1\times11}+K^*_{1\times1}+K^*_{1\times12}+K^*_{1\times2})\\+\frac{1}{4}\left(\frac{1}{2}+\frac{3\beta}{4}\right)(K^*_{1\times11}+K^*_{1\times12}+K^*_{1\times1}+K^*_{1\times2})\\+\frac{1}{4}\left(\frac{1}{2}+\frac{\beta}{4}\right)(K^*_{12\times11}+K^*_{12\times12}+K^*_{12\times1}+K^*_{12\times2})\\+\frac{1}{4}\left(\frac{3\beta}{4}\right)(K^*_{2\times11}+K^*_{2\times12}+K^*_{2\times1})\end{array}\right]\frac{\hat{\eta}_2}{3} \qquad (3.13a)$$

$$+\left[\frac{1}{2}(K^*_{12\times12}+K^*_{12\times2})+\frac{\beta}{2}K^*_{2\times12}\right]\left(\frac{\hat{\eta}_3}{3}\right)+\left[\left(\frac{1}{2}+\frac{\beta}{2}\right)(K^*_{12\times12}+K^*_{12\times1}+K^*_{1\times12}+K^*_{1\times1})\right]\frac{\hat{\eta}_4}{3}$$

$$+\left[\begin{array}{l}\frac{1}{4}\left(\frac{1}{2}+\frac{\beta}{4}\right)(K^*_{12\times12}+K^*_{12\times22}+K^*_{12\times1}+K^*_{12\times2}+K^*_{1\times12}+K^*_{1\times22}+K^*_{1\times1}+K^*_{1\times2})\\+\frac{1}{4}\left(\frac{\beta}{4}\right)(K^*_{22\times12}+K^*_{22\times1}+K^*_{2\times12}+K^*_{2\times1})\end{array}\right]\frac{\hat{\eta}_5}{3},$$

where $K^*_{ij\times k}$, $K^*_{i\times jk}$ and $K^*_{i\times j}$ are defined analogously to $K^*_{ij\times kl}$ and

$$\hat{\eta}_1=\frac{\beta^2}{(2-\beta)(4-3\beta)},\qquad \hat{\eta}_2=\frac{4\beta(1-\beta)}{(2-\beta)(4-3\beta)},\qquad \hat{\eta}_3=\frac{2(1-\beta)}{(2-\beta)},$$

$$\hat{\eta}_4=\frac{2\beta(1-\beta)}{(2-\beta)(4-3\beta)},\qquad \hat{\eta}_5=\frac{4(1-\beta)}{(2-\beta)}. \qquad (3.13b)$$

Compared to weak selection in genotypic values, the hypothesis of weak selection in viabilities does not yield a simple expression for $\dot{\rho}(0)$. In the next section however, we shall consider sufficient conditions which considerably simplify equations (3.11a), (3.12a) and (3.13a).

3.5 A kin selection perspective

In Section 3.4, we have provided formulas for $\dot{\rho}(0)$, under three specific models of partial inbreeding with weak selection, which allow to determine conditions for protection of a rare mutant allele. These formulas were presented under the conventional approach of viability selection models. Nevertheless, it is possible to put these results into a kin selection perspective, since pairwise interactions between sibs affect their reproductive success. In the following, we treat the two hypotheses of weak selection separately.

3.5.1 Case of small differences in mixed strategies

Equations (3.8a), (3.9a) and (3.10a) all include coefficients

$$\begin{aligned} K &= h^2 m_{11} + h(1-h)(m_{12}+m_{21}) + (1-h)^2 m_{22}, \\ A(h) &= h(m_{11}-m_{21}) + (1-h)(m_{12}-m_{22}), \\ B(h) &= h(m_{11}-m_{12}) + (1-h)(m_{21}-m_{22}). \end{aligned} \tag{3.14}$$

We can interpret K as the mean fitness of pairwise interactions between offspring in the population. On the other hand, $A(h)$ approximates the rate of increase in the fitness of an offspring with respect to an increase in the probability for this offspring to adopt strategy 1, while $B(h)$ approximates the rate of increase in the fitness of an offspring with respect to an increase in the probability for a sib interacting with this offspring to adopt strategy 1. Equation (3.8a) for the partial selfing model can alternatively be expressed as

$$\dot{\rho}(0) = \frac{1}{K}\left[R_{I\to I}A(h) + R_{I\to J}B(h)\right]\left[Fd_{11} + (1-F)d_{12}\right],$$

where

$$R_{I\to I} = 1, \quad R_{I\to J} = \frac{1+\alpha}{2}.$$

Here, $R_{I\to I}$ is the coefficient of relatedness of an offspring I with itself, whereas $R_{I\to J}$ is the coefficient of relatedness of an offspring I with a sib J, both calculated in absence of selection. The coefficient of relatedness measures the genetic relationship of an individual with another and plays a central role in kin selection theory.

The coefficient of relatedness of an individual I to an individual J has been generally defined in inbred populations as a covariance ratio, actually the covariance between the frequency of a given allele in J and the genotypic value in I over the covariance between these two quantities in I (Michod and Hamilton, 1980). In the case of inbreeding caused by partial selfing or partial sib-mating, it has been shown that the coefficient of relatedness in absence of selection reduces to a pedigree index, namely the coefficient of kinship of I with J over the coefficient of kinship of I with itself (Lessard, 1990, 1992), the coefficient of kinship of I with J being defined as the probability that a gene chosen at random in I be identical by descent to a gene chosen at random at the same locus in J (Malécot, 1948). This pedigree index corresponds to the coefficient of regression of the frequency of a given allele in J to the frequency of that allele in I (Hamilton, 1972).

Since K is always positive, the increase in frequency of a rare mutant allele ($\dot{\rho}(0)>0$) depends upon the product of two factors: a "structural" factor and a "viability-analogous" factor (this terminology comes from Uyenoyama *et al.*, 1981). The structural factor reflects the changes in fitness produced by the diverse interactions between sibs, while the viability-analogous factor refers to the adaptive topography proposed by Wright (1942) for partially inbred populations under weak selection in classical viability models. In the partial selfing model, the structural factor approximates the rate of increase $A(h)$ in the fitness of a randomly chosen offspring I and the rate of increase $B(h)$ of its sib J weighted by the coefficient of relatedness of I to J, since an offspring contributes to the reproductive success of a sib with which it interacts. The viability-analogous factor approximates the change in strategy induced by the substitution of gene A_1 for gene A_2, when A_1 is rare in the

population. The respective change in strategy for homozygotes and heterozygotes are given by d_{11} and d_{12}, weighted respectively by F and $1 - F$.

As for the partial sib-mating model, equation (3.9a) can be rewritten as

$$\dot{p}(0) = \frac{1}{K}[(R_{I\to I} + R_{I\to M})A(h) + (R_{I\to S} + R_{I\to SM})B(h)][Fd_{11} + (1-F)d_{12}],$$

where

$$R_{I\to I} = 1, \quad R_{I\to M} = \frac{\beta}{2-\beta}, \quad R_{I\to S} = \frac{1}{2-\beta}, \quad R_{I\to SM} = \frac{\beta}{2-\beta}.$$

All the coefficients above represent coefficients of relatedness of an offspring I to an individual interacting with the offspring; subscript M stands for its mate, S for one of its sib and SM for its sib's mate.

The difference between the structural factors of the two models, partial selfing versus partial sib-mating, stems from the fact that an offspring who reproduces under partial sib-mating must mate before reproducing; as a consequence, this will directly affect the rate of increase in fitness $A(h)$ of its mate, which mate can bear some genetical relationship with this offspring, possibly being one of its own sibs. In addition, an offspring will influence the rate of increase in fitness $B(h)$ of its sib with which it interacts, but also the rate of increase in fitness $B(h)$ of its sib's mate, which mate can be genetically related to him, possibly being another of its own sibs.

In the partial sib-mating model at a sex-linked locus, sexes are distinguished relatively to their ploidy and genotypic values. Let I designate a female offspring and J a male offspring. Equation (3.10a) can alternatively be expressed as

$$\dot{\rho}(0)=\frac{1}{K}\left\{\begin{array}{l}\left(\frac{2}{3}R_{I\to I}+\frac{1}{3}R_{I\to M}\right)A(h)\\ \\ +\left[\frac{1}{2}\left(\frac{2}{3}R_{I\to S}+\frac{1}{3}R_{I\to SM}\right)+\frac{1}{2}\left(\frac{1}{3}R_{I\to B}+\frac{2}{3}R_{I\to BM}\right)\right]B(h)\end{array}\right\}\left[Fd_{11}+(1-F)d_{12}\right]$$

$$+\frac{1}{K}\left\{\begin{array}{l}\left(\frac{1}{3}R_{J\to J}+\frac{2}{3}R_{J\to M}\right)A(h)\\ \\ +\left[\frac{1}{2}\left(\frac{2}{3}R_{J\to S}+\frac{1}{3}R_{J\to SM}\right)+\frac{1}{2}\left(\frac{1}{3}R_{J\to B}+\frac{2}{3}R_{J\to BM}\right)\right]B(h)\end{array}\right\}d_1,$$

where

$$R_{I\to I}=R_{J\to J}=1,\quad R_{I\to M}=\frac{\beta}{2-\beta},\quad R_{J\to M}=\frac{\beta}{4-3\beta},$$

$$R_{I\to S}=\frac{3-\beta}{2(2-\beta)},\quad R_{J\to S}=\frac{1}{4-3\beta},\quad R_{I\to SM}=\frac{\beta}{2-\beta},\quad R_{J\to SM}=\frac{\beta(2-\beta)}{4-3\beta},$$

$$R_{I\to B}=\frac{1}{2-\beta},\quad R_{J\to B}=\frac{2-\beta}{4-3\beta},\quad R_{I\to BM}=\frac{\beta(3-\beta)}{2(2-\beta)},\quad R_{J\to BM}=\frac{\beta}{4-3\beta}.$$

In the coefficients of relatedness above, *I* represents a female and *J* a male. In addition, subscript *M* stands for mate, *S* for sister, *B* for brother, *SM* for sister's mate and *BM* for brother's mate. Interpretation of the coefficients involved in the sex-linked case is analogous to the autosomal case, the difference being that all rates of increase in fitness must now be weighted by the reproductive values of the sexes: 2/3 for females and 1/3 for males. The fraction 1/2 which appears in the $B(h)$ term simply reflects the implicit hypothesis of equal numbers in females and males at each generation, so that half of the interactions are produced by females and the other half by males.

In general, no restrictions are imposed on the signs of $A(h)$ and $B(h)$. However, suppose that strategy 1 codes for an altruistic behaviour in the context of a kin selection model. Then it seems natural to assume the following inequalities

$$m_{11} < m_{21}, \quad m_{12} < m_{22}$$

and

$$m_{11} > m_{12}, \quad m_{21} > m_{22}.$$

These inequalities clearly imply that $A(h) < 0$ and $B(h) > 0$. Thus, following, e.g., Karlin and Matessi (1983), $-A(h)$ can be viewed as the cost for an offspring who performs an altruistic act (donor) and $B(h)$ as the benefit for an offspring who receives an altruistic act from a sib (recipient). In this specific case, it is now possible to undergo a detailed analysis of equations (3.8a), (3.9a) and (3.10a). We have summarized in Table 3.1 conditions for protection ($\dot{\rho}(0) > 0$) of a rare mutant allele in all three partial inbreeding models considered so far in this paper. Results are grouped according to values of "*cost-benefit ratio*" and change in strategy represented by the signs of d_{1j} for $j = 1, 2$. In Table 3.1, the parameter γ gives the proportion of inbred matings at each generation.

Table 3.1 Conditions for protection of a rare mutant allele under three partial inbreeding models.

cost-benefit ratio / **changes in strategy**	$-\frac{A(h)}{B(h)} < \frac{1}{2}$	$\frac{1}{2} < -\frac{A(h)}{B(h)} < 1$	$-\frac{A(h)}{B(h)} > 1$
$d_{11} > 0,\ d_{12} > 0$	all γ	$\gamma > \gamma_S$	no γ
$d_{11} < 0,\ d_{12} < 0$	no γ	$\gamma < \gamma_S$	all γ
$d_{11} < 0,\ d_{12} > 0$	$\gamma < \gamma_0$	$\min(\gamma_0, \gamma_S) < \gamma < \max(\gamma_0, \gamma_S)$	$\gamma > \gamma_0$
$d_{11} > 0,\ d_{12} < 0$	$\gamma > \gamma_0$	$\gamma < \min(\gamma_0, \gamma_S)$ or $\gamma > \max(\gamma_0, \gamma_S)$	$\gamma < \gamma_0$

To properly use results of Table 3.1, we have to provide the correct expressions for d_{11}, d_{12}, γ, γ_0 and γ_S for all three models. For partial selfing, set

$$d_{11} = \delta_{11} - \delta_{22}, \quad d_{12} = \delta_{12} - \delta_{22}, \quad \gamma = \alpha, \quad \gamma_0 = \frac{2d_{12}}{2d_{12} - d_{11}};$$

for partial sib-mating at an autosomal locus,

$$d_{11} = \delta_{11} - \delta_{22}, \quad d_{12} = \delta_{12} - \delta_{22}, \quad \gamma = \beta, \quad \gamma_0 = \frac{4d_{12}}{4d_{12} - d_{11}};$$

for partial sib-mating at a sex-linked locus,

$$d_{11} = \tfrac{1}{2}(\delta_{11} - \delta_{22}) + \tfrac{1}{2}(\delta_1 - \delta_2), \quad d_{12} = \tfrac{2}{3}(\delta_{12} - \delta_{22}) + \tfrac{1}{3}(\delta_1 - \delta_2),$$

$$\gamma = \beta, \quad \gamma_0 = \frac{3d_{12}}{3d_{12} - d_{11}};$$

finally, in all three models, take $\gamma_S = -2\left[1 + A(h)/B(h)\right]$. A detailed discussion based upon entries of Table 3.1 is deferred to Section 3.6.

3.5.2 Case of small differences in viabilities

Equations (3.11a), (3.12a) and (3.13a) do not exhibit "easy-to-analyze" factors such as in equations (3.8a), (3.9a) and (3.10a). Nonetheless, after many rearrangements of terms, it is possible to express each of these equations in a form which closely resembles (3.8a), (3.9a) and (3.10a). To this end, we define coefficients similar to those given by (3.14):

$$\begin{aligned} A(h_{22}) &= h_{22}(a_{11} - a_{21}) + (1 - h_{22})(a_{12} - a_{22}), \\ B(h_{ij}) &= h_{ij}(a_{11} - a_{12}) + (1 - h_{ij})(a_{21} - a_{22}), \end{aligned} \tag{3.15}$$

for $i, j = 1, 2$. Interpretations are somewhat more specific. The coefficient $A(h_{22})$ approximates the rate of increase in the fitness of an offspring interacting with a sib of genotype A_2A_2 with respect to an increase in the probability for this offspring to adopt strategy 1. The coefficient $B(h_{ij})$ approximates the rate of increase in the fitness of an offspring with respect to an increase in the probability for a sib of genotype A_2A_2

interacting with this offspring to adopt strategy 1. All these rates involve at least one individual of genotype A_2A_2 because, as long as allele A_1 is rare in the population, most pairwise interactions implicate at least one resident homozygote A_2A_2.

Using the coefficients in (3.15), equation (3.11a) obtained in the partial selfing model can be put into the following form:

$$\begin{aligned}\dot{\rho}(0) = &\left[A(h_{22}) + \left(\frac{1+3\alpha}{4}\right)B(h_{11}) + \left(\frac{1-\alpha}{4}\right)B(h_{12})\right]F(h_{11}-h_{22}) \\ &+\left[A(h_{22}) + \left(\frac{\alpha}{4}\right)B(h_{11}) + \left(\frac{2+\alpha}{4}\right)B(h_{12})\right](1-F)(h_{12}-h_{22}),\end{aligned} \tag{3.16}$$

where F is given by (3.8b). This expression looks similar to equation (3.8a), but does not seem to have a clear interpretation based on a kin selection approach. However, a condition can be found such that this equation will successfully match the structure of equation (3.8a).

A sufficient condition consists to equate $B(h_{11})$ and $B(h_{12})$ in equation (3.16), since the coefficients assigned to them sum up to $(1+\alpha)/2$. But, owing to (3.15), this condition entails that

$$a_{11} - a_{12} = a_{21} - a_{22},$$

for $h_{11} \neq h_{12}$. Moreover, it implies that the $A(h_{22})$ and $B(h_{ij})$ coefficients are all constant:

$$\begin{aligned}A(h_{22}) &= a_{11} - a_{21} = a_{12} - a_{22}, \\ B(h_{11}) = B(h_{12}) &= a_{11} - a_{12} = a_{21} - a_{22},\end{aligned}$$

which means that the approximate change in fitness of an offspring adopting strategy 1 over strategy 2 is the same whether a sib interacting with this offspring chooses strategy 1 or 2. Also, the approximate change in fitness of an offspring which

interacts with a sib choosing strategy 1 over strategy 2 is the same, whether this offspring chooses strategy 1 or 2. Additive effects of strategies in viabilities is one hypothesis which meets these requirements.

In the case of partial sib-mating at an autosomal locus, using the coefficients defined in (3.15) and values of F and R in (3.9b) allows to express equation (3.12a) as

$$\dot{\rho}(0)=\left[\begin{array}{l} A(h_{22})+\left(\dfrac{1+\beta+\beta^2}{4-\beta}\right)B(h_{11}) \\ +\left(\dfrac{(1-\beta)(2+\beta)^2}{4(4-\beta)}\right)B(h_{12})+\left(\dfrac{\beta(1-\beta)(2-\beta)}{4(4-\beta)}\right)B(h_{22}) \end{array}\right](1+R)F(h_{11}-h_{22}) \tag{3.17}$$

$$+\left[\begin{array}{l} A(h_{22})+\left(\dfrac{\beta(8+4\beta+\beta^2)}{16(4-\beta)}\right)B(h_{11}) \\ +\left(\dfrac{8+\beta^2-\beta^3}{4(4-\beta)}\right)B(h_{12})+\left(\dfrac{\beta(4-3\beta)}{16}\right)B(h_{22}) \end{array}\right](1+R)(1-F)(h_{12}-h_{22}).$$

To transform equation (3.17) into a structure similar to equation (3.9a), a sufficient condition obtains when $B(h_{11}) = B(h_{12}) = B(h_{22})$, since the coefficients assigned to them sum up to $(1+\beta)/2$.

Finally, for the partial sib-mating model at a sex-linked locus, equation (3.13a) can be written as

$$\dot{\rho}(0)=\left[\begin{array}{l} \dfrac{A(h_{22})+A(h_2)}{2} \\ +\left(\dfrac{4+\beta+\beta^2}{4(4-\beta)}\right)B(h_{11})+\left(\dfrac{(2+\beta)(1+\beta)}{4(4-\beta)}\right)B(h_1) \\ +\left(\dfrac{(2+\beta)(1-\beta)}{4(4-\beta)}\right)B(h_{12})+\left(\dfrac{3\beta(1-\beta)}{4(4-\beta)}\right)B(h_2) \end{array}\right]\left(\frac{2}{3}+\frac{1}{3}R_{I\to M}\right)F(h_{11}-h_{22})$$

$$+\left[\begin{array}{l}\dfrac{A(h_{22})+A(h_2)}{2}+\left(\dfrac{\beta(4+\beta)}{16(4-\beta)}\right)B(h_{11})\\ +\left(\dfrac{2+\beta+\beta^2}{4(4-\beta)}\right)B(h_1)+\left(\dfrac{12-4\beta+\beta^2}{8(4-\beta)}\right)B(h_{12})\\ +\left(\dfrac{\beta(5-3\beta)}{4(4-\beta)}\right)B(h_2)+\left(\dfrac{\beta(4-3\beta)}{16(4-\beta)}\right)B(h_{22})\end{array}\right]\left(\frac{2}{3}+\frac{1}{3}R_{I\to M}\right)(1-F)(h_{12}-h_{22})$$

$$+\left[\begin{array}{l}\dfrac{A(h_{22})+A(h_2)}{2}+\left(\dfrac{\beta(4+\beta+\beta^2)}{4(4-\beta)(2-\beta)}\right)B(h_{11})\\ +\left(\dfrac{4-2\beta+\beta^2}{2(4-\beta)(2-\beta)}\right)B(h_1)+\left(\dfrac{(1-\beta)(4+2\beta+\beta^2}{2(4-\beta)(2-\beta)}\right)B(h_{12})\\ +\left(\dfrac{\beta(1-\beta)}{(4-\beta)(2-\beta)}\right)B(h_2)+\left(\dfrac{\beta(1-\beta)(4-3\beta)}{4(4-\beta)(2-\beta)}\right)B(h_{22})\end{array}\right]\left(\frac{1}{3}+\frac{2}{3}R_{J\to M}\right)(h_1-h_2),\tag{3.18}$$

where F, $R_{I\to M}$ and $R_{J\to M}$ are given by (3.10b). To be equivalent in structure to equation (3.10a), a sufficient condition again consists to equate all coefficients $B(h_{ij})$ and $B(h_i)$, for $i, j = 1, 2$, in (3.18).

3.6 Discussion

We have studied a special type of fitness between kin as proposed by Michod (1980), called family-specific fitnesses based on strategies. Here, strategies refer to social behaviours adopted by an individual when interacting with another individual. In this paper, we have restricted ourselves to two possible pure strategies and to pairwise interactions between offspring within the same sibship. Despite the fact that the choice between the two pure strategies is dictated both by the individual's genotype and its sib's genotype, genotypic distribution of interactions, unlike classical kin selection models, are not necessary to obtain explicit formulas for these fitnesses (see, e.g., Michod, 1982, for an introduction to kin selection theory). Detailed expressions of these fitnesses for diploid individuals are provided in Section 3.2, as well as their haplo-diploid analogues.

Two hypotheses of weak selection, in genotypic values and in viabilities, have been considered, in order to apply results obtained by Lessard and Rocheleau (2002) for the change in frequency of a rare mutant allele. In that paper, we had recourse to three partial inbreeding models with constant selective values. We inferred that the formula for the change in frequency of a rare mutant allele can be interpreted from a kin selection point of view, although there were no fitness interactions as such between kin. Using the three partial inbreeding models cited above and family-specific fitness based on strategies (see Section 3.3), we have obtained conditions for protection of a rare mutant allele under the two foresaid forms of weak selection. A kin selection interpretation has been proposed to describe factors involved in these conditions.

Regarding the weak selection hypothesis in genotypic values, the condition for protection was expressed as the product of two factors: a structural and a viability-analogous factor (named so after Uyenoyama *et al.*, 1981). These factors appear in kin selection models with pure random mating and additive genotypic fitnesses. The

same factorization obtains in some kin selection models with partial inbreeding and additive genotypic fitnesses (Uyenoyama, 1984), relative to conditions for initial increase of a rare mutant allele. A little rearrangement of terms in equations (3.8a), (3.9a) and (3.10a) showed that coefficients of relatedness are involved into conditions for protection of a rare mutant allele. This should not appear too surprising though. A careful examination of fitnesses (3.1), (3.2a) and (3.2b) reveals that, under the hypothesis of small differences in genotypic values as expressed by (3.3), individual genotypic fitnesses are tantamount to fitnesses in additive kin selection models with, in our own models, additive increments defined by $A(h)$ and $B(h)$ coefficients. In the particular context of altruism, the coefficient $-A(h)$ can be viewed as the cost of performing an altruistic act incurred by the donor and the coefficient $B(h)$ as the benefit bestowed to the recipient of such an altruistic act. Coefficients of relatedness mentioned above are derived under selective neutrality of genes and depend on the mating system along with the ploidy of the donor and recipient. Uyenoyama (1984) already noted that these coefficients appear in the initial increase conditions of a rare allele, without any specification on the intensity level of selection.

With particular reference to altruism behaviour, we have deduced explicit restrictions on the proportion of inbred matings which can be written in terms of changes in strategy and cost-benefit ratios (see Table 3.1 of Section 3.5.1). In view of Table 3.1, we can generally assess that small values of cost-benefit ratio (that is, $-\frac{A(h)}{B(h)} < \frac{1}{2}$) tend to increase the frequency of a rare gene favouring more altruism, which completely agrees with kin selection theory of altruism. As the value of cost-benefit ratio increases, conditions for protection of this gene become more stringent. Although this rule seems to be generally valid, it can be altered due to inbreeding. For example, in completely random mating populations ($\gamma = 0$), a small cost-benefit ratio will lead to an increase in the frequency of a rare mutant gene if and only if the mutant heterozygote performs more altruism than the resident homozygote ($d_{12} > 0$). However, the condition $d_{12} > 0$ is no longer sufficient (or neither necessary) to maintain a rare gene whenever there is some inbreeding. In fact, if the mutant

homozygote performs less altruism than the resident homozygote ($d_{11} < 0$), a rare mutant gene cannot be maintained unless the proportion of inbred matings in the population is lower than a given threshold ($\gamma < \gamma_0$). This is a perfect example where a high level of inbreeding does not promote more altruism, as outlined by Uyenoyama (1984) for some partial inbreeding models. On the other hand, when $d_{12} < 0$, a mutant homozygote enhancing altruism compared to the resident homozygote ($d_{11} > 0$) can guarantee the protection of a rare gene as long as the proportion of inbred matings is sufficiently high ($\gamma > \gamma_0$).

As in classical viability models, inbreeding acts as an evolutionary force which may overcome the effects of differential change in strategy by producing more or less homozygotes, depending upon the proportion of inbred matings in the population. For instance, assume that $d_{12} > 0$. Then, to overcome the negative effect on the frequency of a rare gene induced by mutant homozygotes performing less altruism than resident homozygotes ($d_{11} < 0$), inbreeding paradoxically might act *as if* it was favouring the mutant heterozygote by producing just enough homozygotes. This is achieved by keeping the proportion of inbred matings relatively small enough ($\gamma < \gamma_0$). A similar effect was pointed out by Uyenoyama (1984) who attributed the effect to increased within-family variation caused by the greater production of rare homozygotes when there is inbreeding in the population.

For large values of cost-benefit ratio ($-\frac{A(h)}{B(h)} > 1$), the situation is completely reversed to the case of small cost-benefit ratios. Essentially, large cost-benefit ratios will tend to favour a rare mutant gene performing less altruism than the resident homozygote, which is also in agreement with the notion of altruism in kin selection.

A more interesting case is provided by intermediate values of cost-benefit ratio ($\frac{1}{2} < -\frac{A(h)}{B(h)} < 1$), since restrictions on the parameter γ again involve the change in strategy (through γ_0) but also the $A(h)$ and $B(h)$ terms (through γ_S). These restrictions can lead to many different conditions upon γ for which a rare mutant gene can be

protected. To illustrate this, consider the case of underdominance where the mutant homozygote has a slight advantage over the resident homozygote (d_{11} is positive, but near 0, and $d_{12} < 0$). Then, for small cost-benefit ratios it becomes very difficult (since the value of γ_0 is near 1, in that case) to maintain a rare gene in the population unless the proportion of inbred matings is very high (look at the last row of Table 3.1). In contrast, for large cost-benefit ratios it will be protected for almost every value of γ. For intermediate values of cost-benefit ratio, the whole picture can dramatically change though. For instance, a cost-benefit ratio barely higher than 1/2 can produce more values of γ for which protection is guaranteed (because, in that case, $\min(\gamma_0, \gamma_S) = \gamma_S$ and $\max(\gamma_0, \gamma_S) = \gamma_0$). Since γ_S is near 0 and γ_0 is near 1, this implies that a rare gene might be protected for *either* small values of γ *or* large values of γ. This example shows that inbreeding is one factor among others which contribute to the fate of a rare mutant allele.

An obvious statement emerges from our analysis: kin selection **does not** necessarily promote altruism, which agrees with some observations made by Uyenoyama (1984). This author showed that increasing inbreeding may increase the within-family variance by producing more rare homozygotes, resulting in more stringent conditions for the evolution of greater levels of altruism. We have provided a similar example where inbreeding must not be too high, allowing thus the production of more altruistic heterozygotes at the expense of homozygotes, whenever the mutant homozygote performs less altruim than the resident homozygote.

The weak selection hypothesis in viabilities did not provide readily interpretable conditions for protection. However, it is possible to express equations (3.11a), (3.12a) and (3.13a) in a form which closely mimics equations (3.8a), (3.9a) and (3.10a). Unfortunately, simple conditions on the proportion of inbred matings cannot be obtained analytically unless severe restrictions are imposed on $A(h_{22})$ and $B(h_{ij})$ coefficients. Additive effects of strategies in viabilities is one such restriction which considerably simplifies these equations. Under this additive pattern in

viabilities, conditions are equivalent to the ones deduced in the case of weak selection hypothesis in genotypic values. However, assuming additivity appears to be very restrictive in view of all the possible effects strategies might induce.

Straightforward extensions of fitnesses based on strategies could include more strategies as well as particular patterns in viabilities. Interactions could also be restricted to specific members of the population (e.g., brother-to-sister, sister-to-all-sibs, etc.), following the kin selection models studied by Uyenoyama (1984). Furthermore, not only altruism but other types of social behaviour could be considered between kin. The concept of family-specific fitness based on strategies allows flexibility regarding the types of behaviours between sibs. Finally, as shown by Lessard (1992), the partial selfing and partial sib-mating models exhibit peculiar properties which make coefficients of relatedness between sibs totally independent of gene frequencies and genotypic values. Therefore, considering mating models with other form (regular or irregular) of inbreeding could be of great theoretical interest.

Conclusion

Cette thèse a été consacrée à l'étude de deux modèles avec consanguinité partielle et sélection les plus couramment utilisés, soit le modèle avec autofécondation partielle et le modèle avec accouplement frère-sœur partiel. Ces modèles permettent d'analyser les effets conjoints de la sélection et de la consanguinité sur la structure génétique d'une population.

À cet égard, le présent ouvrage a fait ressurgir la complexité induite par l'introduction de valeurs sélectives assignées aux génotypes. En effet, sans sélection, les équations de récurrence décrivant le passage d'une génération à la suivante convergent vers un équilibre polymorphique stable qui ne dépend que des fréquences alléliques originalement présentes dans la population. Cependant, en présence de sélection, l'analyse dynamique des équations de récurrence s'avère plus ardue car les fluctuations des fréquences génotypiques d'une génération à l'autre modifient les fréquences alléliques dans la population.

Au Chapitre 1, une étude exhaustive du modèle d'autofécondation partielle avec sélection constante a été réalisée pour un locus à deux allèles. À cet effet, le tableau 1.2 résume bien les résultats obtenus. On a montré qu'un équilibre polymorphique existe seulement dans les cas de surdominance ou de sousdominance des hétérozygotes et pour des intervalles spécifiques de la probabilité d'autofécondation. En outre, lorsqu'il existe, cet équilibre polymorphique est unique. Toutefois, une analyse locale de l'équilibre polymorphique et des points de fixation révèle que seule la surdominance peut conduire à un polymorphisme protégé. Dans certains cas, une analyse plus fine de type quadratique s'est avérée nécessaire lorsque l'analyse linéaire était non concluante.

Pour certaines combinaisons particulières de valeurs sélectives, telles la sélection directionnelle, la dominance d'un allèle, l'égalité des valeurs sélectives des homozygotes ou la létalité d'un des génotypes, des critères de convergence globale

ont pu être établis, ce qui représente l'une des grandes contributions de cette thèse à l'étude du modèle avec autofécondation partielle.

Par ailleurs, une comparaison entre le modèle d'autofécondation partielle et le modèle panmictique a permis de mettre en lumière les quelques différences qualitatives entre les deux types de reproduction. D'une part, lorsque la probabilité d'autofécondation n'est pas trop "élevée", les deux modèles montrent des comportements similaires, de sorte qu'on peut affirmer que seule la sélection, dans ce cas, détermine la structure génétique ultime et si possible, la préservation d'un polymorphisme dans la population. D'autre part, lorsque la probabilité d'autofécondation dépasse un certain seuil (déterminé par la magnitude des valeurs sélectives), aucun équilibre polymorphique n'existe et la reproduction par autofécondation devient ainsi le principal facteur susceptible de compromettre un éventuel polymorphisme dans la population.

Enfin, il faut noter que les résultats déduits au Chapitre 1 s'accordent avec ceux obtenus par Nagylaki (1997) sous l'hypothèse de sélection faible et ce, malgré un traitement analytique fort différent de celui préconisé dans cette thèse. Entre autres, dans le cas de surdominance, on a pu vérifier que la sélection faible diminuait les chances de préservation d'un polymorphisme dans la population, contrairement à une sélection d'intensité arbitraire telle que supposée au Chapitre 1. On explique ce phénomène par le fait qu'une sélection d'intensité plus élevée produit un éventail plus grand de valeurs sélectives que la sélection faible.

L'étude exhaustive du modèle d'accouplement frère-sœur partiel avec sélection se heurte à des difficultés supplémentaires, car les fréquences génotypiques ne suffisent plus à décrire le passage d'une génération d'individus à une autre; il faut alors entreprendre une investigation des fréquences des couples reproducteurs, ce qui augmente de manière appréciable la dimension du traitement analytique à effectuer. Pour simplifier l'analyse du modèle, on a donc considéré une hypothèse de sélection faible et concentré l'attention sur les conditions d'invasion ou d'extinction d'un allèle

mutant introduit en petite quantité dans une population originalement fixée pour un allèle donné. La méthode proposée consiste à observer le changement dans la fréquence des couples contenant l'allèle mutant près de l'état de fixation au moyen de la dérivée, par rapport à l'intensité de sélection s, de la plus grande valeur propre $\rho(s)$ de la matrice $\mathbf{M}(s)$ des approximations linéaires de ces fréquences. Sous certaines conditions de régularité de la matrice $\mathbf{M}(s)$, le signe de la dérivée de la plus grande valeur propre $\rho(s)$ est le même que le signe de la dérivée du polynôme caractéristique de $\mathbf{M}(s)$ (Courteau & Lessard, 2000). Étant donné qu'il est généralement beaucoup plus facile d'établir la matrice $\mathbf{M}(s)$ que de calculer l'expression de $\rho(s)$, la nouvelle méthode suggérée au Chapitre 2 simplifie grandement l'analyse requise pour déterminer l'évolution d'un allèle mutant rare. À cet effet, le Résultat 2.1 du Chapitre 2 fournit un critère simple à vérifier: si la dérivée de $\rho(s)$ évaluée à $s = 0$ est positive, l'allèle mutant sera maintenu dans la population; dans le cas contraire, c'est-à-dire si la dérivée est négative, l'allèle sera éventuellement éliminé de la population. L'expression de cette dérivée est attribuée à Taylor (1985).

Jumelé au Résultat 2.1, le Résultat 2.2 du Chapitre 2 donne une approximation du changement dans la fréquence d'un allèle mutant rare d'une génération à la suivante. Taylor (1989) avait déjà souligné l'évidence apparente d'une telle approximation, mais une preuve rigoureuse (telle qu'effectuée dans l'Appendice B) devenait nécessaire. Quelques réserves s'imposent toutefois quant à la validité générale de cette approximation. En particulier, les termes d'ordre différent de ps doivent obligatoirement être assez petits, afin que l'approximation demeure précise et ceci, même après qu'un nombre suffisant de générations se soient écoulées. Par conséquent, la fréquence de l'allèle mutant doit demeurer suffisamment petite, même après quelques générations, et la sélection en vigueur dans la population doit être réputée suffisamment faible.

Quelques applications des Résultats 2.1 et 2.2 ont été effectuées pour les modèles avec consanguinité partielle évoqués plus haut. Ces applications ont confirmé les résultats obtenus pour un locus autosome et sous sélection faible, entre

autres, par Pollak & Sabran (1992) et Nagylaki (1997) dans le modèle d'autofécondation partielle, et par Pollak (1995) dans le modèle d'accouplement frère-sœur partiel. Dans le modèle panmictique, il est connu qu'un allèle mutant rare envahit une population fixée si et seulement si l'hétérozygote mutant possède un avantage sélectif sur l'homozygote résident. On démontre au Chapitre 2 que cette condition n'est plus suffisante, ni nécessaire, lorsque la probabilité d'autofécondation ou d'accouplement frère-sœur est suffisamment élevée. Encore une fois, on constate que la consanguinité peut contrer les effets de la sélection dans les situations de surdominance ou sousdominance des hétérozygotes, mais non dans le cas de sélection directionnelle. Ces observations demeurent qualitativement valides pour un locus lié au sexe dans le modèle d'accouplement frère-sœur partiel.

Ces applications ont aussi permis d'infirmer la formule de Wright (1942) proposée pour décrire le changement dans la fréquence d'un gène donné dans une population sujette aux effets simultanés de la consanguinité et de la sélection faible. Dans le modèle avec autofécondation partielle, la formule de Wright prédit correctement le changement dans la fréquence d'un allèle mutant rare sous un régime de sélection faible. Cependant, tel que déduit par Pollak (1995), la formule de Wright n'est plus valide quantitativement dans le modèle d'accouplement frère-sœur partiel. En effet, celle-ci doit être multipliée par un facteur faisant intervenir le coefficient de corrélation entre les fréquences respectives de l'allèle mutant chez les individus formant un couple reproducteur. On peut néanmoins conclure à la validité qualitative de la formule de Wright pour un locus autosome, puisque ce facteur est toujours positif. Par contre, dans le cas d'un locus lié au sexe, la formule de Wright est totalement invalidée. Cette fois, des coefficients de régression de la fréquence de l'allèle mutant chez un membre d'un couple reproducteur sur la fréquence de cet allèle chez l'autre membre du couple apparaissent dans l'approximation du changement dans la fréquence de l'allèle mutant. Ces coefficients de régression, calculés en absence de sélection, sont interprétés comme des coefficients d'apparentement rencontrés dans les modèles de sélection de parentèle, même en absence d'interactions entre individus apparentés pouvant affecter directement leurs valeurs sélectives. Cette interprétation

est justifiée par le fait que des interactions entre individus apparentés se produisent bel et bien au moment de l'accouplement, ce qui modifie du même coup le succès reproductif espéré de chaque membre d'un couple reproducteur.

Dans le but de pousser l'investigation de ces effets engendrés par l'apparentement entre les individus formant un couple reproducteur, des valeurs sélectives comportant des interactions deux-à-deux entre individus issus d'une même famille ont été étudiées au Chapitre 3. S'inspirant de la théorie sur les équilibres évolutionnairement stables (ESS), la valeur sélective d'un individu est déterminée principalement par la stratégie qu'il adopte en réponse à la stratégie adoptée par son frère ou sa sœur. La probabilité (ou valeur génotypique) correspondant au choix de l'une des deux stratégies est établie par son génotype au locus concerné.

Afin d'utiliser les Résultats 2.1 et 2.2 du Chapitre 2, l'hypothèse de sélection faible doit être supposée. Dans le Chapitre 3, deux hypothèses de sélection faible ont été envisagées: une première hypothèse supposant de petites différences entre les stratégies mixtes (définies par la valeur génotypique), et une deuxième supposant de petites différences entre les viabilités. Sous l'hypothèse de petites différences entre les stratégies mixtes, le Résultat 3.1 procure une condition garantissant la protection d'un allèle mutant rare, condition qui peut être factorisée à la manière des modèles de sélection de parentèle avec valeurs sélectives additives (Uyenoyama, 1984). Tel qu'anticipée, cette factorisation implique des coefficients d'apparentement ainsi que deux taux d'accroissement pouvant s'interpréter comme le coût et le bénéfice rencontrés dans les modèles d'altruisme. En outre, en supposant qu'une des stratégies définit un comportement altruiste chez l'individu, on a déterminé des conditions de protection d'un allèle mutant rare, exprimées en termes de probabilité d'autofécondation ou d'accouplement frère-sœur (désignées au Chapitre 3 par la proportion d'accouplements consanguins) et d'un rapport coût-bénéfice inspiré de Karlin & Matessi (1983). Le Tableau 3.1 résume ces conditions de protection et peut s'utiliser aussi bien dans le modèle d'autofécondation partielle que dans le modèle d'accouplement frère-sœur partiel (locus autosome ou lié au sexe).

Pour de petites valeurs du rapport coût-bénéfice (plus petit que ½), les conditions de protection sont similaires à celles obtenues dans le Chapitre 2 avec des valeurs sélectives constantes. Règle générale, on peut affirmer que de petites valeurs du rapport coût-bénéfice auront tendance à augmenter la fréquence d'un allèle mutant favorisant plus d'altruisme, ce qui s'accorde complètement avec les modèles de sélection de parentèle basés sur l'altruisme. Toutefois, la consanguinité permet d'enfreindre cette règle. Par exemple, dans une population panmictique, un petit rapport coût-bénéfice entraîne une augmentation dans la fréquence de l'allèle mutant si et seulement si l'hétérozygote mutant produit plus d'altruisme que l'homozygote résident. En présence de consanguinité cependant, cette condition n'est plus nécessaire, ni même suffisante, pour maintenir l'allèle mutant dans la population. Dans le cas où l'homozygote mutant engendre moins d'altruisme que l'homozygote résident, la proportion d'accouplements consanguins devra être suffisamment petite afin de protéger l'allèle mutant. Uyenoyama (1984) attribue cet effet à une plus grande variabilité génétique intra-familiale causée par une plus grande production d'homozygotes mutants, lorsqu'il y a consanguinité.

Pour de grandes valeurs du rapport coût-bénéfice (plus grand que 1), on obtient exactement la situation inverse du cas où les valeurs du rapport sont petites. Essentiellement, ceci signifie qu'un coût associé à un comportement altruiste plus grand que le bénéfice procuré ne saurait favoriser un allèle mutant rare produisant plus d'altruisme, ce qui est en parfait accord avec la notion même d'altruisme.

Le cas le plus intéressant s'avère sans aucun doute celui des valeurs intermédiaires (plus grand que ½ mais plus petit que 1) du rapport coût-bénéfice, puisqu'il mène à plusieurs scénarios possibles. Un exemple est donné où l'allèle mutant peut être protégé aussi bien pour une petite que pour une grande proportion d'accouplements consanguins. La consanguinité représente donc une force parmi d'autres contribuant à l'évolution d'un allèle mutant. Aussi, une consanguinité accrue ne garantit pas une augmentation des comportements altruistes, comme l'avait indiqué Uyenoyama (1984).

L'hypothèse de petites différences entre les viabilités ne fournit pas de conditions de protection pouvant se prêter à des interprétations aussi élégantes que sous l'autre hypothèse de sélection faible. Tout au plus, on peut trouver une simplification permettant de se ramener aux conditions énoncées sous l'hypothèse de petites différences entre les stratégies mixtes. Mais cette simplification est obtenue en supposant des effets additifs des stratégies sur les viabilités, ce qui semble restrictif dans la formulation des modèles.

Une possible extension des recherches concerne les modèles de populations structurées en groupes. En réalité, les modèles avec consanguinité partielle étudiés dans cette thèse font partie de cette classe de modèles, où la structure des groupes est de type familiale. L'Appendice E présente une étude préparatoire de modèles où la population est subdivisée en petits groupes avec migration partielle avant ou après accouplement (voir, p. ex., Bulmer, 1986 et Taylor, 1988b). On suggère la possibilité d'utiliser, dans la formule du changement de fréquence d'un allèle mutant rare et sous l'hypothèse de sélection faible, un coefficient d'apparentement indépendant des fréquences alléliques et des valeurs génotypiques. Ce coefficient est toutefois calculé en absence de sélection et son implication dans le changement de fréquence d'un allèle mutant reste à démontrer.

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Appendice A: Preuves du Chapitre 1

A.1 Proof of Result 1.5

We show that $H(\beta, \hat{p})$ is strictly positive. We have to consider separately the cases $0 < b < \min(\frac{1}{2}, a) < 1$ and $\frac{1}{2} \leq b < a < 1$. In the case $0 < b < \min(\frac{1}{2}, a) < 1$, we have exhibited (see Result 1.3) the condition $0 < \beta < \beta_0$ for the existence of a polymorphic equilibrium $(\hat{p}, \hat{F})$, where $0 < \hat{p} < \frac{1}{2}$. We first examine the limiting values $\beta = 0$ and $\beta = \beta_0$. When $\beta = 0$, random mating prevails in the population. Results for this model are well known in population genetics (see, e.g., Jacquard, 1974) and in particular, for $0 < b < a < 1$, it is known that there exists a unique polymorphic equilibrium with the frequency of A_1 given by $\hat{p}_R = b/(a+b) < \frac{1}{2}$ (this result could have also been obtained by letting $\beta = 0$ in equation (1.7)). For these specific values of β and p, we have

$$H(0, \hat{p}_R) = a + b > 0, \tag{A.1}$$

When $\beta = \beta_0$, we have (see Section 1.3) $\hat{p}_- = 0$, i.e. the polymorphic equilibrium degenerates to the fixation of A_2. These values of β and p yield

$$H(\beta_0, 0) = \left(\frac{1}{1-b}\right)[a(1-b) - b^2] > 0. \tag{A.2}$$

We also find that

$$H(0, 0) = a + b > 0 \tag{A.3}$$

and

$$H(\beta_0, \hat{p}_R) = \left[\frac{a+b}{(a+b-ab)^2}\right]\{(a+b)[(a-b)(1-b) + b(1-a)] + a^2b^2\} > 0. \tag{A.4}$$

In addition, the partial derivatives with respect to β and p satisfy

$$\frac{\partial}{\partial \beta} H(\beta, p) = -\frac{K}{2}\left[\frac{a-(a+b)p}{a(1-b)-Kp}\right]^2 < 0$$

and (A.5)

$$\frac{\partial}{\partial p} H(\beta, p) = \frac{\beta Kab(a-b)[a-(a+b)p]}{[a(1-b)-Kp]^3} > 0,$$

for β in the open interval $(0, \beta_0)$ and p in the open interval $(0, \hat{p}_R)$. We conclude that the function $H(\beta, p)$ is strictly positive in the whole rectangle $[0, \beta_0] \times [0, \hat{p}_R]$, since it is strictly positive at the four corners, monotonically decreasing with respect to β and monotonically increasing with respect to p.

In the case $\frac{1}{2} \leq b < a < 1$, we have shown that there exists a unique polymorphic equilibrium $(\hat{p}, \hat{F})$, where $0 < \hat{p} < \frac{1}{2}$, for all $0 < \beta < 1$. We first look at the limiting values $\beta = 0$ and $\beta = 1$. When $\beta = 0$, (A.1) remains valid. When $\beta = 1$, the population reproduces by complete selfing. The expression for $\hat{p}$ at the polymorphic equilibrium is obtained by letting $\beta = 1$ in equation (1.7). This expression is given by

$$\hat{p}_S = \frac{a(2b-1)}{a(2b-1)+b(2a-1)}.$$

One can easily verify that $0 < \hat{p}_S < \hat{p}_R < \frac{1}{2}$. Then, we have

$$H(1, \hat{p}_S) = a(2b-1)+b(2a-1) > 0.$$

Moreover, one can calculate and observe that

$$H(0, \hat{p}_S) = a+b > 0 \quad \text{and} \quad H(1, \hat{p}_R) = \left(\frac{a+b}{2}\right)\left[1+\frac{a^2b^2}{(a+b-ab)^2}\right] > 0.$$

Also, the sign of the partial derivatives of $H(\beta, p)$, given in (A.5), remains unchanged for β in the open interval (0, 1) and p in the open interval $(\hat{p}_S, \hat{p}_R)$. Hence, using arguments as above, we conclude that the function $H(\beta, p)$ is strictly positive in the whole rectangle $[0, 1]\times[\hat{p}_S, \hat{p}_R]$.

A.2 Proof of Result 1.6

We show that $m(1) < 0$ in the case $a < b < 0$. As observed in equation (1.15), the sign of $m(1)$ is the same as that of $H(\beta, \hat{p})$. We have determined earlier (see Result 1.3) the condition $0 < \beta < \beta_0$ that allows for the existence of a polymorphic equilibrium $(\hat{p}, \hat{F})$, where $0 < \hat{p} < \frac{1}{2}$. Using (A.1) to (A.4), one can trivially obtain that

$$H(0, 0) < 0, \quad H(0, \hat{p}_R) < 0, \quad H(\beta_0, 0) < 0, \quad H(\beta_0, \hat{p}_R) < 0.$$

It is also easy to verify that the partial derivatives of $H(\beta, p)$, given in (A.5), are both strictly positive for β in the open interval $(0, \beta_0)$ and p in the open interval $(0, \hat{p}_R)$. Therefore, we conclude that the function $H(\beta, p)$ is strictly negative in the whole rectangle $[0, \beta_0]\times[0, \hat{p}_R]$ and consequently that $m(1) < 0$.

A.3 Proof of Result 1.8

In the degenerate case $\beta = \beta_0$, the greatest eigenvalue of $\mathbf{L}_2$ equals 1. Lessard and Karlin (1981) exhibited a general criterion for stability-instability at fixation states when the greatest eigenvalue of the matrix of the linear approximation is one. Using their notation, we let the vector $\underline{\mathbf{x}} = (x_1, x_2) = (P_{11}, P_{12})$ be such that $\underline{\mathbf{0}} = (0, 0)$ corresponds to the fixation event (F) of A_2. Let $T\underline{\mathbf{x}} = (U_1(\underline{\mathbf{x}}), U_2(\underline{\mathbf{x}})) = (P'_{11}, P'_{12})$, where T is the transformation defined by the recursive equations (1.3). We have that $T(\underline{\mathbf{x}}) = \underline{\mathbf{0}}$ if and only if $\underline{\mathbf{x}} = \underline{\mathbf{0}}$ and T is smooth enough in the neighborhood of $\underline{\mathbf{0}}$.

The matrix $\mathbf{L}_2$ is an irreducible aperiodic nonnegative matrix. Hence, by the theorem of Perron-Frobenius, the components of the left and right eigenvectors, $\underline{\xi}$ and $\underline{\eta}$, of $\mathbf{L}_2$ corresponding to the eigenvalue one are strictly positive:

$$\underline{\xi}\mathbf{L}_2 = \underline{\xi} = (\xi_1, \xi_2) > \underline{0} \qquad \text{and} \qquad \mathbf{L}_2\underline{\eta} = \underline{\eta} = (\eta_1, \eta_2) > \underline{0}.$$

Without loss of generality, we assume $\langle\langle \underline{\xi}, \underline{\eta} \rangle\rangle = \sum_{j=1}^{2} \xi_j \eta_j = 1$. Then we define the quantity $S = \langle\langle \underline{\xi}, \underline{\theta} \rangle\rangle$ as the inner product of the vectors $\underline{\xi}$ and $\underline{\theta} = (\theta_1, \theta_2)$, where

$$\theta_i = \sum_{\lambda,\mu=1}^{2} \frac{\partial^2 U_i(\underline{0})}{\partial x_\lambda \partial x_\mu} \eta_\lambda \eta_\mu, \qquad \text{for} \quad i = 1, 2.$$

The general criterion for stability-instability stipulates that the fixation event F is stable if $S < 0$ and unstable if $S > 0$.

Now, let $b = 1 - w_{22}$, $c = 2w_{22} - 1$ and $d = w_{22} - w_{11}$. Note that b, c, $d > 0$ in the case at hand. The matrix of the linear approximation is

$$\mathbf{L}_2 = \frac{1}{K}\begin{bmatrix} 2w_{11}b & \dfrac{b}{2} \\ \dfrac{2w_{11}cd}{w_{22}} & \dfrac{w_{11}b + w_{22}d}{w_{22}} \end{bmatrix}.$$

The eigenvalues of $\mathbf{L}_2$ are

$$\lambda_1 = 1 > \lambda_2 = \frac{w_{11}b}{w_{22}K} > 0.$$

The left and right eigenvectors of $\mathbf{L}_2$ corresponding to the eigenvalue one are

$$\underline{\xi} = \left(\frac{2w_{11}c}{w_{22}}, 1\right) > 0 \quad \text{and} \quad \underline{\eta} = \left(\frac{b}{2d}, 1\right) > 0 .$$

After some rather tedious calculus, we find that

$$\frac{\partial^2 U_1(\underline{0})}{\partial x_1^2} = \frac{2w_{11}d}{w_{22}^2 K}\left(w_{11}c + 2w_{22}b\right), \qquad \frac{\partial^2 U_1(\underline{0})}{\partial x_2^2} = \frac{1}{2w_{22}^2 K}\left(cd - 2w_{22}b^2\right),$$

$$\frac{\partial^2 U_1(\underline{0})}{\partial x_1 \partial x_2} = \frac{1}{w_{22}^2 K}\left[w_{11}cd - 2w_{22}b\left(w_{11}b - \tfrac{1}{4}d\right)\right],$$

$$\frac{\partial^2 U_2(\underline{0})}{\partial x_1^2} = \frac{4w_{11}(d - w_{11})cd}{w_{22}^2 K}, \qquad \frac{\partial^2 U_2(\underline{0})}{\partial x_2^2} = \frac{-1}{w_{22}^2 K}\left[2w_{22}b^2 + (1 + 2b)cd\right],$$

$$\frac{\partial^2 U_2(\underline{0})}{\partial x_1 \partial x_2} = \frac{d}{w_{22}^2 K}\left[w_{22}b - c(3w_{11} - w_{11}c - d)\right].$$

With some algebra, one finally obtains

$$\mathrm{S} = \frac{K\left|b^2 - w_{22}(1 - w_{11})\right|}{w_{22}^2 d\langle\langle \underline{\xi}, \underline{\eta} \rangle\rangle}. \tag{A.6}$$

In the case at hand, it is trivial to show that $\mathrm{S} < 0$ and consequently that the fixation of A_2 is stable.

A.4 Proof of Result 1.10

This proof is very similar to the above proof of Result 1.8. In this case, however, we have $b, d < 0$ and $c > 0$. Equation (A.6) clearly shows that $\mathrm{S} > 0$, and consequently that the fixation of A_2 is unstable.

A.5 Proof of Result 1.11

We first present an interesting result which will be useful in the subsequent proofs.

Let K be a compact set of $\Re^n$ and let T: $K \to K$ be a continuous function. Let v: $\Re^n \to \Re$ be a continuous function such that $v(T\underline{\mathbf{x}}) \leq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$. We define the sequence $\{T^n\underline{\mathbf{x}}\}_{n\geq 0}$ for every $\underline{\mathbf{x}} \in K$. By the compactness of K, v is bounded below and therefore the sequence $\{v(T^n\underline{\mathbf{x}})\}_{n\geq 0}$ converges, that is

$$\lim_{n\to\infty} v(T^n\underline{\mathbf{x}}) = \hat{v}.$$

Let $\hat{\underline{\mathbf{x}}}$ be an accumulation point of $\{T^n\underline{\mathbf{x}}\}_{n\geq 0}$. Then there exists a subsequence $\{T^{n_k}\underline{\mathbf{x}}\}_{k\geq 0}$ which converges to $\hat{\underline{\mathbf{x}}}$, that is

$$\lim_{k\to\infty}\{T^{n_k}\underline{\mathbf{x}}\} = \hat{\underline{\mathbf{x}}}.$$

Then, the following inequalities hold:

$$v(T^{n_{k+1}}\underline{\mathbf{x}}) \leq v(T^{n_k+1}\underline{\mathbf{x}}) \leq v(T^{n_k}\underline{\mathbf{x}}).$$

By the continuity of v,

$$\lim_{k\to\infty} v(T^{n_{k+1}}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T^{n_k}\underline{\mathbf{x}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}.$$

Also, by the continuity of v and T,

$$\lim_{k\to\infty} v(T^{n_k+1}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T\circ T^{n_k}\underline{\mathbf{x}}) = v(T\hat{\underline{\mathbf{x}}}).$$

Hence, we conclude that

$$v(T\hat{\underline{\mathbf{x}}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}.$$

More generally, for every $l \geq 1$, we obtain the following inequalities:

$$v(T^{n_k+l}\underline{\mathbf{x}}) \leq v(T^{n_k+l}\underline{\mathbf{x}}) \leq v(T^{n_k}\underline{\mathbf{x}}).$$

Using the same arguments as before, we obtain

$$\lim_{k\to\infty} v(T^{n_k+l}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T^{n_k}\underline{\mathbf{x}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}$$

and also

$$\lim_{k\to\infty} v(T^{n_k+l}\underline{\mathbf{x}}) = \lim_{k\to\infty} v(T^{l} \circ T^{n_k}\underline{\mathbf{x}}) = v(T^{l}\hat{\underline{\mathbf{x}}}).$$

Hence, for every $l \geq 1$, we conclude that

$$v(T^{l}\hat{\underline{\mathbf{x}}}) = v(\hat{\underline{\mathbf{x}}}) = \hat{v}.$$

Result A.1 *Every accumulation point of* $\{T^n\underline{\mathbf{x}}\}_{n\geq 0}$ *must be invariant with respect to v.*

Note that this result remains valid for a continuous function v such that $v(T\underline{\mathbf{x}}) \geq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$.

We shall demonstrate hereupon that the state for which $P_{12} = 1$ cannot be a point of accumulation of the iterates of the transformation T defined by the recursive equations (1.3) from any starting point $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$ in the case of directional selection ($0 < w_{11} < 1 < w_{22}$). Let $v(\underline{\mathbf{x}}) = p = P_{11} + \frac{1}{2}P_{12}$, for every $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$. Apply the tranformation T to $\hat{\underline{\mathbf{x}}} = (0, 1, 0)$, which corresponds to $P_{12} = 1$. Trivial computations give $T\hat{\underline{\mathbf{x}}} = (\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$ and $v(T\hat{\underline{\mathbf{x}}}) = \frac{1}{2}$. Applying once again the transformation T, one obtains that

$$v(T^2\hat{\underline{\mathbf{x}}}) = \frac{\frac{1}{4}w_{11} + \frac{1}{4}}{\frac{1}{4}w_{11} + \frac{1}{2} + \frac{1}{4}w_{22}} < \frac{1}{2}.$$

But this contradicts Result A.1 above.

A.6 Proof of Result 1.12

We demonstrate that the states for which $P_{11} + P_{12} = 1$, with $P_{11} \neq 0,\ 1$, cannot represent a set of accumulation points of the iterates of the recursive equations (1.3) from any starting point $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$ in the case of complete dominance ($w_{11} = w_{12} = 1$). Let $v(\underline{\mathbf{x}}) = p = P_{11} + \frac{1}{2}P_{12}$ and $\hat{\underline{\mathbf{x}}} = \left(P_{11},\ 1 - P_{11},\ 0\right)$. Then, applying the transformation T to $\hat{\underline{\mathbf{x}}}$, one easily obtains $v(T\hat{\underline{\mathbf{x}}}) = P_{11} + \frac{1}{2}\left(1 - P_{11}\right)$. Applying once again the transformation T, one calculates that

$$v(T^2\hat{\underline{\mathbf{x}}}) = \frac{P_{11} + \frac{1}{2}\left(1 - P_{11}\right)}{1 - \frac{1}{4}\left(1 - w_{22}\right)\left(1 - P_{11}\right)\left[1 - \left(1 - \beta\right)P_{11}\right]} \neq v(\hat{\underline{\mathbf{x}}}),$$

thus contradicting Result A.1.

A.7 Proof of Results 1.13 and 1.14

First, for any value $w \neq 0,\ 1$, we demonstrate that the states for which $P_{11} + P_{22} = 1$, with $P_{11} \neq 0,\ \frac{1}{2}$ or 1, cannot represent a set of accumulation points of the iterates of the recursive equations (1.3) from any starting point $\underline{\mathbf{x}} = (P_{11}, P_{12}, P_{22})$ in the case of symmetric selection ($w_{11} = w_{22} = w \neq 0$ and 1). Let $v(\underline{\mathbf{x}}) = \left|P_{11} - P_{22}\right|$ and $\hat{\underline{\mathbf{x}}} = \left(P_{11},\ 0,\ 1 - P_{11}\right)$. Applying the transformation T to $\hat{\underline{\mathbf{x}}}$, one easily obtains $v(T\hat{\underline{\mathbf{x}}}) = \left|2P_{11} - 1\right|$. Applying once again the transformation T, one can calculate that

$$v(T^2\hat{\underline{\mathbf{x}}}) = \left[\frac{w}{w + 2(1 - w)\left(1 - \beta\right)P_{11}\left(1 - P_{11}\right)}\right]\left|2P_{11} - 1\right| \neq v(\hat{\underline{\mathbf{x}}}),$$

thus contradicting Result A.1.

At this point, we distinguish the cases $w < 1$ and $w > 1$. In the case $w < 1$, posit again $v(\underline{\mathbf{x}}) = |P_{11} - P_{22}|$. From Section 1.6.3, we know that $v(T\underline{\mathbf{x}}) \leq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$. Let $\hat{v} = 0$ and $\hat{\underline{\mathbf{x}}} = (P_{11}, 1-2P_{11}, P_{11})$. By induction, it is easy to verify that Result A.1 holds. The vectors $\hat{\underline{\mathbf{x}}}$ located on the manifold $P_{11} = P_{22}$ represent a set of accumulation points of the iterates of the recursive equations (1.3) for the case at hand.

In the case $w > 1$, with $v(\underline{\mathbf{x}}) = |P_{11} - P_{22}|$, we know by Section 1.6.3 that $v(T\underline{\mathbf{x}}) \geq v(\underline{\mathbf{x}})$, for every vector $\underline{\mathbf{x}} \in K$. Two distinct cases must be considered:

(i) If $P_{11} > P_{22}$, then let $\hat{v} = 1$ and $\hat{\underline{\mathbf{x}}} = (1, 0, 0)$.

(ii) If $P_{11} < P_{22}$, then let $\hat{v} = 1$ and $\hat{\underline{\mathbf{x}}} = (0, 0, 1)$.

In both cases, it is trivial to verify that Result A.1 holds.

In the case $w < 1$, we have shown that the solution of the system of recursive equations (1.3) converges, except from the fixation states, to the manifold $P_{11} = P_{22}$. We shall prove convergence to the polymorphic equilibrium located on this manifold. In effect, if the sequence $\{T^l \hat{\underline{\mathbf{x}}}\}_{l \geq 0}$ converges to $\hat{\underline{\mathbf{z}}}$ (here the polymorphic equilibrium) for $\hat{\underline{\mathbf{x}}}$ on the manifold $P_{11} = P_{22}$ and $\hat{\underline{\mathbf{z}}}$ is locally stable, then the sequence $\{T^l \underline{\mathbf{x}}\}_{l \geq 0}$ will converge to $\hat{\underline{\mathbf{z}}}$ for any $\underline{\mathbf{x}}$ in a certain neighborhood of $\hat{\underline{\mathbf{x}}}$ by the continuity of T. This will be the case for any $\underline{\mathbf{x}}$, taking $\hat{\underline{\mathbf{x}}}$ as an accumulation point of $\{T^l \underline{\mathbf{x}}\}_{l \geq 0}$ which must be on the manifold $P_{11} = P_{22}$. In Section 1.6.3, we have shown that the sequence $\{T^l \hat{\underline{\mathbf{x}}}\}_{l \geq 0}$ converges to the polymorphic equilibrium $\hat{\underline{\mathbf{z}}}$. The last step is to show that the polymorphic equilibrium is locally stable. In this purpose, we employ the method exposed in Section 1.4.

We develop the linear part of the recursive equations (1.3) in the vicinity of the polymorphic equilibrium $(\hat{p},\hat{F})$. The matrix of the linear approximation is expressed as

$$\mathbf{M}=\begin{bmatrix} m_{11} & m_{12} \\ m_{21} & m_{22} \end{bmatrix}=\begin{bmatrix} \dfrac{2w}{2-(1-w)(1+\hat{F})} & 0 \\ 0 & \beta\left\{\dfrac{2w}{\left[2-(1-w)(1+\hat{F})\right]^2}\right\} \end{bmatrix},$$

using the still valid entries given in (1.13) and recalling that $\hat{p}=\hat{q}=\frac{1}{2}$. Since $-1<\hat{F}<1$, all the entries of **M** are found positive. The characteristic polynomial of **M** simply reads as

$$m(\lambda)=(\lambda-m_{11})(\lambda-m_{22}),$$

with strictly positive eigenvalues. Note that these two eigenvalues are continuous with respect to β and equal to 0 and $m_{11}>0$ for $\beta=0$. Moreover, $m_{11}<1$ if and only if $w<1$, which always holds in the case at hand. Thus, using arguments as in the proof of Result 1.5, it suffices to show that $m(0)>0$ and $m(1)>0$, for $0<\beta<1$, to prove that the greatest eigenvalue of **M** is smaller than 1. We have

$$m(0)=m_{11}m_{22}>0$$

and

$$m(1)=\frac{(1-w)(1-\hat{F})}{\left[2-(1-w)(1+\hat{F})\right]^3}H(\beta,\hat{F}),$$

where

$$H(\beta,F)=\left[2-(1-w)(1+F)\right]^2-2\beta w.$$

The sign of $m(1)$ depends upon the sign of $H(\beta,\hat{F})$. We must divide the subsequent analysis in two cases, $0<w<\frac{1}{2}$ and $\frac{1}{2}\le w<1$, even though they shall lead to the same result.

Before going any further, we have to outline an essential fact that concerns the value of F at equilibrium, that is,

$$\hat{F} = 4\hat{P}_{11} - 1 = \frac{1 + w(1-\beta) - \sqrt{[3 - w(1+\beta)]^2 - 8(1-w)}}{2(1-w)}.$$

For fixed $w > 0$, the value of $\hat{F}$ increases as β increases over the interval (0, 1). This is deduced by taking the derivative of $\hat{F}$ with respect to β, expressed as

$$\frac{\mathrm{d}}{\mathrm{d}\beta}\hat{F} = \frac{w(1+\hat{F})}{\sqrt{[3 - w(1+\beta)]^2 - 8(1-w)}} > 0. \qquad \text{(A.7)}$$

Let us now return to the function $H(\beta, \hat{F})$. In the case $0 < w < \frac{1}{2}$, when $\beta = 0$, the classical result asserts that $\hat{F} = 0$, since no inbreeding is generated by the panmictic model. When $\beta = 1$, the value of F at equilibrium becomes $\hat{F} = w/(1-w)$ (this value follows from Nagylaki, 1977). Easy computations yield

$$H(0, \hat{F}) = (1+w)^2 > 0 \quad \text{and} \quad H(1, \hat{F}) = 1 - 2w > 0.$$

Using (A.7), one can trivially verify that the derivative of $H(\beta, \hat{F})$ is such that

$$\frac{\mathrm{d}}{\mathrm{d}\beta}H(\beta, \hat{F}) = -2w - 2(1-w)\left[2 - (1-w)(1+\hat{F})\right]\left(\frac{\mathrm{d}}{\mathrm{d}\beta}\hat{F}\right) < 0. \qquad \text{(A.8)}$$

The sign of this derivative ensures that $H(\beta, \hat{F}) > 0$, for all $0 < \beta < 1$. Therefore, we conclude that $m(1) > 0$ in the case $0 < w < \frac{1}{2}$.

In the case $\frac{1}{2} \leq w < 1$, when $\beta = 0$, the above conclusions remain valid. However, when $\beta = 1$, the value of F at equilibrium is $\hat{F} = 1$. Direct calculations yield

$$H(0,\ 1) = (1+w)^2 > 0 \quad \text{and} \quad H(1,\ 1) = 2w(2w-1) \geq 0.$$

Using (A.8), we conclude that $H(\beta, \hat{F}) > 0$, for all $0 < \beta < 1$ and consequently that $m(1) > 0$ in the case $\frac{1}{2} \leq w < 1$. Therefore, we have proved that the greatest eigenvalue of **M** is smaller than 1 and consequently that the polymorphic equilibrium $(\hat{p}, \hat{F})$ is locally stable in the case $w < 1$.

Appendice B: Preuves et compléments du Chapitre 2

B.1 Proof of Result 2.1

For a better understanding of our analysis, we state the Perron-Frobenius theorem for primitive matrices (see, e.g., Seneta, 1981, or Gantmacher, 1959, for a proof).

Perron-Frobenius theorem. *Suppose* $\mathbf{M}$ *is a* $n \times n$ *non-negative primitive matrix. Then there exists an eigenvalue* ρ *such that:*

(a) ρ *is real, strictly positive and is a simple root of the characteristic equation of* $\mathbf{M}$;

(b) $\rho > |\lambda|$ *for every eigenvalue* $\lambda \neq \rho$;

(c) *associated to* ρ *are strictly positive left and right eigenvectors,* ξ *and* η*, which are unique to constant multiples; in fact,* ρ *is the only eigenvalue of* $\mathbf{M}$ *which admits strictly positive eigenvectors*;

(d) *as* $k \to \infty$, $\dfrac{\mathbf{M}^k}{\rho^k} \to \dfrac{\eta \xi^{\mathsf{T}}}{\langle \xi, \eta \rangle}$, *where* $\langle \xi, \eta \rangle = \sum_i \xi_i \eta_i$.

Since the non-negative matrix $\mathbf{M}(s)$ is supposed to be primitive, by assertion (c) of the Perron-Frobenius theorem, there exist strictly positive eigenvectors associated to $\rho(s)$, the greatest eigenvalue of $\mathbf{M}(s)$ in modulus. Let $\xi(s)^{\mathsf{T}} = (\xi_1(s),.....,\xi_n(s))$ and $\eta(s)^{\mathsf{T}} = (\eta_1(s),.....,\eta_n(s))$ be strictly positive left and right eigenvectors, respectively, associated to $\rho(s)$. For the sake of simplicity, assume that the scalar product of these eigenvectors equals 1, that is, $\langle \xi(s), \eta(s) \rangle = \sum_i \xi_i(s)\eta_i(s) = 1$. More explicitly, we have

$$\xi(s)^{\mathsf{T}}\mathbf{M}(s) = \rho(s)\xi(s)^{\mathsf{T}}$$

and (B.1)

$$\mathbf{M}(s)\eta(s) = \rho(s)\eta(s),$$

where the superscript T denotes matrix transposition. Taking the derivative with respect to s on both sides of the second equation in (B.1) (this is feasible since the entries of $\mathbf{M}(s)$ are supposed smooth enough), we obtain

$$\dot{\mathbf{M}}(s)\boldsymbol{\eta}(s) + \mathbf{M}(s)\dot{\boldsymbol{\eta}}(s) = \dot{\rho}(s)\boldsymbol{\eta}(s) + \rho(s)\dot{\boldsymbol{\eta}}(s).$$

Hence, multiplying on the left by $\boldsymbol{\xi}(s)^{\mathrm{T}}$, we find

$$\boldsymbol{\xi}(s)^{\mathrm{T}}\dot{\mathbf{M}}(s)\boldsymbol{\eta}(s) + \boldsymbol{\xi}(s)^{\mathrm{T}}\mathbf{M}(s)\dot{\boldsymbol{\eta}}(s) = \dot{\rho}(s)\boldsymbol{\xi}(s)^{\mathrm{T}}\boldsymbol{\eta}(s) + \rho(s)\boldsymbol{\xi}(s)^{\mathrm{T}}\dot{\boldsymbol{\eta}}(s). \qquad \text{(B.2)}$$

But, from the first equality in (B.1) and since $\boldsymbol{\xi}(s)^{\mathrm{T}}\boldsymbol{\eta}(s) = 1$, equation (B.2) reduces to

$$\dot{\rho}(s) = \boldsymbol{\xi}(s)^{\mathrm{T}}\dot{\mathbf{M}}(s)\boldsymbol{\eta}(s).$$

Developing $\rho(s)$ in Taylor series around 0 yields

$$\rho(s) = \rho(0) + \dot{\rho}(0)s + O(s^2), \qquad \text{(B.3)}$$

with $\dot{\rho}(0) = \boldsymbol{\xi}(0)^{\mathrm{T}}\dot{\mathbf{M}}(0)\boldsymbol{\eta}(0)$.

It remains to show that $\rho(0) = 1$. To this end, we express the frequency of the rare mutant gene in the population as $p = \mathbf{f}^{\mathrm{T}}\mathbf{x}$, where $\mathbf{f}$ denotes the vector of the rare mutant gene frequency in the different mutant types and $\mathbf{x}$ is the vector of the frequencies of the different types containing the rare mutant gene. With no selection in the population, that is, when $s = 0$, there is invariance of the allelic frequencies, that is, the allelic frequencies remain unchanged from one generation to the next (this is the first part of the Hardy-Weinberg law). Formally, we have $p' = \mathbf{f}^{\mathrm{T}}\mathbf{x}' = \mathbf{f}^{\mathrm{T}}\mathbf{x} = p$, and therefore, $\mathbf{f}^{\mathrm{T}}\mathbf{M}(0)\mathbf{x} = \mathbf{f}^{\mathrm{T}}\mathbf{x}$, which yields

$$\mathbf{f}^{\mathrm{T}}\mathbf{M}(0) = \mathbf{f}^{\mathrm{T}}, \quad \text{for all } \mathbf{x} \geq \mathbf{0}.$$

This implies that $\lambda = 1$ is one of the eigenvalues of $\mathbf{M}(0)$. But, since $\mathbf{f}$ has strictly positive entries by definition and that a strictly positive eigenvector is necessarily one associated to the greatest eigenvalue $\rho(0)$, this implies that $\rho(0) = 1$. Moreover, by part (c) of the Perron-Frobenius theorem, we have that $\xi(0)$, the left eigenvector of $\mathbf{M}(0)$, is a multiple of the vector $\mathbf{f}$. It will be assumed throughout, without loss of generality, that $\xi(0) = \mathbf{f}$ and $\sum_i \xi_i(s) = \sum_i f_i$, for every $s \geq 0$. This completes the proof of Result 2.1.

B.2 Proof of Result 2.2

As in the proof of Result 2.1, $\mathbf{M}(s)$ is non-negative and primitive. In the complex vector space $\mathbf{C}^n$, one can always represent the matrix $\mathbf{M}(s)$ in a Jordan canonical form, that is,

$$\mathbf{M}(s) = \mathbf{P}(s)\mathbf{J}(s)\mathbf{P}(s)^{-1}.$$

Let $\lambda_1(s), \lambda_2(s), \ldots, \lambda_n(s)$ be the eigenvalues (not necessarily distinct) of $\mathbf{M}(s)$. Let

$$\mathbf{P}(s) = [\varphi_1(s), \varphi_2(s), \ldots, \varphi_n(s)],$$
$$\mathbf{P}(s)^{-1} = [\psi_1(s), \psi_2(s), \ldots, \psi_n(s)]^{\mathrm{T}}.$$

By the Perron-Frobenius theorem, the right (and the left) eigenvectors associated to the greatest eigenvalue in modulus $\rho(s)$ of $\mathbf{M}(s)$ forms a one-dimensional subspace of $\mathbf{C}^n$. Without loss of generality, let $\lambda_1(s) = \rho(s)$, $\varphi_1(s) = \eta(s)$ and $\psi_1(s) = \xi(s)$. Then, we can write

$$\mathbf{M}(s) = [\eta(s), \varphi_2(s), \ldots, \varphi_n(s)] \begin{bmatrix} \rho(s) & \mathbf{0} \\ \mathbf{0} & \mathbf{B}(s) \end{bmatrix} [\xi(s), \psi_2(s), \ldots, \psi_n(s)]^{\mathrm{T}},$$

where $\mathbf{B}(s)$ is a $(n-1) \times (n-1)$ matrix formed of Jordan blocks associated to the eigenvalues of $\mathbf{M}(s)$ different from $\rho(s)$. Because the column vectors of $\mathbf{P}(s)$ form a

basis of the whole space, we can express each vector $\mathbf{x} \neq \mathbf{0}$ of the space as a linear combination of these vectors. Actually, we have

$$\mathbf{x} = c_1 \eta(s) + \sum_{i \geq 2} c_i \varphi_i(s), \tag{B.4}$$

where $c_1 = \xi(s)^{\mathrm{T}} \mathbf{x}$, $c_i = \psi_i(s)^{\mathrm{T}} \mathbf{x}$, for $i = 2, \ldots, n$, and at least one of the c_i is different from 0.

In the following, we shall use, for each $s > 0$ fixed, the norm $\|\cdot\|$ defined by $\|\mathbf{x}\| = \sum_i \xi_i(s)|x_i|$ for every vector $\mathbf{x}$. The norm of the matrix $\mathbf{M}(s)$ is defined as

$$\|\mathbf{M}(s)\| = \sup_{\mathbf{x} \neq 0} \frac{\|\mathbf{M}(s)\mathbf{x}\|}{\|\mathbf{x}\|}. \tag{B.5}$$

Note that

$$\|\mathbf{M}^k(s)\mathbf{x}\| \leq \|\mathbf{M}^k(s)\| \|\mathbf{x}\|, \tag{B.6}$$

for every vector $\mathbf{x}$ and every integer $k \geq 1$. We have also the following lemma.

Lemma 1. *For any integer* $k \geq 1$, $\|\mathbf{M}^k(s)\| = \rho^k(s)$.

Proof of lemma 1. Let $k = 1$. Using equation (B.5), we obtain

$$\begin{aligned}
\|\mathbf{M}(s)\| &= \sup_{\mathbf{x} \neq 0} \frac{\sum_i \xi_i(s) \left| \sum_j m_{ij}(s) x_j \right|}{\|\mathbf{x}\|} \\
&\leq \sup_{\mathbf{x} \neq 0} \frac{\sum_i \xi_i(s) \sum_j m_{ij}(s) |x_j|}{\|\mathbf{x}\|} \\
&= \sup_{\mathbf{x} \neq 0} \frac{\sum_j \sum_i \xi_i(s) m_{ij}(s) |x_j|}{\|\mathbf{x}\|} \\
&= \sup_{\mathbf{x} \neq 0} \frac{\sum_j \rho(s) \xi_j(s) |x_j|}{\|\mathbf{x}\|} \\
&= \rho(s) \sup_{\mathbf{x} \neq 0} \frac{\|\mathbf{x}\|}{\|\mathbf{x}\|} \\
&= \rho(s).
\end{aligned}$$

Moreover, letting $\mathbf{x} = \eta(s)$ in equation (B.6) gives

$$\rho(s) = \|\rho(s)\eta(s)\| = \|\mathbf{M}(s)\eta(s)\| \le \|\mathbf{M}(s)\|\,\|\eta(s)\| = \|\mathbf{M}(s)\|,$$

since $\|\eta(s)\| = 1$. The rest of the proof is easily achieved by induction on k.

A crucial result ensues from Lemma 1 and is provided below.

Lemma 2. *For* $\mathbf{x} \ge \mathbf{0}$, $\mathbf{x} \ne \mathbf{0}$ *sufficiently close to* $\mathbf{0}$, *we have* $\|\mathbf{x}'\| < \|\mathbf{x}\|$ *if* $\rho(s) < 1$ *and* $\|\mathbf{x}'\| > \|\mathbf{x}\|$ *if* $\rho(s) > 1$.

Proof of lemma 2. Taking the scalar product with $\xi(s)$ on both sides of equation (2.1) yields

$$\|\mathbf{x}'\| = \rho(s)\|\mathbf{x}\| + O(\|\mathbf{x}\|^2).$$

If $\rho(s) < 1$, then it suffices to choose $\|\mathbf{x}\|$ sufficiently small so that $O(\|\mathbf{x}\|^2) < (1 - \rho(s))\|\mathbf{x}\|$ to have $\|\mathbf{x}'\| < \|\mathbf{x}\|$. If $\rho(s) > 1$, then $\|\mathbf{x}'\| > \|\mathbf{x}\|$ as soon as $\|\mathbf{x}\|$ is small enough to have $O(\|\mathbf{x}\|^2) > (1 - \rho(s))\|\mathbf{x}\|$. This completes the proof of Lemma 2.

Now, let $\mathbf{x}^{(k)} > \mathbf{0}$ denote the vector of frequencies in the k^{th} generation. Then, iterating equation (2.1) gives

$$\mathbf{x}^{(k)} = \mathbf{M}^k(s)\mathbf{x}^{(0)} + \mathbf{M}^{k-1}(s)O(\|\mathbf{x}^{(0)}\|^2) + \mathbf{M}^{k-2}(s)O(\|\mathbf{x}^{(1)}\|^2) + \ldots + O(\|\mathbf{x}^{(k-1)}\|^2). \quad \text{(B.7)}$$

But the above expression can be simplified, as stated in the following result.

Lemma 3. *If* $\rho(s) < 1$, *then* $\mathbf{x}^{(k)} = \mathbf{M}^k(s)\mathbf{x}^{(0)} + O(\|\mathbf{x}^{(0)}\|^2)$, *for* $\mathbf{x}^{(0)}$ *sufficiently close to* $\mathbf{0}$, *where the function* $O(\|\mathbf{x}^{(0)}\|^2)$ *does not depend upon the value of k. On the other hand, if* $\rho(s) > 1$, *then* $\mathbf{x}^{(k)} = \mathbf{M}^k(s)\mathbf{x}^{(0)} + O(\|\mathbf{x}^{(k-1)}\|^2)$ *for* $\mathbf{x}^{(k-1)}$ *sufficiently close to* $\mathbf{0}$.

Proof of lemma 3. First, let us examine the case $\rho(s) < 1$. We shall show that the sum

$$S = \mathbf{M}^{k-1}(s)O(\|\mathbf{x}^{(0)}\|^2) + \mathbf{M}^{k-2}(s)O(\|\mathbf{x}^{(1)}\|^2) + \ldots + O(\|\mathbf{x}^{(k-1)}\|^2) \qquad \text{(B.8)}$$

in equation (B.7) is a function of order $\|\mathbf{x}^{(0)}\|^2$ and does not depend upon the value of k. Using Lemma 1 and Lemma 2, we have that

$$\begin{aligned}
\frac{\|S\|}{\|\mathbf{x}^{(0)}\|^2} &\le \frac{\|\mathbf{M}^{k-1}(s)\|\|O(\|\mathbf{x}^{(0)}\|^2)\| + \|\mathbf{M}^{k-2}(s)\|\|O(\|\mathbf{x}^{(1)}\|^2)\| + \ldots + \|O(\|\mathbf{x}^{(k-1)}\|^2)\|}{\|\mathbf{x}^{(0)}\|^2} \\
&= \rho^{k-1}(s)\frac{\|O(\|\mathbf{x}^{(0)}\|^2)\|}{\|\mathbf{x}^{(0)}\|^2} + \rho^{k-2}(s)\frac{\|O(\|\mathbf{x}^{(1)}\|^2)\|}{\|\mathbf{x}^{(1)}\|^2}\frac{\|\mathbf{x}^{(1)}\|^2}{\|\mathbf{x}^{(0)}\|^2} + \ldots + \frac{\|O(\|\mathbf{x}^{(k-1)}\|^2)\|}{\|\mathbf{x}^{(k-1)}\|^2}\frac{\|\mathbf{x}^{(k-1)}\|^2}{\|\mathbf{x}^{(0)}\|^2} \\
&\le \rho^{k-1}(s)\,c + \rho^{k-2}(s)\,c + \ \ldots\ + c \\
&\le \frac{c}{1-\rho(s)},
\end{aligned}$$

for some constant c, as soon as $\|\mathbf{x}^{(0)}\|^2$ is small enough. On the other hand, if $\rho(s) > 1$, the function in (B.8) can be shown to be of order $\|\mathbf{x}^{(k-1)}\|^2$ as long as $\|\mathbf{x}^{(k-1)}\|^2$ is small enough. This clearly shows that (B.8) depends upon k only in the case $\rho(s) > 1$. This completes the proof of Lemma 3.

Two other important results are provided below.

Lemma 4. *If* $\rho(s) < 1$, *then* $\mathbf{x}^{(k)} = \|\mathbf{x}^{(k)}\|(\eta(s) + O(s))$, *for k large enough. On the other hand, if* $\rho(s) > 1$, *the above equality remains valid for k large enough but not too large.*

Proof of lemma 4. Let us write $\mathbf{x}^{(0)} = \|\mathbf{x}^{(0)}\|\eta(s) + \left[\mathbf{x}^{(0)} - \|\mathbf{x}^{(0)}\|\eta(s)\right]$. Multiplying on the left by $\mathbf{M}^k(s)$ and using Lemma 3 in the case $\rho(s) < 1$, we find that

$$\mathbf{x}^{(k)} = \rho^k(s)\left\|\mathbf{x}^{(0)}\right\|\left[\eta(s) + \frac{\mathbf{M}^k(s)}{\rho^k(s)}\left(\frac{\mathbf{x}^{(0)}}{\left\|\mathbf{x}^{(0)}\right\|} - \eta(s)\right)\right] + O(\left\|\mathbf{x}^{(0)}\right\|^2).$$

But it can be shown, using (B.4) and assertion (d) of the Perron-Frobenius theorem, that

$$\nu = \frac{\mathbf{M}^k(s)}{\rho^k(s)}\left(\frac{\mathbf{x}^{(0)}}{\left\|\mathbf{x}^{(0)}\right\|} - \eta(s)\right) \to \mathbf{0}, \quad \text{as } k \to \infty,$$

uniformly for $\mathbf{x}^{(0)} \geq \mathbf{0}$, $\mathbf{x}^{(0)} \neq \mathbf{0}$. Thus, there exists an integer N such that, for $k \geq$ N, all the entries of ν are smaller than s in absolute value. If we let $\left\|\mathbf{x}^{(0)}\right\| < \left(\rho^{\mathrm{N}}(s)\right)s$, then $\mathbf{x}^{(\mathrm{N})} = \rho^{\mathrm{N}}(s)\left\|\mathbf{x}^{(0)}\right\|(\eta(s) + O(s))$. Therefore, $\left\|\mathbf{x}^{(\mathrm{N})}\right\| = \rho^{\mathrm{N}}(s)\left\|\mathbf{x}^{(0)}\right\|(1 + O(s))$, which implies that $\mathbf{x}^{(\mathrm{N})} = \left\|\mathbf{x}^{(\mathrm{N})}\right\|(\eta(s) + O(s))$. Finally, for $k \geq$ N, we conclude that $\mathbf{x}^{(k)} = \left\|\mathbf{x}^{(k)}\right\|(\eta(s) + O(s))$, since $\left\|\mathbf{x}^{(k-\mathrm{N})}\right\| \leq \left\|\mathbf{x}^{(0)}\right\| < \left(\rho^{\mathrm{N}}(s)\right)s$. The case $\rho(s) > 1$ is treated analogously, the difference being that k must be large enough so that all the entries of ν are bounded by s, but not too large so that $\left\|\mathbf{x}^{(k)}\right\| < \left(\rho^{\mathrm{N}}(s)\right)s$. This completes the proof of Lemma 4.

Lemma 5. *For s small enough, we have* $\|\mathbf{x}\| = p(1 + O(s))$.

Proof of lemma 5. For s small enough, $\mathbf{x} \geq \mathbf{0}$, $\mathbf{x} \neq \mathbf{0}$ and $p = \sum_i f_i x_i$, we can write

$$\|\mathbf{x}\| = \sum_i \xi_i(s) x_i = \sum_i (f_i + O(s)) x_i = p + O(s)\left[\frac{\sum_i x_i}{\sum_i f_i x_i}\right] p = p(1 + O(s)),$$

since $\sum_i x_i / \sum_i f_i x_i$ is the same for all multiples of $\mathbf{x}$ and continuous on the compact set $\mathbf{x} \geq \mathbf{0}$, $\mathbf{x} \neq \mathbf{0}$, $\|\mathbf{x}\| = 1$, and is therefore bounded. This completes the proof of Lemma 5.

We are now ready to complete the proof of Result 2.2. Using Lemma 5, equation (2.1) for s small enough can be expressed as

$$\mathbf{x}' = \mathbf{M}(s)\mathbf{x} + O(p^2). \tag{B.9}$$

Therefore, recalling that Δp is defined as the change in frequency of the rare mutant gene from one generation to the next, we get

$$\Delta p = p' - p = \mathbf{f}^{\mathrm{T}}(\mathbf{x}' - \mathbf{x}) = \mathbf{f}^{\mathrm{T}}(\mathbf{M}(s) - \mathbf{I})\mathbf{x} + O(p^2). \tag{B.10}$$

When $s = 0$, we know that $\Delta p = 0$ and, consequently, we must have $O(p^2) = 0$, which implies that $O(p^2)$ in (B.10) is in fact a function $O(p^2)$ s, if it is assumed smooth enough. Thus, using Lemma 5, equation (B.10) can be rewritten as

$$\begin{aligned}
\Delta p &= \mathbf{f}^{\mathrm{T}}(\mathbf{M}(s) - \mathbf{M}(0))\mathbf{x} + s\,O(p^2) \\
&= \mathbf{f}^{\mathrm{T}}\left(\dot{\mathbf{M}}(0)\,s + O(s^2)\right)\mathbf{x} + s\,O(p^2) \\
&= \mathbf{f}^{\mathrm{T}}\dot{\mathbf{M}}(0)\mathbf{x}\,s + \left(\mathbf{f}^{\mathrm{T}}O(s^2)\frac{\mathbf{x}}{\|\mathbf{x}\|}\right)\|\mathbf{x}\| + s\,O(p^2) \\
&= \mathbf{f}^{\mathrm{T}}\dot{\mathbf{M}}(0)\mathbf{x}\,s + p\,O(s^2) + s\,O(p^2).
\end{aligned}$$

Finally, for values of k as defined in Lemma 4, we conclude from Lemma 5 that

$$\begin{aligned}
p^{(k+1)} - p^{(k)} &= \mathbf{f}^{\mathrm{T}}\dot{\mathbf{M}}(0)\mathbf{x}^{(k)}s + p^{(k)}O(s^2) + s\,O(p^{(k)^2}) \\
&= \mathbf{f}^{\mathrm{T}}\dot{\mathbf{M}}(0)\left[\|\mathbf{x}^{(k)}\|(\eta(s) + O(s))\right]s + p^{(k)}O(s^2) + s\,O(p^{(k)^2}) \\
&= \mathbf{f}^{\mathrm{T}}\dot{\mathbf{M}}(0)\left[p^{(k)}(1 + O(s))(\eta(0) + O(s))\right]s + p^{(k)}O(s^2) + s\,O(p^{(k)^2}) \\
&= \mathbf{f}^{\mathrm{T}}\dot{\mathbf{M}}(0)\eta(0)p^{(k)}s + p^{(k)}O(s^2) + s\,O(p^{(k)^2}) \\
&= \dot{\rho}(0)p^{(k)}s + p^{(k)}O(s^2) + s\,O(p^{(k)^2}).
\end{aligned}$$

This completes the proof of Result 2.2.

B.3 Coefficients of regression for the partial sib-mating models

Let X be the random variable that gives the frequency of A_1 genes carried by the female of a mated couple chosen at random in a diploid population. The random variable Y is defined analogously for the male of the same mated couple. In the following, we shall use the fact that the inbreeding coefficient F is the coefficient of correlation between two uniting gametes, the value assigned to a gamete being the number, 0 or 1, of gene A_1 that it carries (Wright, 1922). If there is no selection and the population is at equilibrium, this coefficient is equal to the probability that the two uniting gametes are identical by descent (Malécot, 1948; see, e.g., Crow and Kimura, 1970). In the partial sib-mating model, it is known (Ghai, 1969) that $F = \beta/(4-3\beta)$.

Autosomal genes. When females and males are both diploid at the locus considered, let $X = (X_1 + X_2)/2$ and $Y = (Y_1 + Y_2)/2$, where subscript 1 refers to a female gamete and subscript 2 to a male gamete. Hence, the random variables X_1, X_2, Y_1 and Y_2 take on values 1 or 0 depending upon the gene A_1 is carried or not by the corresponding gamete. By definition, we have that

$$r = \frac{\mathrm{Cov}(X,Y)}{\sqrt{\mathrm{Var}(X)}\sqrt{\mathrm{Var}(Y)}} = \frac{\mathrm{Cov}(X_1+X_2, Y_1+Y_2)}{\mathrm{Var}(X_1+X_2)},$$

because Var(X) = Var(Y), since the frequency of A_1 at equilibrium is the same in both female and male populations. Therefore, we infer that

$$r = \frac{4\mathrm{Cov}(X_1,Y_1)}{2\mathrm{Var}(X_1)+2\mathrm{Cov}(X_1,X_2)} = \frac{2F}{1+F} = r_{Y\to X} = r_{X\to Y} = \frac{\beta}{2-\beta},$$

since $F = \dfrac{\mathrm{Cov}(X_1,X_2)}{\mathrm{Var}(X_1)} = \dfrac{\mathrm{Cov}(X_1,Y_1)}{\mathrm{Var}(X_1)}$. In the above equation, $r_{Y\to X}$ is the coefficient of regression of the frequency of A_1 genes carried by the male of a mated

couple (Y) on the frequency of A_1 genes carried by the female of this couple (X). Likewise, $r_{X\to Y}$ represents the coefficient of regression of the frequency of A_1 genes carried by the female of a mated couple (X) on the frequency of A_1 genes carried by the male of this couple (Y).

Sex-linked genes. This time, we define $X = (X_1 + X_2)/2$ and $Y = Y_1$, so that

$$r_{Y\to X} = \frac{\mathrm{Cov}(X,Y)}{\mathrm{Var}(X)} = \frac{2\mathrm{Cov}(X_1,Y_1)}{\mathrm{Var}(X_1)+\mathrm{Cov}(X_1,X_2)} = \frac{2F}{1+F} = \frac{\beta}{2-\beta},$$

$$r_{X\to Y} = \frac{\mathrm{Cov}(X,Y)}{\mathrm{Var}(Y)} = \frac{\mathrm{Cov}(X_1,Y_1)}{\mathrm{Var}(Y_1)} = F = \frac{\beta}{4-3\beta}.$$

B.4 Matrix of linear approximation for autosomal genes in partial sib-mating populations

$$
\begin{bmatrix}
\beta\left(1+d_{11}^{f}s+d_{11}^{m}s\right) & \frac{\beta}{4}\left(1+d_{11}^{f}s+d_{11}^{m}s\right) & \frac{\beta}{4}\left(1+d_{11}^{f}s+d_{11}^{m}s\right) & 0 & 0 & \frac{\beta}{16}\left(1+d_{11}^{f}s+d_{11}^{m}s\right) & 0 & 0 \\
0 & \frac{\beta}{4}\left(1+d_{12}^{f}s+d_{11}^{m}s\right) & \frac{\beta}{4}\left(1+d_{12}^{f}s+d_{11}^{m}s\right) & 0 & 0 & \frac{\beta}{8}\left(1+d_{12}^{f}s+d_{11}^{m}s\right) & 0 & 0 \\
0 & \frac{\beta}{4}\left(1+d_{11}^{f}s+d_{12}^{m}s\right) & \frac{\beta}{4}\left(1+d_{11}^{f}s+d_{12}^{m}s\right) & 0 & 0 & \frac{\beta}{8}\left(1+d_{11}^{f}s+d_{12}^{m}s\right) & 0 & 0 \\
(1-\beta)\left(1+d_{11}^{m}s\right) & \left(\frac{1-\beta}{2}\right)\left(1+d_{11}^{m}s\right) & \left(\frac{1-\beta}{2}\right)\left(1+d_{11}^{m}s\right) & 0 & 0 & \left(\frac{4-3\beta}{16}\right)\left(1+d_{11}^{m}s\right) & 0 & 0 \\
(1-\beta)\left(1+d_{11}^{f}s\right) & \left(\frac{1-\beta}{2}\right)\left(1+d_{11}^{f}s\right) & \left(\frac{1-\beta}{2}\right)\left(1+d_{11}^{f}s\right) & 0 & 0 & \left(\frac{4-3\beta}{16}\right)\left(1+d_{11}^{f}s\right) & 0 & 0 \\
0 & \frac{\beta}{4}\left(1+d_{12}^{f}s+d_{12}^{m}s\right) & \frac{\beta}{4}\left(1+d_{12}^{f}s+d_{12}^{m}s\right) & \beta\left(1+d_{12}^{f}s+d_{12}^{m}s\right) & \beta\left(1+d_{12}^{f}s+d_{12}^{m}s\right) & \frac{\beta}{4}\left(1+d_{12}^{f}s+d_{12}^{m}s\right) & \frac{\beta}{4}\left(1+d_{12}^{f}s+d_{12}^{m}s\right) & \frac{\beta}{4}\left(1+d_{12}^{f}s+d_{12}^{m}s\right) \\
0 & \left(\frac{1-\beta}{2}\right)\left(1+d_{12}^{m}s\right) & \left(\frac{1-\beta}{2}\right)\left(1+d_{12}^{m}s\right) & (1-\beta)\left(1+d_{12}^{m}s\right) & (1-\beta)\left(1+d_{12}^{m}s\right) & \left(\frac{4-3\beta}{8}\right)\left(1+d_{12}^{m}s\right) & \left(\frac{2-\beta}{4}\right)\left(1+d_{12}^{m}s\right) & \left(\frac{2-\beta}{4}\right)\left(1+d_{12}^{m}s\right) \\
0 & \left(\frac{1-\beta}{2}\right)\left(1+d_{12}^{f}s\right) & \left(\frac{1-\beta}{2}\right)\left(1+d_{12}^{f}s\right) & (1-\beta)\left(1+d_{12}^{f}s\right) & (1-\beta)\left(1+d_{12}^{f}s\right) & \left(\frac{4-3\beta}{8}\right)\left(1+d_{12}^{f}s\right) & \left(\frac{2-\beta}{4}\right)\left(1+d_{12}^{f}s\right) & \left(\frac{2-\beta}{4}\right)\left(1+d_{12}^{f}s\right)
\end{bmatrix}
$$

Appendice C: Matrices d'approximation linéaire pour les modèles d'accouplement frère-soeur partiel du Chapitre 3

C.1 Case of small differences in mixed strategies (autosomal locus)

$$
\begin{bmatrix}
\beta\left[1+\frac{2s}{K}d_{11}\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right] & \frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}2d_{11}A(h)+\\(d_{11}+d_{12})B(h)\end{pmatrix}\right] & 0 & \frac{\beta}{16}\left[1+\frac{s}{K}\begin{pmatrix}2d_{11}A(h)+\\(\frac{1}{2}d_{11}+d_{12})B(h)\end{pmatrix}\right] & 0 \\
0 & \frac{\beta}{2}\left[1+\frac{s}{K}(d_{11}+d_{12})\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right] & 0 & \frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}(d_{11}+d_{12})A(h)\\+(\frac{1}{2}d_{11}+d_{12})B(h)\end{pmatrix}\right] & 0 \\
2(1-\beta)\left[1+\frac{s}{K}d_{11}\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right] & (1-\beta)\left[1+\frac{s}{K}\begin{pmatrix}d_{11}A(h)+\\\frac{1}{2}(d_{11}+d_{12})B(h)\end{pmatrix}\right] & 0 & \begin{matrix}\frac{(1-\beta)}{2}\left[1+\frac{s}{K}\begin{pmatrix}d_{11}A(h)+\\(\frac{1}{4}d_{11}+\frac{1}{2}d_{12})B(h)\end{pmatrix}\right]\\+\frac{\beta}{8}\left[1+\frac{s}{K}\begin{pmatrix}d_{11}A(h)+\\(\frac{1}{2}d_{11}+d_{12})B(h)\end{pmatrix}\right]\end{matrix} & 0 \\
0 & \frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}2d_{12}A(h)+\\(d_{11}+d_{12})B(h)\end{pmatrix}\right] & \beta\left[1+\frac{2s}{K}d_{12}\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right] & \frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}2d_{12}A(h)+\\(\frac{1}{2}d_{11}+d_{12})B(h)\end{pmatrix}\right] & \frac{\beta}{4}\left[1+\frac{s}{K}d_{12}\begin{pmatrix}2A(h)\\+B(h)\end{pmatrix}\right] \\
0 & (1-\beta)\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\\frac{1}{2}(d_{11}+d_{12})B(h)\end{pmatrix}\right] & 2(1-\beta)\left[1+\frac{s}{K}d_{12}\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right] & \begin{matrix}(1-\beta)\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\(\frac{1}{4}d_{11}+\frac{1}{2}d_{12})B(h)\end{pmatrix}\right]\\+\frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\(\frac{1}{2}d_{11}+d_{12})B(h)\end{pmatrix}\right]\end{matrix} & \begin{matrix}(1-\beta)\left[1+\frac{s}{K}d_{12}\begin{pmatrix}A(h)+\\\frac{1}{2}B(h)\end{pmatrix}\right]\\+\frac{\beta}{2}\left[1+\frac{s}{K}d_{12}\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right]\end{matrix}
\end{bmatrix}
$$

C.2 Case of small differences in mixed strategies (sex-linked locus)

$$
\begin{bmatrix}
\beta\left[1+\frac{s}{K}(d_{11}+d_1)\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right] & \frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}(d_{11}+d_1)A(h)+\\ \frac{1}{2}(d_{11}+d_{12}+d_1)B(h)\end{pmatrix}\right] & 0 & 0 & 0 \\
0 & \frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}(d_{12}+d_1)A(h)+\\ \frac{1}{2}(d_{11}+d_{12}+d_1)B(h)\end{pmatrix}\right] & 0 & \beta\left[1+\frac{s}{K}(d_{12}+d_1)\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right] & \frac{\beta}{4}\left[1+\frac{s}{K}(d_{12}+d_1)\begin{pmatrix}A(h)+\\ \frac{1}{2}B(h)\end{pmatrix}\right] \\
(1-\beta)\left[1+\frac{s}{K}\begin{pmatrix}d_1A(h)+\\ \frac{1}{2}(d_{11}+d_1)B(h)\end{pmatrix}\right] & \frac{(1-\beta)}{2}\left[1+\frac{s}{K}\begin{pmatrix}d_1A(h)+\\ \frac{1}{4}(d_{11}+d_{12}+d_1)B(h)\end{pmatrix}\right] & 0 & (1-\beta)\left[1+\frac{s}{K}\begin{pmatrix}d_1A(h)+\\ \frac{1}{2}(d_{12}+d_1)B(h)\end{pmatrix}\right] & \begin{matrix}\frac{(1-\beta)}{2}\left[1+\frac{s}{K}\begin{pmatrix}d_1A(h)+\\ \frac{1}{4}(d_{12}+d_1)B(h)\end{pmatrix}\right]\\ +\frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}d_1A(h)+\\ \frac{1}{2}(d_{12}+d_1)B(h)\end{pmatrix}\right]\end{matrix} \\
(1-\beta)\left[1+\frac{s}{K}\begin{pmatrix}d_{11}A(h)+\\ \frac{1}{2}(d_{11}+d_1)B(h)\end{pmatrix}\right] & \begin{matrix}\frac{(1-\beta)}{2}\left[1+\frac{s}{K}\begin{pmatrix}d_{11}A(h)+\\ \frac{1}{4}(d_{11}+d_{12}+d_1)B(h)\end{pmatrix}\right]\\ +\frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}d_{11}A(h)+\\ \frac{1}{2}(d_{11}+d_{12}+d_1)B(h)\end{pmatrix}\right]\end{matrix} & 0 & 0 & 0 \\
0 & \begin{matrix}\frac{(1-\beta)}{2}\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\ \frac{1}{4}(d_{11}+d_{12}+d_1)B(h)\end{pmatrix}\right] & (1-\beta)\left[1+\frac{s}{K}d_{12}\begin{pmatrix}A(h)+\\ \frac{1}{2}B(h)\end{pmatrix}\right]\\ +\frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\ \frac{1}{2}(d_{11}+d_{12}+d_1)B(h)\end{pmatrix}\right] & +\beta\left[1+\frac{s}{K}d_{12}\begin{pmatrix}A(h)\\+B(h)\end{pmatrix}\right]\end{matrix} & (1-\beta)\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\ \frac{1}{2}(d_{12}+d_1)B(h)\end{pmatrix}\right] & \begin{matrix}\frac{(1-\beta)}{2}\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\ \frac{1}{4}(d_{12}+d_1)B(h)\end{pmatrix}\right]\\ +\frac{\beta}{4}\left[1+\frac{s}{K}\begin{pmatrix}d_{12}A(h)+\\ \frac{1}{2}(d_{12}+d_1)B(h)\end{pmatrix}\right]\end{matrix}
\end{bmatrix}
$$

C.3 Case of small differences in viabilities (autosomal locus)

$$
\begin{bmatrix}
\beta\left[1+2sK^{*}_{11\times11}\right] & \frac{\beta}{4}\left[1+s(K^{*}_{11\times11}+K^{*}_{11\times12})\right] & 0 & \frac{\beta}{16}\left[1+\frac{s}{2}(K^{*}_{11\times11}+2K^{*}_{11\times12}+K^{*}_{11\times22})\right] & 0 \\
0 & \frac{\beta}{2}\left[1+\frac{s}{2}\begin{pmatrix}K^{*}_{11\times11}+K^{*}_{11\times12}\\+K^{*}_{12\times11}+K^{*}_{12\times12}\end{pmatrix}\right] & 0 & \frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{*}_{11\times11}+2K^{*}_{11\times12}+K^{*}_{11\times22}\\+K^{*}_{12\times11}+2K^{*}_{12\times12}+K^{*}_{12\times22}\end{pmatrix}\right] & 0 \\
2(1-\beta)\left[1+sK^{*}_{11\times11}\right] & (1-\beta)\left[1+\frac{s}{2}(K^{*}_{11\times11}+K^{*}_{11\times12})\right] & 0 & \begin{matrix}\frac{(1-\beta)}{2}\left[1+\frac{s}{4}(K^{*}_{11\times11}+2K^{*}_{11\times12}+K^{*}_{11\times22})\right]\\+\frac{\beta}{8}\left[1+\frac{s}{4}\begin{pmatrix}K^{*}_{11\times11}+2K^{*}_{11\times12}+K^{*}_{11\times22}\\+K^{*}_{22\times11}+2K^{*}_{22\times12}\end{pmatrix}\right]\end{matrix} & 0 \\
0 & \frac{\beta}{4}\left[1+s(K^{*}_{12\times11}+K^{*}_{12\times12})\right] & \beta\left[1+2sK^{*}_{12\times12}\right] & \frac{\beta}{4}\left[1+\frac{s}{2}(K^{*}_{12\times11}+2K^{*}_{12\times12}+K^{*}_{12\times22})\right] & \frac{\beta}{4}\left[1+s(K^{*}_{12\times12}+K^{*}_{12\times22})\right] \\
0 & (1-\beta)\left[1+\frac{s}{2}(K^{*}_{12\times11}+K^{*}_{12\times12})\right] & 2(1-\beta)\left[1+sK^{*}_{12\times12}\right] & \begin{matrix}(1-\beta)\left[1+\frac{s}{4}(K^{*}_{12\times11}+2K^{*}_{12\times12}+K^{*}_{12\times22})\right]\\+\frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{*}_{12\times11}+2K^{*}_{12\times12}+K^{*}_{12\times22}\\+K^{*}_{22\times11}+2K^{*}_{22\times12}\end{pmatrix}\right]\end{matrix} & \begin{matrix}(1-\beta)\left[1+\frac{s}{2}(K^{*}_{12\times12}+K^{*}_{12\times22})\right]\\+\frac{\beta}{2}\left[1+\frac{s}{2}(K^{*}_{12\times12}+K^{*}_{12\times22}+K^{*}_{22\times12})\right]\end{matrix}
\end{bmatrix}
$$

C.4 Case of small differences in viabilities (sex-linked locus)

$$
\begin{bmatrix}
\beta\left[1+\frac{s}{2}\begin{pmatrix}K^{\bullet}_{11\times11}+K^{\bullet}_{11\times1}\\+K^{\bullet}_{1\times11}+K^{\bullet}_{1\times1}\end{pmatrix}\right] & \frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{\bullet}_{11\times11}+K^{\bullet}_{11\times12}+K^{\bullet}_{11\times1}+K^{\bullet}_{11\times2}\\+K^{\bullet}_{1\times11}+K^{\bullet}_{1\times12}+K^{\bullet}_{1\times1}+K^{\bullet}_{1\times2}\end{pmatrix}\right] & 0 & 0 & 0 \\
0 & \frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{\bullet}_{12\times11}+K^{\bullet}_{12\times12}+K^{\bullet}_{12\times1}+K^{\bullet}_{12\times2}\\+K^{\bullet}_{1\times11}+K^{\bullet}_{1\times12}+K^{\bullet}_{1\times1}+K^{\bullet}_{1\times2}\end{pmatrix}\right] & 0 & \beta\left[1+\frac{s}{2}\begin{pmatrix}K^{\bullet}_{12\times12}+K^{\bullet}_{12\times1}\\+K^{\bullet}_{1\times12}+K^{\bullet}_{1\times1}\end{pmatrix}\right] & \frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{\bullet}_{12\times12}+K^{\bullet}_{12\times22}+K^{\bullet}_{12\times1}+K^{\bullet}_{12\times2}\\+K^{\bullet}_{1\times12}+K^{\bullet}_{1\times22}+K^{\bullet}_{1\times1}+K^{\bullet}_{1\times2}\end{pmatrix}\right] \\
(1-\beta)\left[1+\frac{s}{2}\left(K^{\bullet}_{1\times11}+K^{\bullet}_{1\times1}\right)\right] & \frac{(1-\beta)}{2}\left[1+\frac{s}{4}\left(K^{\bullet}_{1\times11}+K^{\bullet}_{1\times12}+K^{\bullet}_{1\times1}+K^{\bullet}_{1\times2}\right)\right] & 0 & (1-\beta)\left[1+\frac{s}{2}\left(K^{\bullet}_{1\times12}+K^{\bullet}_{1\times1}\right)\right] & \frac{(1-\beta)}{2}\left[1+\frac{s}{4}\left(K^{\bullet}_{1\times12}+K^{\bullet}_{1\times22}+K^{\bullet}_{1\times1}+K^{\bullet}_{1\times2}\right)\right] \\
 & & & & +\frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{\bullet}_{22\times12}+K^{\bullet}_{22\times1}+K^{\bullet}_{1\times12}\\+K^{\bullet}_{1\times22}+K^{\bullet}_{1\times1}+K^{\bullet}_{1\times2}\end{pmatrix}\right] \\
(1-\beta)\left[1+\frac{s}{2}\left(K^{\bullet}_{11\times11}+K^{\bullet}_{11\times1}\right)\right] & \frac{(1-\beta)}{2}\left[1+\frac{s}{4}\left(K^{\bullet}_{11\times11}+K^{\bullet}_{11\times12}+K^{\bullet}_{11\times1}+K^{\bullet}_{11\times2}\right)\right] & 0 & 0 & 0 \\
 & +\frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{\bullet}_{11\times11}+K^{\bullet}_{11\times12}+K^{\bullet}_{11\times1}+K^{\bullet}_{11\times2}\\+K^{\bullet}_{2\times11}+K^{\bullet}_{2\times12}+K^{\bullet}_{2\times1}\end{pmatrix}\right] & & & \\
0 & \frac{(1-\beta)}{2}\left[1+\frac{s}{4}\left(K^{\bullet}_{12\times11}+K^{\bullet}_{12\times12}+K^{\bullet}_{12\times1}+K^{\bullet}_{12\times2}\right)\right] & (1-\beta)\left[1+\frac{s}{2}\left(K^{\bullet}_{12\times12}+K^{\bullet}_{12\times2}\right)\right] & (1-\beta)\left[1+\frac{s}{2}\left(K^{\bullet}_{12\times12}+K^{\bullet}_{12\times1}\right)\right] & \frac{(1-\beta)}{2}\left[1+\frac{s}{4}\left(K^{\bullet}_{12\times12}+K^{\bullet}_{12\times22}+K^{\bullet}_{12\times1}+K^{\bullet}_{12\times2}\right)\right] \\
 & +\frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{\bullet}_{12\times11}+K^{\bullet}_{12\times12}+K^{\bullet}_{12\times1}+K^{\bullet}_{12\times2}\\+K^{\bullet}_{2\times11}+K^{\bullet}_{2\times12}+K^{\bullet}_{2\times1}\end{pmatrix}\right] & +\beta\left[1+\frac{s}{2}\begin{pmatrix}K^{\bullet}_{12\times12}+K^{\bullet}_{12\times2}\\+K^{\bullet}_{2\times12}\end{pmatrix}\right] & & +\frac{\beta}{4}\left[1+\frac{s}{4}\begin{pmatrix}K^{\bullet}_{12\times12}+K^{\bullet}_{12\times22}+K^{\bullet}_{12\times1}\\+K^{\bullet}_{12\times2}+K^{\bullet}_{2\times12}+K^{\bullet}_{2\times1}\end{pmatrix}\right]
\end{bmatrix}
$$

Appendice D: Calcul des coefficients d'identité et d'apparentement utilisés dans les Chapitres 1, 2 et 3

D.1 Coefficients d'identité par descendance

En faisant fi de l'origine (paternelle ou maternelle) des gènes, il existe 9 situations d'identité, dites restreintes, entre les 4 gènes homologues de deux individus diploïdes I et J (Gillois, 1965, Jacquard, 1974). Dans le diagramme ci-dessous, chaque groupe de points représente les 4 gènes de I et J. Les gènes identiques par descendance sont reliés par une ligne. À chaque situation d'identité est assignée une probabilité $\Delta_i (i = 1, 2, \ldots, 9)$.

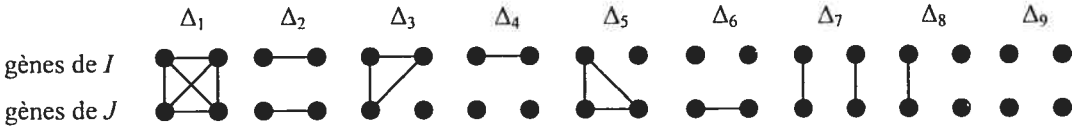

Figure D.1 Situations restreintes d'identité entre les gènes de I et J.

(i) Modèle avec autofécondation partielle

Soit $F^{(n)}$ le coefficient de consanguinité d'un individu choisi au hasard dans la population à la génération n. On peut facilement déduire la relation suivante

$$F^{(n+1)} = \alpha\left[F^{(n)} + \frac{1}{2}\left(1 - F^{(n)}\right)\right],$$

où α est la probabilité de se reproduire par autofécondation. Sous la condition initiale $F^{(0)} = 0$, on peut montrer que

$$F^{(n)} = \left(\frac{\alpha}{2-\alpha}\right)\left[1 - \left(\frac{\alpha}{2}\right)^n\right], \quad n \geq 0.$$

La valeur de $F^{(n)}$ à l'équilibre est donnée par

$$\hat{F} = \lim_{n\to\infty} F^{(n)} = \frac{\alpha}{2-\alpha}.$$

Dans le modèle avec autofécondation partielle, les 9 coefficients d'identité d'une génération donnée peuvent s'exprimer exclusivement en fonction de α et du coefficient de consanguinité de la génération précédente. Si I et J désignent deux individus de la génération $n + 1$ issus d'une même famille, ces coefficients deviennent

$$\Delta_1^{(n+1)} = \alpha F^{(n)} + \frac{\alpha}{8}\left(1-F^{(n)}\right), \qquad \Delta_2^{(n+1)} = \frac{\alpha}{8}\left(1-F^{(n)}\right), \qquad \Delta_3^{(n+1)} = \Delta_5^{(n+1)} = \frac{\alpha}{4}\left(1-F^{(n)}\right),$$

$$\Delta_4^{(n+1)} = \Delta_6^{(n+1)} = 0, \quad \Delta_7^{(n+1)} = \frac{\alpha}{4}\left(1-F^{(n)}\right) + (1-\alpha)\left[(F^{(n)})^2 + F^{(n)}\left(1-F^{(n)}\right) + \frac{1}{4}\left(1-F^{(n)}\right)^2\right],$$

$$\Delta_8^{(n+1)} = (1-\alpha)\left[F^{(n)}\left(1-F^{(n)}\right) + \frac{1}{2}\left(1-F^{(n)}\right)^2\right], \qquad \Delta_9^{(n+1)} = \frac{1}{4}(1-\alpha)\left(1-F^{(n)}\right)^2.$$

À l'équilibre, on obtient

$$\hat{\Delta}_1 = \frac{\alpha(1+3\alpha)}{4(2-\alpha)}, \quad \hat{\Delta}_2 = \frac{\alpha(1-\alpha)}{4(2-\alpha)}, \quad \hat{\Delta}_3 = \hat{\Delta}_5 = \frac{\alpha(1-\alpha)}{2(2-\alpha)}, \quad \hat{\Delta}_4 = \hat{\Delta}_6 = 0,$$

$$\hat{\Delta}_7 = \frac{(1-\alpha)\left(2+2\alpha-\alpha^2\right)}{2(2-\alpha)^2}, \quad \hat{\Delta}_8 = \frac{2(1-\alpha)^2}{(2-\alpha)^2}, \quad \hat{\Delta}_9 = \frac{(1-\alpha)^3}{(2-\alpha)^2}. \tag{D.1}$$

À l'aide des valeurs obtenues en (D.1), on peut facilement vérifier que les coefficients de consanguinité respectifs de I et J sont égaux:

$$\hat{F}_I = \hat{\Delta}_1 + \hat{\Delta}_2 + \hat{\Delta}_3 + \hat{\Delta}_4 = \frac{\alpha}{2-\alpha} \quad \text{et} \quad \hat{F}_J = \hat{\Delta}_1 + \hat{\Delta}_2 + \hat{\Delta}_5 + \hat{\Delta}_6 = \frac{\alpha}{2-\alpha}.$$

De plus, on peut déterminer le coefficient de parenté f_{IJ} à l'équilibre, soit

$$\hat{f}_{IJ} = \hat{\Delta}_1 + \tfrac{1}{2}\left(\hat{\Delta}_3 + \hat{\Delta}_5 + \hat{\Delta}_7\right) + \tfrac{1}{4}\hat{\Delta}_8 = \frac{1+\alpha}{2(2-\alpha)}.$$

On peut également exprimer le coefficient de parenté à l'aide du coefficient de consanguinité, de sorte qu'à la génération n, on trouve que

$$f_{IJ}^{(n)} = \frac{1+\alpha}{2(2-\alpha)}\left[1-\left(\frac{\alpha}{2}\right)^n\right], \qquad n \geq 0.$$

(ii) Modèle avec accouplement frère-soeur partiel: cas diploïde

Dans ce modèle, le coefficient de consanguinité ne suffit pas pour décrire le processus itératif des coefficients d'identité d'une génération à la suivante. Supposons qu'un accouplement frère-sœur se réalise avec probabilité β. Soit $F^{(n)}$ le coefficient de consanguinité d'un individu choisi au hasard dans la population à la génération n. On peut déduire les équations de récurrence suivantes entre deux individus de la génération $n+1$ issus d'une même famille:

$$\Delta_1^{(n+1)} = \beta\left(\Delta_1^{(n)} + \frac{1}{4}\Delta_3^{(n)} + \frac{1}{4}\Delta_5^{(n)} + \frac{1}{8}\Delta_7^{(n)} + \frac{1}{16}\Delta_8^{(n)}\right), \qquad \Delta_2^{(n+1)} = \frac{\beta}{8}\Delta_7^{(n)},$$

$$\Delta_3^{(n+1)} = \Delta_5^{(n+1)} = \beta\left(\frac{1}{4}\Delta_3^{(n)} + \frac{1}{4}\Delta_5^{(n)} + \frac{1}{4}\Delta_7^{(n)} + \frac{1}{8}\Delta_8^{(n)}\right), \qquad \Delta_4^{(n+1)} = \Delta_6^{(n+1)} = \frac{\beta}{16}\Delta_8^{(n)}, \tag{D.2}$$

$$\begin{aligned}\Delta_7^{(n+1)} = {} & \beta\left(\Delta_2^{(n)} + \frac{1}{4}\Delta_3^{(n)} + \frac{1}{2}\Delta_4^{(n)} + \frac{1}{4}\Delta_5^{(n)} + \frac{1}{2}\Delta_6^{(n)} + \frac{1}{4}\Delta_7^{(n)} + \frac{3}{16}\Delta_8^{(n)} + \frac{1}{4}\Delta_9^{(n)}\right) \\ & + (1-\beta)\left[(F^{(n)})^2 + F^{(n)}\left(1-F^{(n)}\right) + \frac{1}{4}\left(1-F^{(n)}\right)^2\right],\end{aligned}$$

$$\Delta_8^{(n+1)} = \beta\left(\frac{1}{2}\Delta_4^{(n)} + \frac{1}{2}\Delta_6^{(n)} + \frac{3}{8}\Delta_8^{(n)} + \frac{1}{2}\Delta_9^{(n)}\right) + (1-\beta)\left[F^{(n)}\left(1-F^{(n)}\right) + \frac{1}{2}\left(1-F^{(n)}\right)^2\right],$$

$$\Delta_9^{(n+1)} = \frac{\beta}{4}\Delta_9^{(n)} + \frac{1}{4}(1-\beta)\left(1-F^{(n)}\right)^2.$$

Le coefficient de consanguinité d'un rejeton I' à la génération n est donnée par la relation

$$F_{I'}^{(n)} = \beta f_{IJ}^{(n-1)}, \tag{D.3}$$

où I et J représentent les parents de I'. Le coefficient de parenté de deux rejetons I' et J' issus d'une même famille peut s'écrire

$$f_{I'J'}^{(n)} = \beta\left[\frac{1}{4} + \frac{1}{4}F_I^{(n-1)} + \frac{1}{2}f_{IJ}^{(n-1)}\right] + (1-\beta)\left[\frac{1}{4} + \frac{1}{4}F_I^{(n-1)}\right],$$

ou, de manière équivalente, comme

$$f_{I'J'}^{(n)} = \frac{1}{4} + \frac{\beta}{2}f_{IJ}^{(n-1)} + \frac{\beta}{4}f_{IJ}^{(n-2)}, \quad n \geq 2. \tag{D.4}$$

L'équation (D.4) forme une équation aux différences finies d'ordre 2. Sous les conditions initiales $f_{IJ}^{(0)} = 0$ and $f_{IJ}^{(1)} = 1/4$, on obtient la solution suivante:

$$f_{IJ}^{(n)} = \frac{1}{4-3\beta} - \left[\frac{2\sqrt{\beta(\beta+4)} + (\beta+4)}{2(4-3\beta)(\beta+4)}\right]\lambda_1^n + \left[\frac{2\sqrt{\beta(\beta+4)} - (\beta+4)}{2(4-3\beta)(\beta+4)}\right]\lambda_2^n, \quad n \geq 0$$

où

$$\lambda_1 = \frac{\beta + \sqrt{\beta(\beta+4)}}{4} \quad \text{et} \quad \lambda_2 = \frac{\beta - \sqrt{\beta(\beta+4)}}{4}.$$

Puisqu'on veut calculer les coefficients d'identité à l'équilibre, on trouve d'abord la valeur du coefficient de parenté à l'équilibre, soit

$$\hat{f}_{IJ} = \lim_{n\to\infty} f_{IJ}^{(n)} = \frac{1}{4-3\beta}, \tag{D.5}$$

car $|\lambda_1|, |\lambda_2| < 1$, et on déduit, à partir de (D.3), que

$$\hat{F}_I = \lim_{n\to\infty} F_I^{(n)} = \frac{\beta}{4-3\beta}, \tag{D.6}$$

En substituant la valeur obtenue en (D.6) dans (D.2) et en solutionnant ce système d'équations linéaires pour Δ_i (i = 1, 2, ..., 9), on obtient les coefficients d'identité à l'équilibre entre deux individus issus de la même famille:

$$\hat{\Delta}_1 = \frac{\beta(2+\beta)}{(2-\beta)(4-\beta)(4-3\beta)}, \qquad \hat{\Delta}_2 = \frac{\beta(1-\beta)(32-24\beta+2\beta^2-\beta^3)}{(2-\beta)(4-\beta)(4-3\beta)^2(8+\beta)},$$

$$\hat{\Delta}_3 = \hat{\Delta}_5 = \frac{4\beta(1-\beta)}{(2-\beta)(4-\beta)(4-3\beta)}, \quad \hat{\Delta}_4 = \hat{\Delta}_6 = \frac{4\beta(1-\beta)^2(8-4\beta-\beta^2)}{(2-\beta)(4-\beta)(4-3\beta)^2(8+\beta)}, \tag{D.7}$$

$$\hat{\Delta}_7 = \frac{8(1-\beta)(32-24\beta+2\beta^2-\beta^3)}{(2-\beta)(4-\beta)(4-3\beta)^2(8+\beta)},$$

$$\hat{\Delta}_8 = \frac{64(1-\beta)^2(8-4\beta-\beta^2)}{(2-\beta)(4-\beta)(4-3\beta)^2(8+\beta)}, \qquad \hat{\Delta}_9 = \frac{16(1-\beta)^3}{(4-\beta)(4-3\beta)^2}.$$

(iii) Modèle avec accouplement frère-soeur partiel: cas haplo-diploïde

Dans le cas d'un locus lié au sexe (*sex-linked locus*) ou d'une population haplo-diploïde, il est nécessaire de distinguer le sexe des individus. Soient I une femelle diploïde et J un mâle haploïde. Les situations d'identité possibles entre les 4

gènes homologues de deux femelles I_1 et I_2 demeurent correctement décrites à la Figure D.1. Toutefois, les situations d'identité entre les 3 gènes homologues d'une femelle I et d'un mâle J, d'une part, et entre les 2 gènes homologues de deux mâles J_1 et J_2, d'autre part, sont décrites à la Figure D.2 ci-dessous.

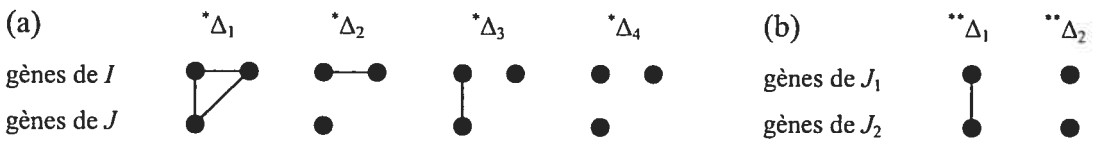

Figure D.2 (a) Situations restreintes d'identité entre les gènes d'une femelle I et d'un mâle J. (b) Situations restreintes d'identité entre les gènes de deux mâles J_1 et J_2.

De façon analogue au cas diploïde, on peut développer les équations de récurrence des coefficients d'identité entre deux individus issus de la même famille, en distinguant cependant le sexe des individus. Ces équations sont

- pour une paire formée d'une femelle et de sa soeur,

$$\Delta_1^{(n+1)} = \beta\left[{}^{*}\Delta_1^{(n)} + \frac{1}{4}{}^{*}\Delta_3^{(n)}\right], \qquad \Delta_3^{(n+1)} = \Delta_5^{(n+1)} = \frac{\beta}{4}{}^{*}\Delta_3^{(n)},$$

$$\Delta_7^{(n+1)} = \beta\left[{}^{*}\Delta_2^{(n)} + \frac{1}{4}{}^{*}\Delta_3^{(n)} + \frac{1}{2}{}^{*}\Delta_4^{(n)}\right] + \frac{1}{2}(1-\beta)\left[F_I^{(n)} + \frac{1}{2}\left(1 - F_I^{(n)}\right)\right],$$

$$\Delta_8^{(n+1)} = \frac{\beta}{2}{}^{*}\Delta_4^{(n)} + \frac{1}{2}(1-\beta)\left(1 - F_I^{(n)}\right), \qquad \Delta_2^{(n+1)} = \Delta_4^{(n+1)} = \Delta_6^{(n+1)} = \Delta_9^{(n+1)} = 0;$$

- pour une paire formée d'une femelle et de son frère (ou d'un mâle et de sa sœur),

$${}^{*}\Delta_1^{(n+1)} = \beta\left[{}^{*}\Delta_1^{(n)} + \frac{1}{4}{}^{*}\Delta_3^{(n)}\right], \qquad {}^{*}\Delta_2^{(n+1)} = \frac{\beta}{4}{}^{*}\Delta_3^{(n)},$$

$${}^{*}\Delta_3^{(n+1)} = \beta\left[{}^{*}\Delta_2^{(n)} + \frac{1}{2}{}^{*}\Delta_3^{(n)} + \frac{1}{2}{}^{*}\Delta_4^{(n)}\right] + \frac{1}{2}(1-\beta)\left[F_I^{(n)} + \frac{1}{2}\left(1 - F_I^{(n)}\right)\right],$$

$$ {}^{*}\Delta_4^{(n+1)} = \frac{\beta}{2}{}^{*}\Delta_4^{(n)} + \frac{1}{2}(1-\beta)\left(1-F_I^{(n)}\right), $$

- pour une paire formée d'un mâle et de son frère,

$$ {}^{**}\Delta_1^{(n+1)} = \beta\left[{}^{*}\Delta_1^{(n)} + {}^{*}\Delta_2^{(n)} + \frac{1}{2}{}^{*}\Delta_3^{(n)} + \frac{1}{2}{}^{*}\Delta_4^{(n)}\right] + \frac{1}{2}(1-\beta)\left[F_I^{(n)} + \frac{1}{2}\left(1-F_I^{(n)}\right)\right], $$

$$ {}^{**}\Delta_2^{(n+1)} = \frac{\beta}{2}\left[{}^{*}\Delta_3^{(n)} + {}^{*}\Delta_4^{(n)}\right] + \frac{1}{2}(1-\beta)\left(1-F_I^{(n)}\right), $$

où $F_I^{(n)}$ désigne le coefficient de consanguinité de la mère I des deux individus (par convention, le coefficient de consanguinité d'un mâle haploïde vaut 1). Un examen attentif de ces équations permet de constater que tous les coefficients d'identité, de la génération courante, entre deux individus issus de la même famille peuvent s'exprimer en termes des coefficients d'identité d'une paire frère/sœur de la génération précédente et du coefficient de consanguinité de leur mère. De plus, les équations (D.3) et (D.4) restent valides pour un rejeton femelle I' et un rejeton mâle J' engendrés par une femelle I et un mâle J. Conséquemment, en s'appuyant sur les limites obtenues en (D.5) et (D.6), on trouve les coefficients d'identité à l'équilibre pour une paire frère/sœur:

$$ {}^{*}\hat{\Delta}_1 = \frac{\beta}{(2-\beta)(4-3\beta)}, \qquad {}^{*}\hat{\Delta}_2 = \frac{\beta(1-\beta)}{(2-\beta)(4-3\beta)}, $$

$$ {}^{*}\hat{\Delta}_3 = \frac{4(1-\beta)}{(2-\beta)(4-3\beta)}, \qquad {}^{*}\hat{\Delta}_4 = \frac{4(1-\beta)^2}{(2-\beta)(4-3\beta)}. \tag{D.8} $$

Par la suite, les autres coefficients d'identité s'obtiennent facilement:

$$\hat{\Delta}_1 = \frac{\beta}{(2-\beta)(4-3\beta)}, \quad \hat{\Delta}_2 = \hat{\Delta}_4 = \hat{\Delta}_6 = \hat{\Delta}_9 = 0, \quad \hat{\Delta}_3 = \hat{\Delta}_5 = \frac{\beta(1-\beta)}{(2-\beta)(4-3\beta)},$$

$$\hat{\Delta}_7 = \frac{(1-\beta)(4-\beta)}{(2-\beta)(4-3\beta)}, \quad \hat{\Delta}_8 = \frac{4(1-\beta)^2}{(2-\beta)(4-3\beta)}, \quad {}^{**}\hat{\Delta}_1 = \frac{2-\beta}{4-3\beta}, \quad {}^{**}\hat{\Delta}_2 = \frac{2(1-\beta)}{4-3\beta}. \tag{D.9}$$

À partir des valeurs obtenues en (D.8) et (D.9), on tire le coefficient de parenté à l'équilibre entre deux sœurs, soit

$$\hat{f}_{I_1 I_2} = \hat{\Delta}_1 + \tfrac{1}{2}\left(\hat{\Delta}_3 + \hat{\Delta}_5 + \hat{\Delta}_7\right) + \tfrac{1}{4}\hat{\Delta}_8 = \frac{3-\beta}{2(4-3\beta)}, \tag{D.10}$$

et le coefficient de parenté à l'équilibre entre deux frères, soit

$$\hat{f}_{J_1 J_2} = {}^{**}\hat{\Delta}_1 = \frac{2-\beta}{4-3\beta}. \tag{D.11}$$

D.2 Coefficients d'apparentement

(i) Cas diploïde

Pour obtenir l'expression générale de ce coefficient, on emploie une méthodologie basée sur l'approche de Michod et Hamilton (1980). Soient p_I et p_J la fréquence du gène A_1 dans les génotypes respectifs des individus I et J. Les quantités G_I et G_J définissent les valeurs génotypiques respectives de I et J. $P_{kl\times mn}$ représente la distribution conjointe des génotypes A_kA_l et A_mA_n de I et J, respectivement. La distribution marginale des génotypes de I et J dans la population sont données par $P_{kl\bullet}$ et $P_{\bullet mn}$, respectivement. Toutes ces quantités sont décrites de façon détaillée dans le Tableau D.1 (adapté du Tableau 1 de Michod et Hamilton, 1980).

Tableau D.1 Distributions conjointe et marginales des génotypes de deux individus *I* et *J*, avec la fréquence du gène A_1 et la valeur génotypique correspondantes.

I \ *J*		p_J	1	½	0	
		G_J	h_{11}	h_{12}	h_{22}	
p_I	G_I	génotype	A_1A_1	A_1A_2	A_2A_2	
1	h_{11}	A_1A_1	$P_{11\times11}$	$P_{11\times12}$	$P_{11\times22}$	$P_{11\bullet} = p^2 + F_I pq$
½	h_{12}	A_1A_2	$P_{12\times11}$	$P_{12\times12}$	$P_{12\times22}$	$P_{12\bullet} = 2pq(1 - F_I)$
0	h_{22}	A_2A_2	$P_{22\times11}$	$P_{22\times12}$	$P_{22\times22}$	$P_{22\bullet} = q^2 + F_I pq$
			$P_{\bullet11} = p^2 + F_J pq$	$P_{\bullet12} = 2pq(1 - F_J)$	$P_{\bullet22} = q^2 + F_J pq$	1

Dans le Tableau D.1, p désigne la fréquence du gène A_1 et $q = 1 - p$ la fréquence du gène A_2 dans la population. Les fréquences $P_{kl\times mn}$ peuvent être exprimées en fonction de p, q et des coefficients d'identité Δ_i illustrés à la Figure D.1 (pour plus de détails, voir par exemple, Jacquard, 1974, Elston et Lange, 1976, Michod et Hamilton 1980). Ainsi, on peut écrire

$$P_{11\times11} = \Delta_1 p + (\Delta_2 + \Delta_3 + \Delta_5 + \Delta_7)p^2 + (\Delta_4 + \Delta_6 + \Delta_8)p^3 + \Delta_9 p^4,$$

$$P_{11\times12} = pq\left[\Delta_3 + (2\Delta_4 + \Delta_8)p + 2\Delta_9 p^2\right], \quad P_{12\times11} = pq\left[\Delta_5 + (2\Delta_6 + \Delta_8)p + 2\Delta_9 p^2\right],$$

$$P_{11\times22} = pq(\Delta_2 + \Delta_4 q + \Delta_6 p + \Delta_9 pq), \quad P_{22\times11} = pq(\Delta_2 + \Delta_4 p + \Delta_6 q + \Delta_9 pq), \tag{D.12}$$

$$P_{12\times12} = pq(2\Delta_7 + \Delta_8 + 4\Delta_9 pq),$$

$$P_{12\times22} = pq\left[\Delta_5 + (2\Delta_6 + \Delta_8)q + 2\Delta_9 q^2\right], \quad P_{22\times12} = pq\left[\Delta_3 + (2\Delta_4 + \Delta_8)q + 2\Delta_9 q^2\right],$$

$$P_{22\times22} = \Delta_1 q + (\Delta_2 + \Delta_3 + \Delta_5 + \Delta_7)q^2 + (\Delta_4 + \Delta_6 + \Delta_8)q^3 + \Delta_9 q^4.$$

Il faut rappeler que les équations en (D.12) sont rigoureusement exactes seulement en absence de sélection. Toutefois, sous l'hypothèse de sélection faible, on considère généralement que ces équations sont approximativement exactes. Les fréquences $P_{kl\bullet}$ et $P_{\bullet mn}$ apparaissant dans le Tableau D.1 sont facilement déduites à partir des fréquences conjointes (D.12), et où les coefficients de consanguinité respectifs de I et J sont donnés par

$$F_I = \Delta_1 + \Delta_2 + \Delta_3 + \Delta_4 \quad \text{et} \quad F_J = \Delta_1 + \Delta_2 + \Delta_5 + \Delta_6 .$$

Dans les modèles avec sélection de parentèle, le coefficient d'apparentement entre un "donneur" I et un "bénéficiaire" J est habituellement défini par (voir, par exemple, Michod et Hamilton, 1980, Lessard, 1992)

$$R_{I \to J} = \frac{\mathrm{Cov}(p_J, G_I)}{\mathrm{Cov}(p_I, G_I)}.$$

Afin d'obtenir une formule pour $R_{I \to J}$ spécifique à la notation employée au Tableau D.1, il faut d'abord calculer les espérances suivantes:

$$E[p_I] = P_{11\bullet} + \tfrac{1}{2} P_{12\bullet} = p, \tag{D.13a}$$

$$E[p_J] = P_{\bullet 11} + \tfrac{1}{2} P_{\bullet 12} = p, \tag{D.13b}$$

$$\begin{aligned} E[G_I] &= h_{11} P_{11\bullet} + h_{12} P_{12\bullet} + h_{22} P_{22\bullet} \\ &= h_{11} p^2 + 2h_{12} pq + h_{22} q^2 + F_I pq(h_{11} - 2h_{12} + h_{22}), \end{aligned} \tag{D.14a}$$

$$\begin{aligned} E[G_J] &= h_{11} P_{\bullet 11} + h_{12} P_{\bullet 12} + h_{22} P_{\bullet 22} \\ &= h_{11} p^2 + 2h_{12} pq + h_{22} q^2 + F_J pq(h_{11} - 2h_{12} + h_{22}). \end{aligned} \tag{D.14b}$$

De même, on calcule

$$E[p_J G_I] = h_{11} P_{11\times 11} + h_{12} P_{12\times 11} + h_{22} P_{22\times 11} + \tfrac{1}{2}\left(h_{11} P_{11\times 12} + h_{12} P_{12\times 12} + h_{22} P_{22\times 12}\right). \tag{D.15}$$

En incorporant les équations (D.12) dans (D.15), on obtient

$$E[p_J G_I] = p\begin{bmatrix}\delta_{IJ}h_{11} + \gamma_{IJ}(h_{11}p + h_{12}q) + (\Delta_2 + \tfrac{1}{2}\Delta_3 + \Delta_4)(h_{11}p + h_{22}q) \\ + (\Delta_6 + \tfrac{1}{2}\Delta_8 + \Delta_9)(h_{11}p^2 + 2h_{12}pq + h_{22}q^2)\end{bmatrix}, \qquad \text{(D.16)}$$

où

$$\delta_{IJ} = \Delta_1 + \tfrac{1}{2}\Delta_3 \quad \text{et} \quad \gamma_{IJ} = \Delta_5 + \Delta_7 + \tfrac{1}{2}\Delta_8. \qquad \text{(D.17)}$$

Le coefficient δ_{IJ} représente la probabilité qu'un gène choisi au hasard chez J soit identique par descendance à tous les gènes de I au même locus, tandis que γ_{IJ} représente la probabilité qu'un gène choisi au hasard chez J soit identique par descendance à un et un seul gène de I au même locus (Lessard, 1992). En utilisant (D.16), (D.13b), (D.14a) et en réorganisant les termes, on trouve que

$$\begin{aligned}\mathrm{Cov}(p_J, G_I) &= E[p_J G_I] - E[p_J]E[G_I] \\ &= pq[(h_{11} - h_{12})(\delta_{IJ} + p\gamma_{IJ}) + (h_{12} - h_{22})(\delta_{IJ} + q\gamma_{IJ})].\end{aligned} \qquad \text{(D.18)}$$

Ensuite, on détermine sans peine que

$$\begin{aligned}E[p_I G_I] &= h_{11}P_{11\bullet} + \tfrac{1}{2}h_{12}P_{12\bullet} \\ &= h_{11}p^2 + h_{12}pq + F_I pq(h_{11} - h_{12}),\end{aligned}$$

ce qui, avec les équations (D.13a) et (D.14a), donne

$$\begin{aligned}\mathrm{Cov}(p_I, G_I) &= E[p_I G_I] - E[p_I]E[G_I] \\ &= pq\{(h_{11} - h_{12})[F_I + p(1 - F_I)] + (h_{12} - h_{22})[F_I + q(1 - F_I)]\} \\ &= pq[(h_{11} - h_{12})(\delta_{II} + p\gamma_{II}) + (h_{12} - h_{22})(\delta_{II} + q\gamma_{II})],\end{aligned} \qquad \text{(D.19)}$$

en observant que

$$\delta_{II} = F_I = \Delta_1 + \Delta_2 + \Delta_3 + \Delta_4 \quad \text{et} \quad \gamma_{II} = 1 - F_I = \Delta_5 + \Delta_6 + \Delta_7 + \Delta_8 + \Delta_9. \qquad \text{(D.20)}$$

Finalement, le rapport de (D.18) sur (D.19) conduit directement à

$$R_{I\to J} = \frac{(h_{11}-h_{12})(\delta_{IJ}+p\gamma_{IJ})+(h_{12}-h_{22})(\delta_{IJ}+q\gamma_{IJ})}{(h_{11}-h_{12})(\delta_{II}+p\gamma_{II})+(h_{12}-h_{22})(\delta_{II}+q\gamma_{II})}. \qquad \text{(D.21)}$$

(ii) Cas haplo-diploïde

Par analogie au cas diploïde, on peut développer des coefficients d'apparentement entre des individus dont la ploïdie diffère au locus étudié. L'approche proposée requiert cependant l'emploi des coefficients d'identité décrits plus haut à la Figure D.2. Rappelons que I désigne une femelle diploïde et J un mâle haploïde. Le Tableau D.2 fournit toutes les informations nécessaires afin d'évaluer les coefficients d'apparentement entre une femelle et un mâle d'une part, et entre deux mâles d'autre part. Il faut noter que le coefficient d'apparentement exprimé en (D.21) demeure valide pour deux femelles diploïdes, mais l'égalité $R_{I\to J} = R_{J\to I}$ n'est généralement pas vérifiée pour une femelle diploïde I et un mâle haploïde J.

Tableau D.2 Distributions conjointe et marginales des génotypes (a) d'une femelle I et d'un mâle J, (b) de deux mâles J_1 et J_2, avec la fréquence du gène A_1 et la valeur génotypique correspondantes.

(a)

J / I		p_J	1	0	
		G_J	h_1	h_2	
p_I	G_I	génotype	A_1	A_2	
1	h_{11}	A_1A_1	$P_{11\times1}$	$P_{11\times2}$	$P_{11\bullet} = p^2 + F_I pq$
½	h_{12}	A_1A_2	$P_{12\times1}$	$P_{12\times2}$	$P_{12\bullet} = 2pq(1-F_I)$
0	h_{22}	A_2A_2	$P_{22\times1}$	$P_{22\times2}$	$P_{22\bullet} = q^2 + F_I pq$
			$P_{\bullet1} = p$	$P_{\bullet2} = q$	1

(b)

J_2 / J_1		p_{J_2}	1	0	
		G_{J_2}	h_1	h_2	
p_{J_1}	G_{J_1}	génotype	A_1	A_2	
1	h_1	A_1	$P_{1\times1}$	$P_{1\times2}$	$P_{1\bullet} = p$
0	h_2	A_2	$P_{2\times1}$	$P_{2\times2}$	$P_{2\bullet} = q$
			$P_{\bullet1} = p$	$P_{\bullet2} = q$	1

Les fréquences conjointes des génotypes peuvent s'écrire de la façon suivante:

$$P_{11\times1}={}^{*}\Delta_1 p+({}^{*}\Delta_2+{}^{*}\Delta_3)p^2+{}^{*}\Delta_4 p^3, \qquad P_{11\times2}=pq({}^{*}\Delta_2+{}^{*}\Delta_4 p),$$

$$P_{12\times1}=pq({}^{*}\Delta_3+2{}^{*}\Delta_4 p), \qquad P_{12\times2}=pq({}^{*}\Delta_3+2{}^{*}\Delta_4 q), \tag{D.22a}$$

$$P_{22\times1}=pq({}^{*}\Delta_2+{}^{*}\Delta_4 q), \qquad P_{22\times2}={}^{*}\Delta_1 q+({}^{*}\Delta_2+{}^{*}\Delta_3)q^2+{}^{*}\Delta_4 q^3,$$

$$P_{1\times1}={}^{**}\Delta_1 p+{}^{**}\Delta_2 p^2, \quad P_{1\times2}=P_{2\times1}={}^{**}\Delta_2 pq, \quad P_{2\times2}={}^{**}\Delta_1 q+{}^{**}\Delta_2 q^2. \tag{D.22b}$$

Calculons dans un premier temps le coefficient d'apparentement $R_{I\to J}$ entre une femelle I et un mâle J. On trouve que

$$\begin{aligned} E[p_J G_I] &= h_{11}P_{11\times1}+h_{12}P_{12\times1}+h_{22}P_{22\times1} \\ &= p\begin{bmatrix} \delta_{IJ}h_{11}+\gamma_{IJ}(h_{11}p+h_{12}q)+{}^{*}\Delta_2(h_{11}p+h_{22}q) \\ +{}^{*}\Delta_4(h_{11}p^2+2h_{12}pq+h_{22}q^2) \end{bmatrix}, \end{aligned} \tag{D.23}$$

où

$$\delta_{IJ}={}^{*}\Delta_1 \quad \text{et} \quad \gamma_{IJ}={}^{*}\Delta_3. \tag{D.24}$$

Les coefficients δ_{IJ} et γ_{IJ} sont définis de façon analogue au cas diploïde étudié plus tôt, sauf qu'ils s'expriment maintenant en fonction des coefficients d'identité ${}^{*}\Delta_i$. À l'aide des équations (D.14a) et (D.23), on vérifie que

$$\begin{aligned} \mathrm{Cov}(p_J,G_I) &= E[p_J G_I]-E[p_J]E[G_I] \\ &= pq[(h_{11}-h_{12})(\delta_{IJ}+p\gamma_{IJ})+(h_{12}-h_{22})(\delta_{IJ}+q\gamma_{IJ})], \end{aligned}$$

dont la forme est identique à l'équation (D.18). Étant donné que (D.19) est valide pour une femelle diploïde, on obtient directement l'équation (D.21), avec δ_{IJ} et γ_{IJ} définis en (D.24), et

$$\delta_{II}=F_I={}^{*}\Delta_1+{}^{*}\Delta_2 \quad \text{et} \quad \gamma_{II}=1-F_I={}^{*}\Delta_3+{}^{*}\Delta_4. \tag{D.25}$$

Afin de déterminer le coefficient d'apparentement $R_{J\to I}$ entre un mâle J et une femelle I, on utilise à nouveau les équations (D.22a) et le Tableau D.2(a). On peut vérifier que

$$\begin{aligned} E[p_I G_J] &= h_1 P_{11\times 1} + h_2 P_{11\times 2} + \tfrac{1}{2}\left(h_1 P_{12\times 1} + h_2 P_{12\times 2}\right) \\ &= p\left\{\delta_{IJ} h_1 + \gamma_{IJ}\left[h_1(p+\tfrac{1}{2}q)+\tfrac{1}{2}h_2 q\right]+({}^*\Delta_2+{}^*\Delta_4)(h_1 p + h_2 q)\right\}. \end{aligned} \tag{D.26}$$

En combinant (D.13a), (D.26) et

$$E[G_J] = h_1 P_{\bullet 1} + h_2 P_{\bullet 2} = h_1 p + h_2 q\,,$$

on obtient

$$\mathrm{Cov}(p_I, G_J) = pq(h_1 - h_2) f_{IJ}\,, \tag{D.27}$$

où

$$f_{IJ} = {}^*\Delta_1 + \tfrac{1}{2}{}^*\Delta_3\,. \tag{D.28}$$

De plus, on montre de façon triviale que

$$\mathrm{Cov}(p_J, G_J) = pq(h_1 - h_2)\,. \tag{D.29}$$

En divisant (D.27) par (D.29), on établit ainsi que

$$R_{J\to I} = f_{IJ}\,, \tag{D.30}$$

tel que défini en (D.28), en autant que $h_1 \neq h_2$. On remarquera que le coefficient d'apparentement entre un mâle et une femelle est égal au coefficient de parenté entre ceux-ci et ne dépend ni des fréquences des gènes dans la population, ni de la valeur génotypique du mâle.

Finalement, en s'appuyant sur le Tableau D.2(b) et sur les équations (D.22b), le coefficient d'apparentement entre deux mâles J_1 et J_2 est donné par

$$
\begin{aligned}
R_{J_1 \to J_2} &= \frac{\mathrm{Cov}(p_{J_2}, G_{J_1})}{\mathrm{Cov}(p_{J_1}, G_{J_1})} \\
&= \frac{pq(h_1 - h_2)^{**}\Delta_1}{pq(h_1 - h_2)} \\
&= {}^{**}\Delta_1 \\
&= f_{J_1 J_2},
\end{aligned}
\tag{D.31}
$$

où $f_{J_1 J_2}$ est défini comme le coefficient de parenté entre deux mâles. Encore une fois, on remarque que le coefficient d'apparentement entre deux mâles ne dépend ni des fréquences des gènes dans la population, ni de la valeur génotypique des mâles, en autant que $h_1 \neq h_2$.

D.3 Coefficients d'apparentement avec consanguinité partielle

Les modèles avec autofécondation partielle ou accouplement frère-sœur partiel produisent des interactions génétiques entre individus issus d'une même famille. Pour mesurer ces interactions, on utilise les coefficients d'apparentement développés à la section précédente. Cependant, on doit supposer d'emblée que les effets de la sélection sont suffisamment faibles dans la population, de sorte que les coefficients d'identité à l'équilibre, tels qu'obtenus précédemment, s'avèrent approximativement exacts.

(i) Modèle avec autofécondation partielle

Dans ce modèle, on considère une population d'individus diploïdes pouvant se reproduire par autofécondation avec probabilité α. Soient I et J deux individus issus d'une même famille. En utilisant les équations (D.1), (D.17) et (D.20), on trouve que

$$
\hat{\delta}_{IJ} = \frac{\alpha(1+\alpha)}{2(2-\alpha)}, \qquad \hat{\gamma}_{IJ} = \frac{(1-\alpha)(1+\alpha)}{2-\alpha}, \qquad \hat{\delta}_{II} = \frac{\alpha}{2-\alpha}, \qquad \hat{\gamma}_{II} = \frac{2(1-\alpha)}{2-\alpha}.
$$

En substituant les coefficients calculés ci-haut dans l'équation (D.21), on obtient

$$R_{I\to J} = \frac{1+\alpha}{2},$$

en autant que les valeurs génotypiques h_{ij} ne soient pas toutes égales. Étonnamment, ce coefficient ne dépend ni des fréquences des gènes dans la population, ni des valeurs génotypiques individuelles.

(ii) Modèle avec accouplement frère-sœur partiel: cas diploïde

La population est composée d'individus diploïdes pouvant s'accoupler avec un membre de sa propre fratrie avec probabilité β. Encore un fois, I et J désignent deux individus issus de la même famille. En se basant sur (D.7), (D.17) et (D.20), on détermine que

$$\hat{\delta}_{IJ} = \frac{\beta}{(2-\beta)(4-3\beta)}, \qquad \hat{\gamma}_{IJ} = \frac{4(1-\beta)}{(2-\beta)(4-3\beta)},$$
$$\hat{\delta}_{II} = \frac{\beta}{4-3\beta}, \qquad \hat{\gamma}_{II} = \frac{4(1-\beta)}{4-3\beta}. \tag{D.32}$$

Si on introduit ces valeurs dans l'équation (D.21), on obtient

$$R_{I\to J} = \frac{1}{2-\beta}, \tag{D.33}$$

à la condition que les valeurs génotypiques h_{ij} ne soient pas toutes égales entre elles. À l'instar du modèle avec autofécondation partielle, ce coefficient ne dépend ni des fréquences des gènes dans la population, ni des valeurs génotypiques individuelles.

(iii) Modèle avec accouplement frère-sœur partiel: cas haplo-diploïde

Pour deux sœurs (diploïdes) I_1 et I_2, on a montré que le coefficient d'apparentement en (D.21) demeurait valide, en utilisant toutefois les coefficients d'identité calculés en (D.9). Ainsi, l'insertion de (D.9) dans (D.17) et (D.20) donne

$$\hat{\delta}_{I_1I_2} = \frac{\beta(3-\beta)}{2(2-\beta)(4-3\beta)}, \qquad \hat{\gamma}_{I_1I_2} = \frac{2(1-\beta)(3-\beta)}{(2-\beta)(4-3\beta)},$$

$$\hat{\delta}_{I_1I_2} = \frac{\beta}{4-3\beta}, \qquad \hat{\gamma}_{I_1I_2} = \frac{4(1-\beta)}{4-3\beta},$$

lesquels, substitués en (D.21), produisent

$$R_{I_1 \to I_2} = \frac{3-\beta}{2(2-\beta)}, \tag{D.34}$$

en autant que les valeurs génotypiques h_{ij} ne soient pas toutes égales.

Le coefficient d'apparentement entre une femelle (diploïde) I et son frère (haploïde) J est aussi calculé au moyen de l'expression (D.21). Les équations (D.8), (D.24) et (D.25) produisent les mêmes coefficients que ceux déduits en (D.32) qui, lorsque introduits en (D.21), donnent exactement le coefficient d'apparentement (D.33). Quant au coefficient d'apparentement entre un mâle J et sa sœur I, il est égal au coefficient de parenté f_{IJ} entre I et J (voir équations (D.30) et (D.27)):

$$R_{J \to I} = \frac{1}{4-3\beta}.$$

Enfin, le coefficient d'apparentement entre deux frères J_1 et J_2 égale simplement le coefficient de parenté $f_{J_1J_2}$ entre J_1 et J_2 (voir équations (D.31) et (D.11)):

$$R_{J_1 \to J_2} = \frac{2-\beta}{4-3\beta}.$$

Remarque 1. Dans certains cas particuliers, tels des valeurs génotypiques additives ($2h_{12} = h_{11} + h_{22}$) ou des fréquences géniques égales ($p = q = \frac{1}{2}$), plusieurs auteurs ont noté que le coefficient d'apparentement donné en (D.21) se réduisait à un indice basé sur le pedigree de I et J, c'est-à-dire que

$$R_{I \to J} \equiv \frac{2f_{IJ}}{1+F_I}, \tag{D.35}$$

(voir Lessard, 1992, et références jointes). Ce coefficient correspond également au coefficient de régression de la fréquence p_J du gène A_1 chez J sur la fréquence p_I du gène A_1 chez I.

Remarque 2. Il semble fortuit que tous les coefficients évalués dans ces modèles avec consanguinité partielle ne dépendent ni des fréquences des gènes dans la population, ni des valeurs génotypiques individuelles, car ce n'est généralement pas le cas. Cependant, du moins dans les modèles avec autofécondation partielle ou accouplement frère-sœur partiel, Lessard (1992) a montré qu'à l'équilibre, les égalités

$$\frac{\delta_{IJ}}{\delta_{II}} = \frac{\gamma_{IJ}}{\gamma_{II}} = \frac{f_{IJ}}{f_{II}}$$

étaient toujours vérifiées en absence de sélection. Ces égalités, lorsque introduites dans l'équation (D.21), simplifient le coefficient d'apparentement à la forme donnée en (D.35), étant donné que $f_{II} = \frac{1}{2}(1 + F_I)$.

Appendice E: Coefficients d'apparentement pour populations structurées

La population, que l'on suppose de taille infinie, est divisée en un très grand nombre de sous-populations, ou groupes, à l'intérieur desquels chaque individu s'accouple avec un autre individu choisi au hasard (reproduction intra-groupe). Cependant, en raison de la compétition entre femelles pour le nombre limité de sites reproductifs dans chacun des groupes, seulement N d'entre elles vont vraisemblablement se reproduire et ainsi contribuer à la génération suivante. De plus, on suppose que chacune des N femelles ayant "réussi" à acquérir un site reproductif engendre un grand nombre de rejetons, tandis que les femelles ayant "échoué" ne se reproduisent tout simplement pas.

Dans ce qui suit, deux types de dispersion sont considérés et ce, pour une population diploïde et pour une population haplo-diploïde. Dans le modèle de dispersion *après* accouplement, chaque femelle s'accouple avec un mâle né dans le même groupe qu'elle, puis migre dans un autre groupe avec probabilité d ou demeure dans le groupe d'où elle est issue avec probabilité complémentaire $\kappa = 1 - d$. Dans le modèle de dispersion *avant* accouplement, il y a plutôt dispersion des rejetons entre le moment de leur naissance et la phase d'accouplement. Pour généraliser ce type de dispersion, on peut supposer des probabilités de dispersion différentes selon le sexe du rejeton, soient d_1 pour une femelle et d_2 pour un mâle, avec probabilités complémentaires respectives κ_1 et κ_2.

Afin d'évaluer les indices basés sur le pedigree de deux individus choisis au hasard dans la population, il faut d'abord définir certaines quantités, soient

F_I : le coefficient de consanguinité de I, c'est-à-dire la probabilité que les deux gènes de I à un même locus soient identiques par descendance; par convention, on adopte $F_J = 1$ pour un individu haploïde J;

f_{IJ} : le coefficient de parenté entre I et J, c'est-à-dire la probabilité qu'un gène choisi au hasard chez J soit identique par descendance à un gène choisi au hasard au même locus chez I; dans une population haplo-diploïde, les coefficients f_{IJ}, $f_{I_1I_2}$ et $f_{J_1J_2}$ sont définis de façon similaire, respectivement, pour un individu diploïde I et un individu haploïde J, pour deux individus diploïdes I_1 et I_2, et pour deux individus haploïdes J_1 et J_2;

δ_{IJ} : la probabilité qu'un gène choisi au hasard chez J soit identique par descendance à tous les gènes de I au même locus; dans une population haplo-diploïde, le coefficient $\delta_{I_1I_2}$ est défini de façon similaire pour deux individus diploïdes I_1 et I_2; par contre, on pose $\delta_{JI} = f_{JI}$ pour un individu diploïde I et un individu haploïde J;

γ_{IJ} : la probabilité qu'un gène choisi au hasard chez J soit identique par descendance à un et un seul gène de I au même locus; dans une population haplo-diploïde, le coefficient $\gamma_{I_1I_2}$ est défini de façon similaire pour deux individus diploïdes I_1 et I_2; par convention, on suppose que $\gamma_{JI} = 0$ pour un individu diploïde I et un individu haploïde J;

f_{IJK} : la probabilité qu'un gène choisi au hasard chez I soit identique par descendance à un gène choisi au hasard au même locus chez J et identique par descendance à un gène choisi au hasard au même locus chez K; dans une population haplo-diploïde, les coefficients $f_{I_1I_2I_3}$, $f_{I_1I_2J}$, $f_{IJ_1J_2}$ et $f_{J_1J_2J_3}$ sont définis de façon similaire pour des individus diploïdes I, I_1, I_2, I_3 et des individus haploïdes J, J_1, J_2, J_3.

De ces définitions découlent ces quelques relations utiles, valables pour un individu I diploïde et un individu J, diploïde ou haploïde:

$$f_{IJ} = \delta_{IJ} + \tfrac{1}{2}\gamma_{IJ}, \quad \delta_{II} = F_I, \quad \gamma_{II} = 1 - F_I, \quad f_{II} = \tfrac{1}{2}(1 + F_I).$$

(i) Modèle de dispersion après accouplement: cas diploïde

Pour déterminer les divers coefficients à l'équilibre, il faut développer les équations de récurrence d'une génération à la suivante. En utilisant la terminologie introduite plus tôt, on peut affirmer que

$$F_{I'} = f_{IJ},$$

$$f_{I'J'} = \frac{1}{N}\left[\frac{1}{4}+\frac{1}{4}F_I+\frac{1}{2}f_{IJ}\right]+\left(1-\frac{1}{N}\right)\kappa^2 f_{IJ},$$

$$\delta_{I'J'} = \frac{1}{N}\left[\delta_{IJ}+\frac{1}{4}\gamma_{IJ}\right]+\left(1-\frac{1}{N}\right)\kappa^2 f_{IJK},$$

$$\gamma_{I'J'} = \frac{1}{N}\left[\frac{1}{2}(1-f_{IJ})+\frac{1}{2}\left(\frac{1}{2}\gamma_{IJ}+(F_I-\delta_{IJ})\right)\right]+2\left(1-\frac{1}{N}\right)\kappa^2(f_{IJ}-f_{IJK}),$$

$$f_{I'J'K'} = \frac{1}{N^2}\left[\frac{1}{4}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{3}{4}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\kappa^2\left[\frac{1}{2}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)+\frac{1}{2}f_{IJK}\right]+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\kappa^3 f_{IJK}.$$

À l'équilibre, on obtient

$$\hat{F}_I = \hat{f}_{IJ} = \frac{1}{D_1},$$

$$\hat{\delta}_{IJ} = \frac{1}{D_2}\left[4N^2+(N-1)(2N-3)\kappa^2-4(N-1)(N-2)\kappa^3+4(N-1)^2\kappa^4\right],$$

$$\hat{\gamma}_{IJ} = \frac{4(N-1)(1-\kappa)}{D_2}\left[4N^2+4N^2\kappa+(N-1)(4N-3)\kappa^2+5(N-1)\kappa^3\right],$$

$$\hat{f}_{IJK} = \frac{1}{D_2}\left[2N(N+1)+(N-1)(4N+1)\kappa^2\right],$$

où

$$D_1 = (4N-3) - 4(N-1)\kappa^2,$$
$$D_2 = D_1 \times \left[\begin{array}{l} 4N^2(2N-1) - 3(N-1)(4N-1)\kappa^2 \\ -4(N-1)(N-2)(2N-1)\kappa^3 - 6(N-1)^2\kappa^4 \end{array} \right].$$

Conséquemment, on trouve que

$$\hat{f}_{II} = \frac{\left[(2N-1) - 2(N-1)\kappa^2\right]}{D_1}, \quad \hat{\delta}_{II} = \frac{1}{D_1}, \quad \hat{\gamma}_{II} = \frac{4(N-1)(1-\kappa^2)}{D_1},$$

ainsi que les rapports

$$\frac{\hat{f}_{IJ}}{\hat{f}_{II}} = \frac{1}{(2N-1) - 2(N-1)\kappa^2},$$

$$\frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}} = \frac{4N^2 + (N-1)(2N-3)\kappa^2 - 4(N-1)(N-2)\kappa^3 + 4(N-1)^2\kappa^4}{4N^2(2N-1) - 3(N-1)(4N-1)\kappa^2 - 4(N-1)(N-2)(2N-1)\kappa^3 - 6(N-1)^2\kappa^4},$$

$$\frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} = \left(\frac{1-\kappa}{1-\kappa^2}\right)\left[\frac{4N^2 + 4N^2\kappa + (N-1)(4N-3)\kappa^2 + 5(N-1)\kappa^3}{4N^2(2N-1) - 3(N-1)(4N-1)\kappa^2 - 4(N-1)(N-2)(2N-1)\kappa^3 - 6(N-1)^2\kappa^4}\right].$$

Pour $\kappa \neq 0$, 1 et $N \neq 1$, il est trivial de vérifier analytiquement les inégalités

$$\frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} > \frac{\hat{f}_{IJ}}{\hat{f}_{II}} > \frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}};$$

mais les différences semblent petites, tellement petites qu'on peut supposer en pratique l'égalité de ces trois rapports. Pour quelques valeurs fixées de N et κ, la Figure E.1 et le Tableau E.1 donnent un aperçu de l'ordre de grandeur numérique de ces différences.

(ii) Modèle de dispersion après accouplement: cas haplo-diploïde

Dans une population haplo-diploïde, il faut prendre en compte la différence de ploïdie possible pour chaque paire d'individus. Si l'indice *I* représente un individu diploïde et l'indice *J* un individu haploïde, les équations de récurrence sont données par les expressions suivantes:

$$F_{I'} = f_{IJ},$$

$$f_{I_1'I_2'} = \frac{1}{N}\left[\frac{1}{4}+\frac{1}{8}(1+F_I)+\frac{1}{2}f_{IJ}\right]+\left(1-\frac{1}{N}\right)K^2\left[\frac{f_{I_1I_2}+2f_{IJ}+f_{J_1J_2}}{4}\right],$$

$$f_{I'J'} = \frac{1}{N}\left[\frac{1}{4}(1+F_I)+\frac{1}{2}f_{IJ}\right]+\left(1-\frac{1}{N}\right)K^2\left[\frac{f_{I_1I_2}+f_{IJ}}{2}\right],$$

$$f_{J_1'J_2'} = \frac{1}{N}\left[\frac{1}{2}(1+F_I)\right]+\left(1-\frac{1}{N}\right)K^2 f_{I_1I_2},$$

$$\delta_{I'J'} = \frac{1}{N}\left[\delta_{IJ}+\frac{1}{4}\gamma_{IJ}\right]+\left(1-\frac{1}{N}\right)K^2 f_{I_1I_2J},$$

$$\gamma_{I'J'} = \frac{1}{N}\left[\frac{1}{2}(1-f_{IJ})+\frac{1}{2}\left(\frac{1}{2}\gamma_{IJ}+(F_I-\delta_{IJ})\right)\right]+2\left(1-\frac{1}{N}\right)K^2\left[\frac{(f_{I_1I_2}-f_{I_1I_2J})+(f_{IJ}-f_{I_1I_2J})}{2}\right],$$

$$\delta_{I_1'I_2'} = \frac{1}{N}\left[\frac{1}{2}\left(\delta_{IJ}+\frac{1}{4}\gamma_{IJ}\right)+\frac{1}{2}f_{IJ}\right]+\left(1-\frac{1}{N}\right)K^2\left[\frac{f_{I_1I_2J}+f_{IJ_1J_2}}{2}\right],$$

$$\gamma_{I_1'I_2'} = \frac{1}{N}\left[\frac{1}{2}(1-f_{IJ})+\frac{1}{2}\left(\frac{1}{4}\gamma_{IJ}+\frac{1}{2}(F_I-\delta_{IJ})+\frac{1}{2}(1-f_{IJ})\right)\right]$$
$$+2\left(1-\frac{1}{N}\right)K^2\left[\frac{(f_{I_1I_2}-f_{I_1I_2J})+(f_{IJ}-f_{I_1I_2J})+(f_{IJ}-f_{IJ_1J_2})+(f_{J_1J_2}-f_{IJ_1J_2})}{4}\right],$$

$$f_{I_1I_2I_3} = \frac{1}{N^2}\left[\frac{1}{8}+\frac{1}{8}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{3}{8}f_{IJ}+\frac{3}{8}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\kappa^2\left\{\begin{array}{l}\frac{1}{2}\left[\frac{1}{4}f_{IJ}+\frac{1}{4}\left(\frac{1}{2}f_{I_1I_2}+\frac{1}{2}\delta_{I_1I_2}\right)+\frac{1}{2}f_{I_1I_2J}\right]\\ +\frac{1}{2}\left[\frac{1}{4}f_{J_1J_2}+\frac{1}{4}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)+\frac{1}{2}f_{IJ_1J_2}\right]\end{array}\right\}$$
$$+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\kappa^3\left[\frac{f_{I_1I_2I_3}+3f_{I_1I_2J}+3f_{IJ_1J_2}+f_{J_1J_2J_3}}{8}\right],$$

$$f_{I_1I_2J} = \frac{1}{N^2}\left[\frac{1}{4}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{1}{4}f_{IJ}+\frac{1}{2}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\kappa^2\left\{\begin{array}{l}\frac{1}{3}\left[\frac{1}{4}f_{IJ}+\frac{1}{4}\left(\frac{1}{2}f_{I_1I_2}+\frac{1}{2}\delta_{I_1I_2}\right)+\frac{1}{2}f_{I_1I_2J}\right]\\ +\frac{2}{3}\left[\frac{1}{4}\left(\frac{1}{2}f_{I_1I_2}+\frac{1}{2}\delta_{I_1I_2}\right)+\frac{1}{4}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)+\frac{1}{4}f_{I_1I_2J}+\frac{1}{4}f_{IJ_1J_2}\right]\end{array}\right\}$$
$$+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\kappa^3\left[\frac{f_{I_1I_2I_3}+2f_{I_1I_2J}+f_{IJ_1J_2}}{4}\right],$$

$$f_{IJ_1J_2} = \frac{1}{N^2}\left[\frac{1}{2}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{1}{2}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\kappa^2\left\{\begin{array}{l}\frac{1}{3}\left[\frac{1}{2}\left(\frac{1}{2}f_{I_1I_2}+\frac{1}{2}\delta_{I_1I_2}\right)+\frac{1}{2}\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)\right]\\ +\frac{2}{3}\left[\frac{1}{2}\left(\frac{1}{2}f_{I_1I_2}+\frac{1}{2}\delta_{I_1I_2}\right)+\frac{1}{2}f_{I_1I_2J}\right]\end{array}\right\}$$
$$+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\kappa^3\left[\frac{f_{I_1I_2I_3}+f_{I_1I_2J}}{2}\right],$$

$$f_{J_1J_2J_3} = \frac{1}{N^2}\left[\frac{1}{4}+\frac{3}{4}F_I\right]+\frac{3}{N}\left(1-\frac{1}{N}\right)\kappa^2\left[\frac{1}{2}f_{I_1I_2}+\frac{1}{2}\delta_{I_1I_2}\right]+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\kappa^3 f_{I_1I_2I_3},$$

Remarque. Il y a bien entendu quelques regroupements de termes possibles qui simplifieraient un peu l'écriture de ces équations, mais on perdrait alors une logique permettant au lecteur de vérifier par lui-même l'exactitude de celles-ci.

A l'équilibre, on obtient

$$\hat{f}_{I_1I_2}=\frac{(3N-1)-(N-1)\kappa^2}{2D_3},\qquad \hat{F}_I=\hat{f}_{IJ}=\frac{N}{D_3},\qquad \hat{f}_{J_1J_2}=\frac{(2N-1)-(N-1)\kappa^2}{D_3},$$

$$\hat{\delta}_{IJ}=\frac{N}{D_4}\begin{bmatrix}64N^8+32N^7(N-1)\kappa^2-40N^6(N-1)(N-2)\kappa^3\\+16N^4(N-1)^2(3N-1)(2N+1)\kappa^4+2N^4(N-1)^2(N-2)(16N-27)\kappa^5\\-2N^3(N-1)^2(23N^3-92N^2+83N+1)\kappa^6\\+2N^2(N-1)^3(N-2)(19N^2+9N-5)\kappa^7\\+N^2(N-1)^3(8N^3-69N^2+78N-12)\kappa^8\\-N(N-1)^3(N-2)(11N^3+2N^2-10N-8)\kappa^9\\-(N-1)^4(N-2)^2(7N^2+4N-2)\kappa^{10}-(N-1)^4(N-2)(N+2)(5N-6)\kappa^{11}\\-(N-1)^4(N-2)^2(3N^2+2N-6)\kappa^{12}-(N-1)^5(N-2)^3\kappa^{13}\end{bmatrix},$$

$$\hat{\gamma}_{IJ}=\frac{4N(N-1)(1-\kappa)}{D_4}\begin{bmatrix}64N^8+64N^8\kappa+16N^6(N-1)(4N-1)\kappa^2\\+8N^6(N-1)(3N+8)\kappa^3+4N^4(N-1)(6N^3-9N^2-7N+4)\kappa^4\\+8N^4(N-1)^2(3N^2-11N+11)\kappa^5\\-2N^3(N-1)^2(3N^3-20N^2+32N+2)\kappa^6\\-2N^2(N-1)^2(N^2-2N+2)(3N^2-2N+2)\kappa^7\\-2N^2(N-1)^3(N-2)(3N^2-3N+4)\kappa^8\\-N(N-1)^3(N-2)(N^3+6N^2-12N-4)\kappa^9\\-(N-1)^3(N-2)(N^4-6N^2+10N-4)\kappa^{10}\\-(N-1)^4(N-2)^2(N^2-N+4)\kappa^{11}-(N-1)^4(N-2)^3\kappa^{12}\end{bmatrix},$$

$$\hat{\delta}_{I_1I_2}=\frac{1}{2D_4}\begin{bmatrix}64N^8(3N-1)+32N^6(N-1)^2(3N-1)\kappa^2-40N^6(N-1)(N-2)(3N-1)\kappa^3\\+8N^4(N-1)^2(24N^3-14N^2-3N+1)\kappa^4\\+2N^4(N-1)^2(N-2)(N-3)(24N-7)\kappa^5\\-2N^3(N-1)^2(69N^4-247N^3+272N^2-62N-2)\kappa^6\\+2N^2(N-1)^3(N-2)(39N^3-25N^2+7N-2)\kappa^7\\+N^2(N-1)^3(N-2)^2(25N-9)\kappa^8\\-N(N-1)^3(N-2)(9N^4+47N^3-92N^2+28N-2)\kappa^9\\-(N-1)^4(15N^5-71N^4+88N^3-11N^2-20N+4)\kappa^{10}\\+(N-1)^4(N-2)(7N^3-36N^2+44N-8)\kappa^{11}\\+(N-1)^4(N-2)^2(3N^3-21N^2+26N-6)\kappa^{12}\\-(N-1)^5(N-2)(3N-4)(N^2-4N+2)\kappa^{13}-(N-1)^6(N-2)^2\kappa^{14}\end{bmatrix},$$

$$\hat{\gamma}_{I_1I_2}=\frac{(N-1)(1-\kappa)}{D_4}\begin{bmatrix}128N^8(3N-1)+128N^8(3N-1)\kappa\\+32N^6(N-1)(8N^2-9N+2)\kappa^2+16N^6(N-1)(N^2+17N-6)\kappa^3\\+8N^4(N-1)(2N^4-13N^3-4N^2+14N-3)\kappa^4\\+4N^4(N-1)^2(24N^3-154N^2+169N-40)\kappa^5\\-2N^3(N-1)^2(42N^4-158N^3+174N^2-35N-5)\kappa^6\\-4N^2(N-1)^2(21N^5-82N^4+89N^3-4N^2-15N+3)\kappa^7\\-2N^2(N-1)^3(12N^4-53N^3+107N^2-116N+26)\kappa^8\\+2N(N-1)^3(3N^5-25N^4+74N^3-77N^2+21N-2)\kappa^9\\+(N-1)^3(N-2)(6N^5-32N^4+69N^3-76N^2+41N-6)\kappa^{10}\\-(N-1)^4(N-2)(4N^4-33N^3+80N^2-69N+14)\kappa^{11}\\+(N-1)^4(N-2)(2N^4-10N^3+20N^2-17N+6)\kappa^{12}\\+(N-1)^4(N-2)^2(2N^3-8N^2+10N-3)\kappa^{13}+(N-1)^5(N-2)^3\kappa^{14}\end{bmatrix},$$

$$\hat{f}_{I_1I_2I_3}=\frac{1}{4D_4}\begin{bmatrix}64N^8(5N-1)+8N^5(N-1)(52N^3-35N^2+26N-3)\kappa^2\\+24N^5(N-1)(N-2)(2N^2+3N-1)\kappa^3\\-2N^3(N-1)^2(80N^4-20N^3-49N^2-39N+12)\kappa^4\\+2N^3(N-1)^2(N-2)(72N^3-49N^2+59N-18)\kappa^5\\-2N^2(N-1)^2(36N^5-85N^4+146N^3-142N^2+61N-4)\kappa^6\\-N^2(N-1)^3(N-2)(24N^3+152N^2-57N+3)\kappa^7\\-N(N-1)^3(48N^5-275N^4+145N^3+192N^2-60N+6)\kappa^8\\-(N-1)^3(N-2)(8N^5-169N^4+262N^3-109N^2+13N-1)\kappa^9\\+N(N-1)^4(36N^4-198N^3+387N^2-246N+4)\kappa^{10}\\-(N-1)^4(N-2)(8N^4-49N^3+13N^2+46N-10)\kappa^{11}\\+(N-1)^5(21N^3-100N^2+130N-40)\kappa^{12}\\+(N-1)^5(N-2)(4N^3-18N^2+31N-15)\kappa^{13}+2(N-1)^6(N-2)^2\kappa^{14}\end{bmatrix},$$

$$\hat{f}_{I_1I_2J}=\frac{N^2}{D_4}\begin{bmatrix}16N^5(2N^2+3N-1)+4N^4(N-1)(8N-1)(3N+1)\kappa^2\\+2N^3(N-1)(N-2)(16N^2-5N+1)\kappa^3\\-2N^2(N-1)^2(8N^3-28N^2+7N-1)\kappa^4\\+2N(N-1)^2(N-2)(19N^3+2N^2-10N+3)\kappa^5\\+N(N-1)^2(8N^4-85N^3+161N^2-110N+20)\kappa^6\\-2(N-1)^3(N-2)(8N^3-5N^2+5N-2)\kappa^7\\-N(N-1)^3(N-2)^2(7N+3)\kappa^8-(N-1)^3(N-2)(9N^2-16N+8)\kappa^9\\-4N(N-1)^4(N-2)^2\kappa^{10}-(N-1)^4(N-2)^3\kappa^{11}\end{bmatrix},$$

$$\hat{f}_{IJ_1J_2}=\frac{N}{D_4}\begin{bmatrix}64N^8+8N^4(N-1)(4N-1)(3N^2+1)\kappa^2\\+8N^4(N-1)(N-2)(2N^2+2N-1)\kappa^3\\-2N^3(N-1)^2(16N^3-4N^2-3N-1)\kappa^4\\+2N^2(N-1)^2(N-2)(20N^3-29N^2+11N-1)\kappa^5\\-2N^2(N-1)^2(4N^4-35N^3+45N^2-15N+4)\kappa^6\\-2N(N-1)^3(N-2)(4N^3+4N^2-6N+1)\kappa^7\\-(N-1)^3(8N^5-42N^4+66N^3-49N^2+28N-4)\kappa^8\\+(N-1)^3(N-2)(4N^3+3N^2-12N+4)\kappa^9\\+2N(N-1)^4(N-2)^2(2N-3)\kappa^{10}\\-(N-1)^4(N-2)(2N^3-11N^2+14N-4)\kappa^{11}-(N-1)^5(N-2)^2\kappa^{12}\end{bmatrix},$$

$$\hat{f}_{J_1J_2J_3} = \frac{1}{D_4}\begin{bmatrix} 64N^8(2N-1)+16N^6(N-1)(8N^2-7N+1)\kappa^2 \\ +24N^6(N-1)(N-2)\kappa^3-8N^4(N-1)^2(N+1)(8N^2+8N-3)\kappa^4 \\ +2N^3(N-1)^2(N-2)(12N^3-100N^2+56N-3)\kappa^5 \\ -2N^2(N-1)^2(24N^5-172N^4+299N^3-166N^2+19N-1)\kappa^6 \\ -2N(N-1)^3(N-2)(52N^3-9N^2-12N+3)\kappa^7 \\ -N(N-1)^3(24N^5-104N^4-2N^3+225N^2-168N+36)\kappa^8 \\ -(N-1)^3(N-2)(8N^5-106N^4+175N^3-112N^2+40N-4)\kappa^9 \\ +4(N-1)^4(6N^5-30N^4+57N^3-51N^2+28N-6)\kappa^{10} \\ -(N-1)^4(N-2)(2N^4-25N^3+28N^2-14N+8)\kappa^{11} \\ +(N-1)^5(N-2)^2(15N-4)\kappa^{12} \\ +2(N-1)^5(N-2)(2N^3-9N^2+14N-6)\kappa^{13}+2(N-1)^6(N-2)^2\kappa^{14} \end{bmatrix},$$

où

$$D_3 = \left[N(4N-3)-(N-1)(5N-1)\kappa^2+(N-1)^2\kappa^4\right]$$

et

$$D_4 = D_3 \times \begin{bmatrix} 64N^8(2N-1)-32N^6(N-1)(4N-1)\kappa^2-40N^6(N-1)(N-2)(2N-1)\kappa^3 \\ -8N^4(N-1)^2(13N^2+5N-2)\kappa^4-10N^4(N-1)^2(N-2)(12N-5)\kappa^5 \\ -2N^3(N-1)^2(30N^4-135N^3+188N^2-65N-3)\kappa^6 \\ -2N^2(N-1)^3(N-2)(5N^2-N+1)\kappa^7 \\ +N^2(N-1)^3(24N^3-97N^2+118N-28)\kappa^8 \\ +N^2(N-1)^3(N-2)(10N^3-45N^2+62N-22)\kappa^9 \\ +(N-1)^4(N-2)^2(5N^2+8N-2)\kappa^{10}+(N-1)^4(N-2)^3(8N-3)\kappa^{11} \\ +(N-1)^4(N-2)^2(2N^3-9N^2+14N-6)\kappa^{12}+(N-1)^5(N-2)^3\kappa^{13} \end{bmatrix}.$$

Contrairement au cas diploïde, les rapports de probabilités donnent lieu à des expressions très complexes difficiles à traiter de façon analytique. Des simulations numériques ont donc été entreprises pour quelques valeurs fixées de N et κ (voir Figure E.3 et Tableau E.1). Les résultats obtenus montrent que les inégalités

$$\frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} > \frac{\hat{f}_{IJ}}{\hat{f}_{II}} > \frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}} \quad \text{et} \quad \frac{\hat{\gamma}_{I_1I_2}}{\hat{\gamma}_{I_1I_1}} > \frac{\hat{f}_{I_1I_2}}{\hat{f}_{I_1I_1}} > \frac{\hat{\delta}_{I_1I_2}}{\hat{\delta}_{I_1I_1}}$$

seraient vérifiées, du moins pour ces valeurs de N. À la Figure E.3, il est cependant difficile d'observer ces inégalités. En effet, ces rapports ne diffèrent pas beaucoup entre eux, si bien qu'on pourrait assumer l'égalité de ces rapports.

Quelques cas particuliers méritent une attention spéciale pour le modèle de dispersion *après* accouplement.

- **Absence de dispersion (d = 0).** Étant donné qu'il n'y a aucune dispersion des femelles inséminées après accouplement avec les mâles issus du même groupe qu'elles, chaque groupe devient génétiquement homogène pour un allèle particulier. À l'équilibre, chaque individu est "complètement" consanguin, c'est-à-dire que ses deux gènes sont identiques par descendance avec probabilité 1. Ces conclusions demeurent valides autant pour une population haplo-diploïde que pour une population diploïde.

- **Dispersion totale (d = 1).** On peut poser directement $\kappa = 0$ dans les expressions obtenues à l'équilibre. Ainsi, on peut vérifier que

$$\frac{\hat{f}_{IJ}}{\hat{f}_{II}} = \frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}} = \frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} = \frac{1}{2N-1} \qquad \text{et} \qquad \frac{\hat{f}_{I_1I_2}}{\hat{f}_{I_1I_1}} = \frac{\hat{\delta}_{I_1I_2}}{\hat{\delta}_{I_1I_1}} = \frac{\hat{\gamma}_{I_1I_2}}{\hat{\gamma}_{I_1I_1}} = \frac{3N-1}{2N(2N-1)},$$

pour deux individus I et J dans une population diploïde, pour des individus I, I_1, I_2 diploïdes et J haploïde dans une population haplo-diploïde.

- **Une femelle par groupe (N = 1).** Ceci équivaut à un modèle avec accouplement frère-sœur répété de génération en génération. Par conséquent, chaque groupe devient de plus en plus homogène génétiquement et à la limite, chaque individu est "complètement" consanguin. Ces résultats demeurent valides autant dans une population haplo-diploïde que diploïde.

(iii) Modèle de dispersion avant accouplement: cas diploïde

Dans ce modèle, les équations de récurrence sont données par

$$F_{I'} = \kappa_1\kappa_2 f_{IJ},$$

$$f_{I'J'} = \frac{1}{N}\left[\frac{1}{4}+\frac{1}{4}F_I+\frac{1}{2}\kappa_1\kappa_2 f_{IJ}\right]+\left(1-\frac{1}{N}\right)\left(\frac{\kappa_1+\kappa_2}{2}\right)^2 f_{IJ},$$

$$\delta_{I'J'} = \frac{1}{N}\left[\kappa_1\kappa_2\delta_{IJ}+\frac{1}{4}\kappa_1\kappa_2\gamma_{IJ}\right]+\left(1-\frac{1}{N}\right)\left(\frac{\kappa_1+\kappa_2}{2}\right)\kappa_1\kappa_2 f_{IJK},$$

$$\gamma_{I'J'} = \frac{1}{N}\left[\frac{1}{2}\left(1-\kappa_1\kappa_2 f_{IJ}\right)+\frac{1}{2}\left(\frac{1}{2}\kappa_1\kappa_2\gamma_{IJ}+\left(F_I-\kappa_1\kappa_2\delta_{IJ}\right)\right)\right]$$
$$+2\left(1-\frac{1}{N}\right)\left[\left(\frac{\kappa_1+\kappa_2}{2}\right)^2 f_{IJ}-\kappa_1\kappa_2\left(\frac{\kappa_1+\kappa_2}{2}\right)f_{IJK}\right],$$

$$f_{I'J'K'} = \frac{1}{N^2}\left[\frac{1}{4}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{3}{4}\left(\frac{1}{2}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\kappa_1\kappa_2\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\left[\frac{1}{2}\left(\frac{\kappa_1+\kappa_2}{2}\right)^2\left(\frac{1}{2}f_{IJ}+\frac{1}{2}\delta_{IJ}\right)+\frac{1}{2}\kappa_1\kappa_2\left(\frac{\kappa_1+\kappa_2}{2}\right)f_{IJK}\right]$$
$$+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\left(\frac{\kappa_1+\kappa_2}{2}\right)^3 f_{IJK}.$$

À l'équilibre, on obtient

$$\hat{F}_I = \kappa_1\kappa_2\hat{f}_{IJ} = \frac{\kappa_1\kappa_2}{D_5},$$

$$\hat{\delta}_{IJ} = \frac{2\kappa_1\kappa_2}{D_6}\left[8N^2+2N(N-1)(\kappa_1+\kappa_2)+(N-1)(\kappa_1^3+\kappa_2^3)\right],$$

$$\hat{\gamma}_{IJ} = \frac{2}{D_6}\begin{bmatrix} 32N^3 - 32N^2\kappa_1\kappa_2 - 4N(N-1)(3N+1)\kappa_1\kappa_2(\kappa_1+\kappa_2) - 3(N-1)^2\kappa_1^2\kappa_2^2(\kappa_1+\kappa_2) \\ -4N(N-1)(N-2)(\kappa_1^3+\kappa_2^3) - (N-1)(N+3)\kappa_1\kappa_2(\kappa_1^3+\kappa_2^3) \end{bmatrix},$$

$$\hat{f}_{IJK} = \frac{1}{D_6}\left[8N^2 + 8N\kappa_1\kappa_2 + 4N(N-1)(\kappa_1+\kappa_2)^2 + (N-1)\kappa_1\kappa_2(\kappa_1+\kappa_2)^2\right],$$

où

$$D_5 = 4N - 3\kappa_1\kappa_2 - (N-1)(\kappa_1+\kappa_2)^2,$$

$$D_6 = D_5 \times \begin{bmatrix} 32N^3 - 16N^2\kappa_1\kappa_2 - 12N^2(N-1)\kappa_1\kappa_2(\kappa_1+\kappa_2) - 3(N-1)^2\kappa_1^2\kappa_2^2(\kappa_1+\kappa_2) \\ -4N(N-1)(N-2)(\kappa_1^3+\kappa_2^3) - (N-1)(N+1)\kappa_1\kappa_2(\kappa_1^3+\kappa_2^3) \end{bmatrix}.$$

Par la suite, pour simplifier le traitement de ces équations, on suppose que $\kappa_1 = \kappa_2 = \kappa$. Les résultats obtenus précédemment se simplifient à

$$\hat{F}_I = \kappa^2 \hat{f}_{IJ} = \frac{\kappa^2}{D_5},$$

$$\hat{\delta}_{IJ} = \frac{\kappa^2}{D_6}\left[4N^2 + 2N(N-1)\kappa + (N-1)\kappa^3\right],$$

$$\hat{\gamma}_{IJ} = \frac{4N(1-\kappa)}{D_6}\left[4N^2 + 4N^2\kappa + 4N(N-1)\kappa^2 + (N-1)\kappa^3 + (N-1)\kappa^4\right],$$

$$\hat{f}_{IJK} = \frac{1}{D_6}\left[2N^2 + 2N(2N-1)\kappa^2 + (N-1)\kappa^4\right],$$

où

$$D_5 = 4N - (4N-1)\kappa^2,$$

$$D_6 = D_5 \times \left[8N^3 - 4N^2\kappa^2 - 4N(N-1)(2N-1)\kappa^3 - (N-1)(2N-1)\kappa^5\right].$$

De même, on trouve que

$$\hat{f}_{II} = \frac{\left[2N-(2N-1)\kappa^2\right]}{D_5}, \quad \hat{\delta}_{II} = \frac{\kappa^2}{D_5}, \quad \hat{\gamma}_{II} = \frac{4N\left(1-\kappa^2\right)}{D_5},$$

et

$$\frac{\hat{f}_{IJ}}{\hat{f}_{II}} = \frac{1}{2N-(2N-1)\kappa^2},$$

$$\frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}} = \frac{4N^2+2N(N-1)\kappa+(N-1)\kappa^3}{8N^3-4N^2\kappa^2-4N(N-1)(2N-1)\kappa^3-(N-1)(2N-1)\kappa^5},$$

$$\frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} = \left(\frac{1-\kappa}{1-\kappa^2}\right)\left[\frac{4N^2+4N^2\kappa+4N(N-1)\kappa^2+(N-1)\kappa^3+(N-1)\kappa^4}{8N^3-4N^2\kappa^2-4N(N-1)(2N-1)\kappa^3-(N-1)(2N-1)\kappa^5}\right].$$

Pour $\kappa \neq 0$, 1 et $N \neq 1$, il est trivial de vérifier analytiquement les inégalités

$$\frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}} > \frac{\hat{f}_{IJ}}{\hat{f}_{II}} > \frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}};$$

mais les différences s'avèrent petites, de sorte qu'à l'instar du modèle diploïde de dispersion *après* accouplement, on peut supposer l'égalité de ces trois rapports. Pour quelques valeurs fixées de N et κ, la Figure E.2 et le Tableau E.2 donnent un aperçu de l'ordre de grandeur numérique des différences entre ces rapports.

(iv) Modèle de dispersion avant accouplement: cas haplo-diploïde

Les équations de récurrence peuvent s'exprimer de la façon suivante:

$$F_{I'} = \kappa_1 \kappa_2 f_{IJ},$$

$$f_{I_1'I_2'} = \frac{1}{N}\left[\frac{1}{4}+\frac{1}{8}(1+F_I)+\frac{1}{2}\kappa_1\kappa_2 f_{IJ}\right]+\left(1-\frac{1}{N}\right)\left[\frac{\kappa_1^2 f_{I_1I_2}+2\kappa_1\kappa_2 f_{IJ}+\kappa_2^2 f_{J_1J_2}}{4}\right],$$

$$f_{I'J'} = \frac{1}{N}\left[\frac{1}{4}(1+F_I)+\frac{1}{2}\kappa_1\kappa_2 f_{IJ}\right]+\left(1-\frac{1}{N}\right)\left[\frac{\kappa_1^2 f_{I_1I_2}+\kappa_1\kappa_2 f_{IJ}}{2}\right],$$

$$f_{J_1'J_2'} = \frac{1}{N}\left[\frac{1}{2}(1+F_I)\right]+\left(1-\frac{1}{N}\right)\kappa_1\kappa_2 f_{I_1I_2},$$

$$\delta_{I'J'} = \frac{1}{N}\left[\kappa_1\kappa_2\delta_{IJ}+\frac{1}{4}\kappa_1\kappa_2\gamma_{IJ}\right]+\left(1-\frac{1}{N}\right)\kappa_1^2\kappa_2 f_{I_1I_2J},$$

$$\gamma_{I'J'} = \frac{1}{N}\left[\frac{1}{2}(1-\kappa_1\kappa_2 f_{IJ})+\frac{1}{2}\left(\frac{1}{2}\kappa_1\kappa_2\gamma_{IJ}+(F_I-\kappa_1\kappa_2\delta_{IJ})\right)\right] + 2\left(1-\frac{1}{N}\right)\left[\frac{\left(\kappa_1^2 f_{I_1I_2}-\kappa_1^2\kappa_2 f_{I_1I_2J}\right)+\left(\kappa_1\kappa_2 f_{IJ}-\kappa_1^2\kappa_2 f_{I_1I_2J}\right)}{2}\right],$$

$$\delta_{I_1'I_2'} = \frac{1}{N}\left[\frac{1}{2}\left(\kappa_1\kappa_2\delta_{IJ}+\frac{1}{4}\kappa_1\kappa_2\gamma_{IJ}\right)+\frac{1}{2}\kappa_1\kappa_2 f_{IJ}\right]+\left(1-\frac{1}{N}\right)\left[\frac{\kappa_1^2\kappa_2 f_{I_1I_2J}+\kappa_1\kappa_2^2 f_{IJ_1J_2}}{2}\right],$$

$$\gamma_{I_1'I_2'} = \frac{1}{N}\left[\frac{1}{2}(1-\kappa_1\kappa_2 f_{IJ})+\frac{1}{2}\left(\frac{1}{4}\kappa_1\kappa_2\gamma_{IJ}+\frac{1}{2}(F_I-\kappa_1\kappa_2\delta_{IJ})+\frac{1}{2}(1-\kappa_1\kappa_2 f_{IJ})\right)\right] + 2\left(1-\frac{1}{N}\right)\left[\frac{\begin{array}{c}\left(\kappa_1^2 f_{I_1I_2}-\kappa_1^2\kappa_2 f_{I_1I_2J}\right)+\left(\kappa_1\kappa_2 f_{IJ}-\kappa_1^2\kappa_2 f_{I_1I_2J}\right)\\ +\left(\kappa_1\kappa_2 f_{IJ}-\kappa_1\kappa_2^2 f_{IJ_1J_2}\right)+\left(\kappa_2^2 f_{J_1J_2}-\kappa_1\kappa_2^2 f_{IJ_1J_2}\right)\end{array}}{4}\right],$$

$$f_{I_1I_2I_3} = \frac{1}{N^2}\left[\frac{1}{8}+\frac{1}{8}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{3}{8}\kappa_1\kappa_2 f_{IJ}+\frac{3}{8}\left(\frac{1}{2}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\kappa_1\kappa_2\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\left\{\begin{array}{l}\frac{1}{2}\left[\frac{1}{4}\kappa_1\kappa_2 f_{IJ}+\frac{1}{4}\left(\frac{1}{2}\kappa_1^2 f_{I_1I_2}+\frac{1}{2}\kappa_1^2\delta_{I_1I_2}\right)+\frac{1}{2}\kappa_1^2\kappa_2 f_{I_1I_2J}\right]\\ +\frac{1}{2}\left[\frac{1}{4}\kappa_2^2 f_{J_1J_2}+\frac{1}{4}\left(\frac{1}{2}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\kappa_1\kappa_2\delta_{IJ}\right)+\frac{1}{2}\kappa_1\kappa_2^2 f_{IJ_1J_2}\right]\end{array}\right\}$$
$$+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\left[\frac{\kappa_1^3 f_{I_1I_2I_3}+3\kappa_1^2\kappa_2 f_{I_1I_2J}+3\kappa_1\kappa_2^2 f_{IJ_1J_2}+\kappa_2^3 f_{J_1J_2J_3}}{8}\right],$$

$$f_{I_1I_2J} = \frac{1}{N^2}\left[\frac{1}{4}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{1}{4}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\left(\frac{1}{2}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\kappa_1\kappa_2\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\left\{\begin{array}{l}\frac{1}{3}\left[\frac{1}{4}\kappa_1\kappa_2 f_{IJ}+\frac{1}{4}\left(\frac{1}{2}\kappa_1^2 f_{I_1I_2}+\frac{1}{2}\kappa_1^2\delta_{I_1I_2}\right)+\frac{1}{2}\kappa_1^2\kappa_2 f_{I_1I_2J}\right]\\ +\frac{2}{3}\left[\begin{array}{l}\frac{1}{4}\left(\frac{1}{2}\kappa_1^2 f_{I_1I_2}+\frac{1}{2}\kappa_1^2\delta_{I_1I_2}\right)+\frac{1}{4}\left(\frac{1}{2}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\kappa_1\kappa_2\delta_{IJ}\right)\\ +\frac{1}{4}\kappa_1^2\kappa_2 f_{I_1I_2J}+\frac{1}{4}\kappa_1\kappa_2^2 f_{IJ_1J_2}\end{array}\right]\end{array}\right\}$$
$$+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\left[\frac{\kappa_1^3 f_{I_1I_2I_3}+2\kappa_1^2\kappa_2 f_{I_1I_2J}+\kappa_1\kappa_2^2 f_{IJ_1J_2}}{4}\right],$$

$$f_{IJ_1J_2} = \frac{1}{N^2}\left[\frac{1}{2}\left(\frac{1}{4}+\frac{3}{4}F_I\right)+\frac{1}{2}\left(\frac{1}{2}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\kappa_1\kappa_2\delta_{IJ}\right)\right]$$
$$+\frac{3}{N}\left(1-\frac{1}{N}\right)\left\{\begin{array}{l}\frac{1}{3}\left[\frac{1}{2}\left(\frac{1}{2}\kappa_1^2 f_{I_1I_2}+\frac{1}{2}\kappa_1^2\delta_{I_1I_2}\right)+\frac{1}{2}\left(\frac{1}{2}\kappa_1\kappa_2 f_{IJ}+\frac{1}{2}\kappa_1\kappa_2\delta_{IJ}\right)\right]\\ +\frac{2}{3}\left[\frac{1}{2}\left(\frac{1}{2}\kappa_1^2 f_{I_1I_2}+\frac{1}{2}\kappa_1^2\delta_{I_1I_2}\right)+\frac{1}{2}\kappa_1^2\kappa_2 f_{I_1I_2J}\right]\end{array}\right\}$$
$$+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\left[\frac{\kappa_1^3 f_{I_1I_2I_3}+\kappa_1^2\kappa_2 f_{I_1I_2J}}{2}\right],$$

$$f_{J_1J_2J_3} = \frac{1}{N^2}\left[\frac{1}{4}+\frac{3}{4}F_I\right]+\frac{3}{N}\left(1-\frac{1}{N}\right)\left[\frac{1}{2}\kappa_1^2 f_{I_1I_2}+\frac{1}{2}\kappa_1^2\delta_{I_1I_2}\right]+\left(1-\frac{1}{N}\right)\left(1-\frac{2}{N}\right)\kappa_1^3 f_{I_1I_2I_3}.$$

À l'équilibre, les coefficients de parenté s'obtiennent sans trop de peine:

$$\hat{f}_{I_1I_2} = \frac{N\left[6N-(N+1)\kappa_1\kappa_2+2(N-1)\kappa_2^2-(N-1)\kappa_1\kappa_2^3\right]}{D_7},$$

$$\hat{f}_{IJ} = \frac{4N^2+2N(N-1)\kappa_1^2+(N-1)^2\kappa_1^2\kappa_2^2-(N-1)^2\kappa_1\kappa_2^3}{D_7},$$

$$\hat{f}_{J_1J_2} = \frac{\left[2N+(N-1)\kappa_1\kappa_2\right]\left[4N-(N+1)\kappa_1\kappa_2-(N-1)\kappa_1^2\right]}{D_7},$$

où

$$\begin{aligned} D_7 = {} & 16N^3-4N^2(N-1)\kappa_1^2-4N^2(2N+1)\kappa_1\kappa_2-4N(N-1)^2\kappa_1\kappa_2^3 \\ & -2N^2(N-1)\kappa_1^3\kappa_2-(N-1)^2\kappa_1^3\kappa_2^3+(N-1)^2(2N+1)\kappa_1^2\kappa_2^4. \end{aligned}$$

Toutefois, comme il devient très difficile de calculer les autres coefficients à l'équilibre, on pose $\kappa_1=\kappa_2=\kappa$ pour la suite. On obtient alors les solutions suivantes:

$$\hat{f}_{I_1I_2} = \frac{3-\kappa^2}{2D_7}, \quad \hat{f}_{IJ} = \frac{1}{D_7}, \quad \hat{f}_{J_1J_2} = \frac{2-\kappa^2}{D_7},$$

$$\hat{\delta}_{IJ} = \frac{\kappa^2}{D_8}\begin{bmatrix} 32N^5+16N^4(N-1)\kappa+4N^3(N-1)(7N-2)\kappa^3+16N^2(N-1)^3\kappa^4 \\ -8N^3(N-1)^2\kappa^5+4N^3(N-1)^2\kappa^6+4N(N-1)^3(N-2)\kappa^7 \\ -8N(N-1)^4\kappa^8-N(N-1)^3(N-2)\kappa^9-2(N-1)^4(N-2)\kappa^{11} \end{bmatrix},$$

$$\hat{\gamma}_{IJ} = \frac{2(1-\kappa)}{D_8}\begin{bmatrix} 64N^6+64N^6\kappa+64N^5(N-1)\kappa^2+24N^5(N-1)\kappa^3+24N^5(N-1)\kappa^4 \\ +12N^3(N-1)^2(2N-3)\kappa^5-2N^2(N-1)^2(3N^2-4N+8)\kappa^6 \\ -2N^2(N-1)^2(3N^2-8N+2)\kappa^7-2N(N-1)^3(3N^2-8N+8)\kappa^8 \\ -N(N-1)^3(N^2+6N-8)\kappa^9-N^2(N-1)^3(N-2)\kappa^{10} \\ -N(N-1)^4(N-2)\kappa^{11}-2(N-1)^4(N-2)\kappa^{12} \end{bmatrix},$$

$$\hat{\delta}_{I_1I_2} = \frac{\kappa^2}{D_8}\begin{bmatrix} 48N^5 + 24N^4(N-1)\kappa - 16N^4\kappa^2 + 2N^3(N-1)(9N-10)\kappa^3 \\ +12N^2(N-1)^2(N-2)\kappa^4 - 2N^2(N-1)(6N^2-3N-2)\kappa^5 \\ -N(N-1)^2(N-2)(3N+4)\kappa^6 + 4N^2(N-1)^2\kappa^7 \\ -N(N-1)^2(N-2)(6N-7)\kappa^8 + 2(N-1)^3(N-2)\kappa^{10} \end{bmatrix},$$

$$\hat{\gamma}_{I_1I_2} = \frac{(1-\kappa)}{D_8}\begin{bmatrix} 192N^6 + 192N^6\kappa + 64N^5(2N-3)\kappa^2 + 8N^5(N-9)\kappa^3 \\ +8N^4(N-1)(N-4)\kappa^4 + 4N^3(N-1)(12N^2-45N+31)\kappa^5 \\ -2N^2(N-1)(21N^3-33N^2+40N-24)\kappa^6 \\ -2N^2(N-1)^2(21N^2-40N+2)\kappa^7 \\ -4N(N-1)^2(3N^3-14N^2+15N-8)\kappa^8 \\ +N(N-1)^2(N-2)(3N^2-7N+8)\kappa^9 + N(N-1)^3(N-2)(3N-2)\kappa^{10} \\ -2N(N-1)^3(N-2)(N-3)\kappa^{11} + (N-1)^4(N-2)^2\kappa^{12} \\ +(N-1)^4(N-2)^2\kappa^{13} \end{bmatrix},$$

$$\hat{f}_{I_1I_2I_3} = \frac{1}{2D_8}\begin{bmatrix} 80N^5 + 8N^4(13N-15)\kappa^2 + 4N^3(N-1)(3N-8)\kappa^3 \\ -2N^3(N-1)(20N+11)\kappa^4 + 4N^2(N-1)(9N^2-25N+21)\kappa^5 \\ -2N^2(N-1)(9N^2-27N+11)\kappa^6 - N(N-1)^2(6N^2-5N-28)\kappa^7 \\ -2N(N-1)^2(6N^2-17N+8)\kappa^8 - N(N-1)^2(2N^2-34N+33)\kappa^9 \\ +N(N-1)^3(9N-8)\kappa^{10} - 2(N-1)^3(N^2-3N+5)\kappa^{11} \\ +(N-1)^4(N-2)\kappa^{13} \end{bmatrix},$$

$$\hat{f}_{I_1I_2J} = \frac{1}{2D_8}\begin{bmatrix} 32N^5 + 48N^4(2N-1)\kappa^2 + 32N^3(N-1)^2\kappa^3 - 4N^3(4N^2-5N+5)\kappa^4 \\ +2N^2(N-1)(19N^2-38N+24)\kappa^5 + 4N^2(N-1)(2N^2-4N+1)\kappa^6 \\ -2N(N-1)(8N^3-9N^2-6N+8)\kappa^7 - N(N-1)^2(N-2)(7N-4)\kappa^8 \\ +8N(N-1)^3\kappa^9 - N(N-1)^2(N-2)(4N-5)\kappa^{10} - (N-1)^3(N-2)^2\kappa^{11} \\ +2(N-1)^3(N-2)\kappa^{12} \end{bmatrix},$$

$$\hat{f}_{IJ_1J_2} = \frac{1}{D_8}\begin{bmatrix} 32N^5 + 48N^4(N-1)\kappa^2 + 8N^3(N-1)(N-4)\kappa^3 - 4N^3(N-1)(4N-5)\kappa^4 \\ +4N^2(N-1)(5N^2-14N+12)\kappa^5 - 4N^2(N-1)(N^2-5N+5)\kappa^6 \\ -4N(N-1)^2(N^2-2N-4)\kappa^7 - 4N(N-1)^2(N-2)^2\kappa^8 \\ +4N(N-1)^2(N-2)\kappa^9 + 2N(N-1)^3(N-2)\kappa^{10} - (N-1)^3(N-2)^2\kappa^{11} \end{bmatrix},$$

$$\hat{f}_{J_1J_2J_3} = \frac{1}{D_8}\begin{bmatrix} 64N^5 + 32N^4(2N-3)\kappa^2 - 64N^3(N-1)\kappa^3 - 8N^3(N-1)(4N-5)\kappa^4 \\ +4N^2(N-1)(3N^2-26N+24)\kappa^5 - 8N^2(N-1)(3N^2-9N+7)\kappa^6 \\ +16N(N-1)^2(N+2)\kappa^7 - 4N(N-1)^2(3N^2-8N+8)\kappa^8 \\ -4N(N-1)^2(N-2)(N-3)\kappa^9 + 4N(N-1)^3(3N-4)\kappa^{10} \\ -(N-1)^3(N-2)(N-4)\kappa^{11} + 2(N-1)^4(N-2)\kappa^{13} \end{bmatrix},$$

où

$$D_7 = 4N - (5N-2)\kappa^2 + (N-1)\kappa^4$$

et

$$D_8 = D_7 \times \begin{bmatrix} 64N^6 - 32N^5\kappa^2 - 8N^4(N-1)(5N-2)\kappa^3 - 4N^3(N-1)(8N-7)\kappa^5 \\ -2N^2(N-1)^2(15N^2-30N+16)\kappa^6 + 12N^2(N-1)^2\kappa^7 \\ +2N(N-1)^2(N-2)(5N-4)\kappa^8 + N(N-1)^3(N-2)(5N-8)\kappa^9 \\ +(N-1)^4(N-2)^2\kappa^{12} \end{bmatrix}.$$

Les rapports de probabilités donnent lieu encore une fois à des expressions très complexes difficiles à traiter analytiquement. Des simulations numériques ont été effectuées pour quelques valeurs de N et κ (voir Figure E.4 et Tableau E.2). Les résultats obtenus indiquent que les inégalités

$$\frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}} > \frac{\hat{f}_{IJ}}{\hat{f}_{II}} > \frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} \quad \text{et} \quad \frac{\hat{\delta}_{I_1I_2}}{\hat{\delta}_{I_1I_1}} > \frac{\hat{f}_{I_1I_2}}{\hat{f}_{I_1I_1}} > \frac{\hat{\gamma}_{I_1I_2}}{\hat{\gamma}_{I_1I_1}}$$

seraient vérifiées, du moins pour ces valeurs de N. À nouveau, on constate d'après la Figure E.4 que ces rapports de probabilités ne diffèrent pas beaucoup entre eux, si bien qu'on pourrait assumer l'égalité de ces rapports.

Comme pour le modèle de dispersion *après* accouplement, quelques cas particuliers s'avèrent intéressants pour le modèle de dispersion *avant* accouplement.

- **Absence de dispersion (d = 0).** À l'instar du modèle de dispersion *après* accouplement, chaque groupe devient génétiquement homogène pour un allèle particulier. À l'équilibre, chaque individu est "complètement" consanguin, c'est-à-dire que ses deux gènes sont identiques par descendance avec probabilité 1. Ces conclusions demeurent valides autant pour une population haplo-diploïde que pour une population diploïde.

- **Dispersion totale (d = 1).** Étant donné que le nombre de groupes composant la population est très grand, les parents d'un rejeton choisi au hasard dans un groupe ne peuvent être apparentés puisqu'ils proviennent forcément de deux groupes "génétiquement" différents, d'où l'impossibilité pour ce rejeton d'être consanguin. À l'équilibre, chaque individu sera en fait non consanguin, c'est-à-dire que ses deux gènes seront identiques par descendance avec probabilité nulle. On peut vérifier que

$$\frac{\hat{f}_{IJ}}{\hat{f}_{II}} = \frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} = \frac{1}{2N} \qquad \text{et} \qquad \frac{\hat{f}_{I_1I_2}}{\hat{f}_{I_1I_1}} = \frac{\hat{\gamma}_{I_1I_2}}{\hat{\gamma}_{I_1I_1}} = \frac{3}{4N},$$

pour deux individus I et J dans une population diploïde, pour des individus I, I_1, I_2 diploïdes et J haploïde dans une population haplo-diploïde; cependant, les rapports $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\delta}_{I_1I_2}/\hat{\delta}_{I_1I_1}$ sont indéfinis.

- **Une femelle par groupe (N = 1).** Cette situation équivaut au modèle avec accouplement frère-sœur partiel. En effet, un mâle et une femelle qui ne migrent pas et qui, par conséquent, s'accouplent à l'intérieur du groupe d'où ils proviennent, sont obligatoirement frère et sœur. Dans ce cas, la probabilité d'un accouplement frère-sœur est $\kappa_1\kappa_2$. Ainsi, tous les résultats obtenus dans le modèle d'accouplement frère-sœur partiel s'appliquent et en particulier, on peut déduire les égalités suivantes (comparer avec les équations D.33 et D.34) :

$$\frac{\hat{f}_{IJ}}{\hat{f}_{II}} = \frac{\hat{\delta}_{IJ}}{\hat{\delta}_{II}} = \frac{\hat{\gamma}_{IJ}}{\hat{\gamma}_{II}} = \frac{1}{2-\kappa_1\kappa_2} \quad \text{et} \quad \frac{\hat{f}_{I_1I_2}}{\hat{f}_{I_1I_1}} = \frac{\hat{\delta}_{I_1I_2}}{\hat{\delta}_{I_1I_1}} = \frac{\hat{\gamma}_{I_1I_2}}{\hat{\gamma}_{I_1I_1}} = \frac{3-\kappa_1\kappa_2}{2(2-\kappa_1\kappa_2)},$$

pour deux individus I et J dans une population diploïde, pour des individus I, I_1, I_2 diploïdes et J haploïde dans une population haplo-diploïde.

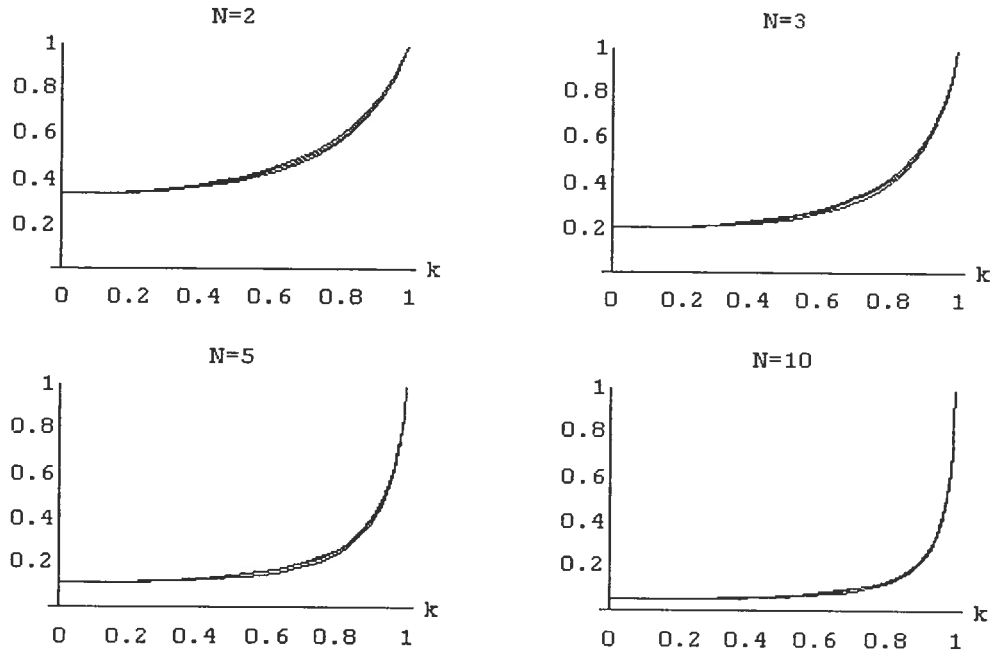

Figure E.1 Courbes des rapports de probabilités $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ obtenus dans le modèle diploïde de *dispersion après accouplement*, en fonction du paramètre κ et pour certaines valeurs fixées de *N*.

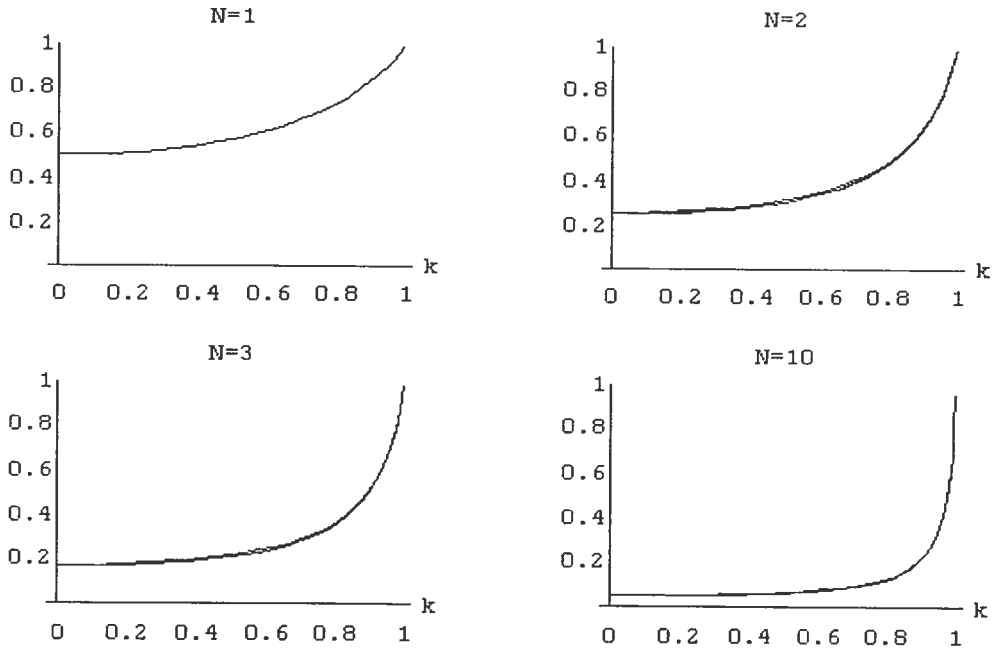

Figure E.2 Courbes des rapports de probabilités $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ obtenus dans le modèle diploïde de *dispersion avant accouplement*, en fonction du paramètre $\kappa = \kappa_1 = \kappa_2$ et pour certaines valeurs fixées de *N*. Pour $N = 1$, les trois courbes sont en tous points identiques.

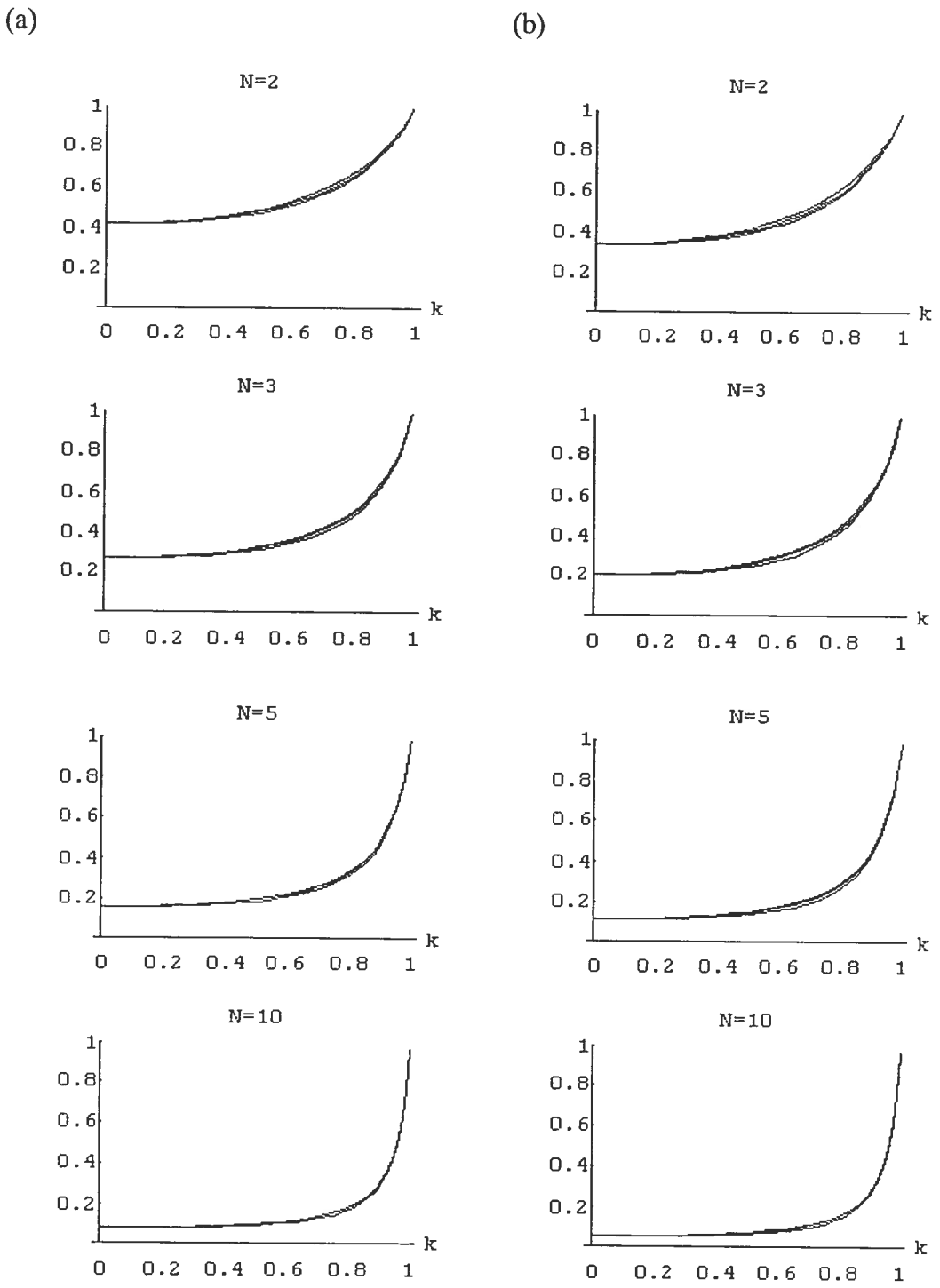

Figure E.3 Courbes des rapports de probabilités (a) $\hat{f}_{I_1I_2}/\hat{f}_{I_1I_1}$, $\hat{\delta}_{I_1I_2}/\hat{\delta}_{I_1I_1}$ et $\hat{\gamma}_{I_1I_2}/\hat{\gamma}_{I_1I_1}$ pour deux individus diploïdes I_1 et I_2, (b) $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ pour un individu diploïde I et un individu haploïde J, obtenus dans le modèle haplo-diploïde de *dispersion après accouplement*, en fonction du paramètre κ et pour certaines valeurs fixées de N.

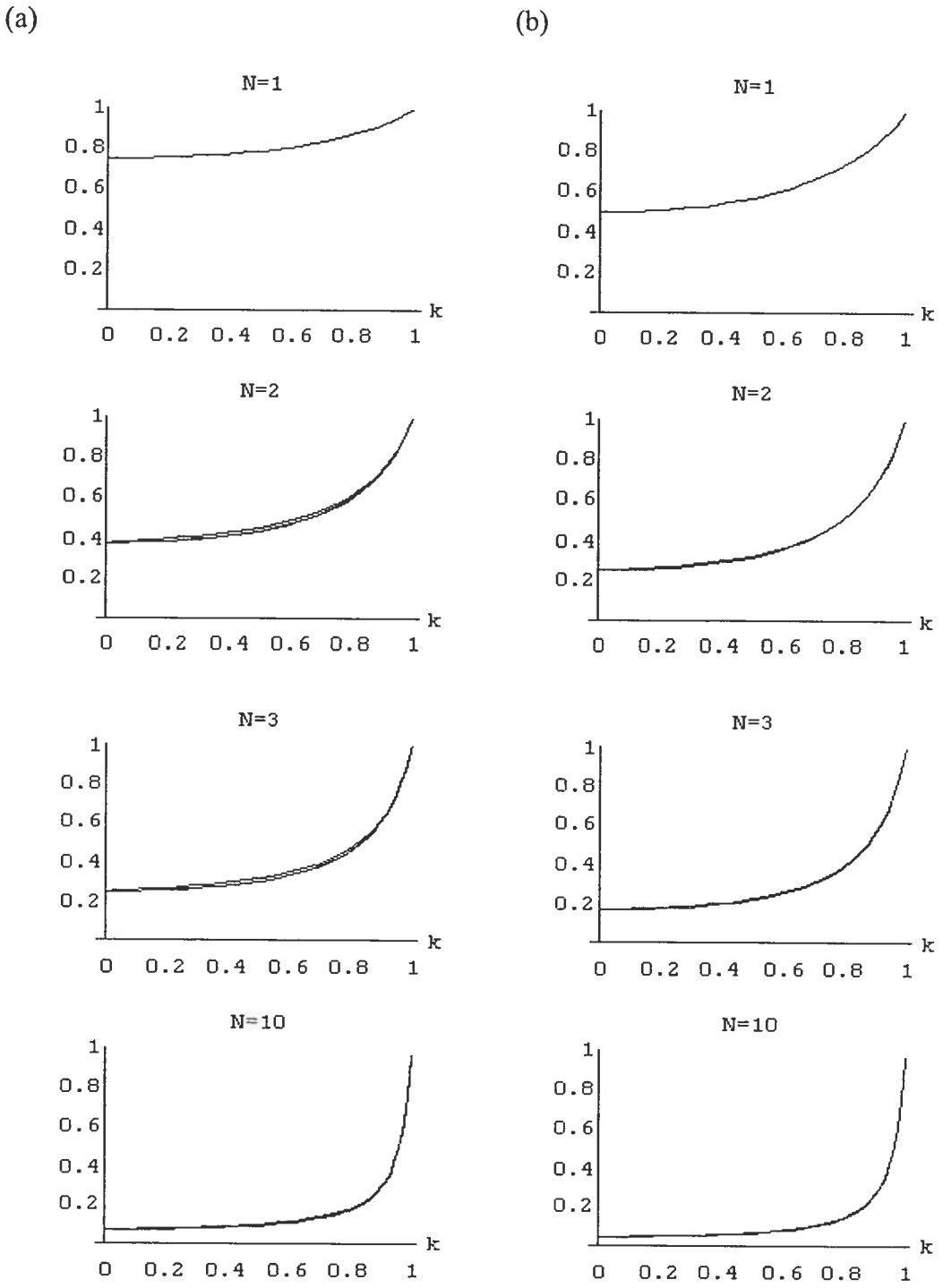

Figure E.4 Courbes des rapports de probabilités (a) $\hat{f}_{I_1I_2}/\hat{f}_{I_1I_1}$, $\hat{\delta}_{I_1I_2}/\hat{\delta}_{I_1I_1}$ et $\hat{\gamma}_{I_1I_2}/\hat{\gamma}_{I_1I_1}$ pour deux individus diploïdes I_1 et I_2, (b) $\hat{f}_{IJ}/\hat{f}_{II}$, $\hat{\delta}_{IJ}/\hat{\delta}_{II}$ et $\hat{\gamma}_{IJ}/\hat{\gamma}_{II}$ pour un individu diploïde I et un individu haploïde J, obtenus dans le modèle haplo-diploïde de *dispersion avant accouplement*, en fonction du paramètre $\kappa = \kappa_1 = \kappa_2$ et pour certaines valeurs fixées de N. Pour $N = 1$, les trois courbes en (a) d'une part, et les trois courbes en (b) d'autre part, sont en tous points identiques.

Tableau E.1 Valeurs numériques des rapports de probabilités dans le modèle de dispersion après accouplement.

$\kappa = 0$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	1	*	1	1	*	1	1	*	1
2	0,3333	0,3333	0,3333	0,4167	0,4167	0,4167	0,3333	0,3333	0,3333
3	0,2000	0,2000	0,2000	0,2667	0,2667	0,2667	0,2000	0,2000	0,2000
5	0,1111	0,1111	0,1111	0,1556	0,1556	0,1556	0,1111	0,1111	0,1111
10	0,0526	0,0526	0,0526	0,0763	0,0763	0,0763	0,0526	0,0526	0,0526

$\kappa = 0,1$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	1	*	1	1	*	1	1	*	1
2	0,3350	0,3358	0,3356	0,4184	0,4193	0,4190	0,3352	0,3362	0,3358
3	0,2011	0,2017	0,2016	0,2679	0,2686	0,2685	0,2012	0,2021	0,2019
5	0,1117	0,1122	0,1121	0,1563	0,1568	0,1568	0,1118	0,1124	0,1123
10	0,0529	0,0531	0,0531	0,0767	0,0770	0,0770	0,0529	0,0533	0,0532

$\kappa = 0,5$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	1	*	1	1	*	1	1	*	1
2	0,3894	0,4071	0,4000	0,4742	0,4909	0,4841	0,3951	0,4163	0,4076
3	0,2389	0,2537	0,2500	0,3114	0,3265	0,3226	0,2441	0,2629	0,2581
5	0,1341	0,1443	0,1429	0,1847	0,1957	0,1940	0,1378	0,1513	0,1493
10	0,0638	0,0693	0,0690	0,0916	0,0978	0,0973	0,0658	0,0733	0,0728

$\kappa = 0,8$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	1	*	1	1	*	1	1	*	1
2	0,5694	0,5981	0,5814	0,6459	0,6705	0,6557	0,5890	0,6204	0,6015
3	0,3937	0,4211	0,4098	0,4760	0,5007	0,4900	0,4201	0,4508	0,4374
5	0,2422	0,2631	0,2577	0,3118	0,3314	0,3258	0,2679	0,2915	0,2848
10	0,1231	0,1353	0,1337	0,1675	0,1793	0,1775	0,1409	0,1549	0,1527

$\kappa = 0,9$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	1	*	1	1	*	1	1	*	1
2	0,7184	0,7411	0,7246	0,7761	0,7946	0,7808	0,7394	0,7629	0,7454
3	0,5577	0,5820	0,5681	0,6335	0,6539	0,6416	0,5935	0,6184	0,6034
5	0,3843	0,4050	0,3968	0,4633	0,4810	0,4732	0,4280	0,4490	0,4398
10	0,2159	0,2293	0,2262	0,2772	0,2890	0,2856	0,2535	0,2669	0,2634

$\kappa = 0,99$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	1	*	1	1	*	1	1	*	1
2	0,9616	0,9652	0,9617	0,9710	0,9737	0,9711	0,9661	0,9696	0,9663
3	0,9259	0,9307	0,9263	0,9436	0,9471	0,9438	0,9373	0,9415	0,9376
5	0,8619	0,8673	0,8627	0,8931	0,8971	0,8936	0,8860	0,8905	0,8865
10	0,7349	0,7402	0,7363	0,7879	0,7917	0,7887	0,7808	0,7849	0,7817

L'astérisque (*) représente une valeur indéfinie.

Tableau E.2 Valeurs numériques des rapports de probabilités dans le modèle de dispersion avant accouplement.

$\kappa = 0$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	*	0,5000	0,5000	*	0,7500	0,7500	*	0,5000	0,5000
2	*	0,2500	0,2500	*	0,3750	0,3750	*	0,2500	0,2500
3	*	0,1667	0,1667	*	0,2500	0,2500	*	0,1667	0,1667
5	*	0,1000	0,1000	*	0,1500	0,1500	*	0,1000	0,1000
10	*	0,0500	0,0500	*	0,0750	0,0750	*	0,0500	0,0500

$\kappa = 0,1$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	0,5025	0,5025	0,5025	0,7513	0,7513	0,7513	0,5025	0,5025	0,5025
2	0,2570	0,2519	0,2519	0,3848	0,3770	0,3770	0,2571	0,2522	0,2522
3	0,1726	0,1681	0,1681	0,2586	0,2517	0,2517	0,1727	0,1683	0,1683
5	0,1042	0,1009	0,1009	0,1562	0,1512	0,1512	0,1042	0,1011	0,1011
10	0,0523	0,0505	0,0505	0,0785	0,0756	0,0756	0,0523	0,0506	0,0506

$\kappa = 0,5$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	0,5714	0,5714	0,5714	0,7857	0,7857	0,7857	0,5714	0,5714	0,5714
2	0,3185	0,3068	0,3077	0,4528	0,4342	0,4356	0,3249	0,3161	0,3168
3	0,2204	0,2100	0,2105	0,3180	0,3004	0,3014	0,2271	0,2187	0,2192
5	0,1363	0,1288	0,1290	0,1993	0,1860	0,1864	0,1419	0,1354	0,1356
10	0,0698	0,0655	0,0656	0,1031	0,0953	0,0954	0,0732	0,0693	0,0694

$\kappa = 0,8$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	0,7353	0,7353	0,7353	0,8676	0,8676	0,8676	0,7353	0,7353	0,7353
2	0,4868	0,4781	0,4808	0,6097	0,5961	0,6006	0,5133	0,5069	0,5090
3	0,3636	0,3552	0,3571	0,4707	0,4554	0,4592	0,3955	0,3871	0,3892
5	0,2413	0,2349	0,2358	0,3236	0,3099	0,3122	0,2715	0,2632	0,2646
10	0,1311	0,1272	0,1276	0,1818	0,1726	0,1734	0,1524	0,1464	0,1470

$\kappa = 0,9$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$
1	0,8403	0,8403	0,8403	0,9202	0,9202	0,9202	0,8403	0,8403	0,8403
2	0,6398	0,6339	0,6369	0,7374	0,7287	0,7334	0,6719	0,6673	0,6698
3	0,5164	0,5103	0,5128	0,6158	0,6046	0,6097	0,5608	0,5535	0,5568
5	0,3726	0,3675	0,3690	0,4634	0,4520	0,4558	0,4218	0,4135	0,4163
10	0,2196	0,2163	0,2169	0,2866	0,2777	0,2795	0,2607	0,2538	0,2553

$\kappa = 0,99$

	Diploïde			Haplo-diploïde					
N	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$f_{I,J}/f_{II}$	$\delta_{I_1I_2}/\delta_{I_1I_1}$	$\gamma_{I_1I_2}/\gamma_{I_1I_1}$	$f_{I_1I_2}/f_{I_1I_1}$	$\delta_{I,J}/\delta_{II}$	$\gamma_{I,J}/\gamma_{II}$	$g_{I,J}/g_{II}$
1	0,9805	0,9805	0,9805	0,9902	0,9902	0,9902	0,9805	0,9805	0,9805
2	0,9437	0,9428	0,9437	0,9620	0,9608	0,9619	0,9525	0,9517	0,9524
3	0,9096	0,9085	0,9095	0,9353	0,9334	0,9351	0,9261	0,9246	0,9259
5	0,8483	0,8471	0,8481	0,8862	0,8836	0,8859	0,8774	0,8752	0,8771
10	0,7260	0,7248	0,7256	0,7834	0,7805	0,7827	0,7757	0,7729	0,7750

L'astérisque (*) représente une valeur indéfinie.

Accords du coauteur

Ghislain Rocheleau

Ph.D. Statistique

1er article: Rocheleau, G., Lessard, S. (2000). Stability analysis of the partial selfing selection model. *Journal of Mathematical Biology*.

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Ghislain Rocheleau inclue cet article dans sa thèse de doctorat qui a pour titre *Effets de la consanguinité dans des modèles de sélection pour des populations structurées en familles*.

Sabin Lessard [redacted] 6 janvier 2003

2ème article: Lessard, S., Rocheleau, G. (2002). Change in frequency of a rare mutant allele: A general formula and applications to partial inbreeding models. *Journal of Mathematical Biology*.

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Ghislain Rocheleau inclue cet article dans sa thèse de doctorat qui a pour titre *Effets de la consanguinité dans des modèles de sélection pour des populations structurées en familles*.

Sabin Lessard [redacted] 6 janvier 2003

3ème article: Rocheleau, G., Lessard, S. New insights into kin selection theory in family-structured populations with inbreeding. Soumis pour publication dans *Theoretical Population Biology*.

À titre de coauteur de l'article identifié ci-dessus, je suis d'accord pour que Ghislain Rocheleau inclue cet article dans sa thèse de doctorat qui a pour titre *Effets de la consanguinité dans des modèles de sélection pour des populations structurées en familles*.

Sabin Lessard [redacted] 6 janvier 2003