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STRATÉGIES D'HISTOIRE DE VIE DANS UNE POPULATION D'ÉCUREUILS ROUX D'AMÉRIQUE DU NORD

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Résumé

Ce travail de doctorat avait comme principal objectif de mieux comprendre les stratégies démographiques au sein des populations animales, en se basant sur l'exemple de l'écureuil roux d'Amérique du Nord (*Tamiasciurus hudsonicus*). La population d'écureuils roux de Kluane (territoire du Yukon, Canada) est étudiée depuis 1987. Chaque année, sur deux aires d'étude témoins, tous les individus, mâles et femelles, sont capturés et pesés régulièrement au cours de l'été. D'autre part, la reproduction de l'ensemble des femelles de ces zones (environ 90 par année) est suivie en détail, et tous les jeunes sont marqués. La faible dispersion et les recaptures généralement faciles font que le sort et l'activité de reproduction de la majorité des écureuils de cette population sont connus. Cette thèse de doctorat s'intéresse tout d'abord aux effets cohortes et à leur influence sur les stratégies de reproduction dans cette population d'écureuils. Elle se concentre ensuite sur les effets de l'âge sur les paramètres démographiques et l'investissement reproducteur, et finalement sur les coûts de la reproduction. L'activité de reproduction des mâles étant inconnu, la majorité de ce travail concerne les femelles.

Les données à long-terme de suivi individuel utilisées dans ce projet ont tout d'abord permis de montrer le rôle joué par la disponibilité alimentaire l'année de naissance sur la qualité phénotypique et les stratégies de reproduction. Plus les conditions alimentaires sont favorables l'année de naissance, plus les individus seront de qualité phénotypique élevée tout au long de leur vie, et plus leur reproduction sera intense en début de vie. Cependant, nos résultats montrent qu'une reproduction intense en début de vie est associée à une survie moins grande et une sénescence plus précoce. Le processus de sénescence est marqué dans notre population, et a des conséquences inter-générationnelles : une femelle âgée a une moins bonne survie, un moins bon succès reproducteur et produit des jeunes de moins bonne qualité, malgré un effort reproducteur plus important. Ce travail de doctorat souligne également le rôle de l'hétérogénéité individuelle au sein d'une population dans l'étude et la compréhension des compromis évolutifs. Il montre notamment que des compromis entre reproduction et survie existent et diffèrent selon l'âge et le comportement de l'individu. En particulier, des coûts significatifs de la reproduction sur la survie des femelles de moins de deux ans et de plus de cinq ans ont été mis en évidence, alors qu'aucun coût de la reproduction n'a pu être détecté pour les femelles entre deux et cinq ans.

Abstract

The main goal of this PhD thesis was to improve our understanding of life-history strategies in free-living animal populations, based on a population of North American red squirrels (*Tamiasciurus hudsonicus*). The red squirrel population at Kluane (Yukon Territory, Canada) is monitored since 1987. All male and female squirrels on two study areas are regularly trapped and weighed throughout the summer. Reproductive status of all the females (90 females are followed every year on average) is known and all the juveniles are tagged as soon as 20-25 days old. Thanks to low dispersion and easy recaptures, fate and breeding activity of almost all squirrels are known with certainty. First, this thesis focuses on short- and long-term cohort effects on individual quality and reproductive activity. Then, it deals with the effects of age on demographic parameters and reproductive investment, and finally, with costs of reproduction. As breeding status of males is generally unknown in this population, this thesis concerns mainly female red squirrels.

This long-term dataset allowed us to show the importance of food availability the first year of life and of individual phenotypic quality on reproductive strategies. Females born a year with high food availability will be of higher quality than females born a year of low food availability, and breed more intensely at the beginning of their life. However, an intense breeding activity early in life is associated to a lower survival and an earlier onset of senescence. The senescence process has been clearly shown in our red squirrel population and has inter-generational effects: an old female has a lower survival, a lower breeding success and produces juveniles of lower quality, despite a higher reproductive effort. This thesis also points out the importance of considering individual heterogeneity within the population to correctly interpret trade-offs between life-history traits. In particular our results show that trade-offs between reproduction and survival exist and vary according to individual's age and behaviour. In particular, we found clear costs of reproduction on survival for the youngest and oldest females, whereas no such cost has been detected for prime-age females.

Chapitre 1 Introduction et cadre théorique

1.1 Théorie d'histoire de vie

1.1.1 Définition

Ce travail de doctorat se place dans le contexte de la théorie d'histoire de vie. La théorie d'histoire de vie se base directement sur les notions de sélection naturelle et d'adaptation (Stearns, 1992) et vise à comprendre les associations entre les traits d'histoire de vie (i.e. les traits reliés à la survie et à la reproduction), les pressions évolutives à l'origine de ces associations, et ainsi la diversité des patrons observés dans ces associations (Partridge & Harvey, 1988). La théorie d'histoire de vie pose le cadre théorique permettant d'étudier et de comprendre « quelles circonstances dans l'environnement font qu'il est plus ou moins avantageux pour un organisme d'augmenter ou non son investissement dans la reproduction » (Fisher, 1930), et donc finalement de comprendre comment les organismes vont répondre à un changement dans cet environnement (Partridge *et al.*, 1988). La théorie d'histoire de vie n'a pas été proposée par un auteur ou à la suite d'une unique publication. Il s'agit plutôt d'un ensemble d'études visant à comprendre l'évolution de certains traits (e.g. Lack, 1947; Cole, 1954; Williams, 1957; Cody, 1966; Williams, 1966b; Mac Arthur & Wilson, 1967), qui ont trouvé un cadre théorique commun avec cette théorie. Le travail de Cole (1954) est l'un des premiers à avoir étudié et quantifié les conséquences de la variation de certains traits d'histoire de vie sur la dynamique des populations (notamment l'importance de l'âge de première reproduction, α), et donc correspond à l'une des premières approches quantitatives concernant l'évolution des traits d'histoire de vie.

La théorie d'histoire de vie traite de l'allocation de l'énergie par les organismes pour assurer leur croissance, leur survie et leur reproduction, « the general life history problem » (Cody, 1966; Williams, 1966a; Schaffer, 1983) et fait donc référence aux patrons d'associations entre les différents traits d'histoire de vie (Stearns, 1976). La théorie d'histoire de vie suppose que ces co-adaptations entre les traits ou paramètres démographiques se sont mises en place au cours de l'évolution par sélection naturelle et qu'elles maximisent l'aptitude phénotypique ou valeur sélective (i.e. *fitness*) de l'organisme dans les conditions environnementales où il a évolué. Dans cette travail, la définition d'aptitude phénotypique sera celle de Danchin *et al.* (2005) et correspondra « à la capacité d'un individu à produire des descendants matures, relativement aux autres individus de la population et au même moment ».

Fondamentalement, la théorie d'histoire de vie a pour but d'interpréter l'énorme variété des cycles de vie et stratégies de reproduction observées dans la nature en tant que réponses à certaines pressions de sélection et contraintes phylogénétiques.

1.1.2 De la théorie d'histoire de vie aux stratégies biodémographiques

Notion de stratégie biodémographique, ou stratégie d'histoire de vie

La théorie d'histoire de vie fait référence aux associations entre les paramètres démographiques. Ces combinaisons ou co-adaptations entre les traits correspondent à la notion de stratégie, ou tactique, biodémographique (Stearns, 1976; Gaillard *et al.*, 1989). Cette notion de stratégie est souvent présentée dans le contexte de la sélection *r*-*K*. Les termes sélection *r* et *K* apparaissent pour la première fois dans les travaux de McArthur (1958; 1962), Cody (1966) et McArthur et Wilson (1967), les termes *r* et *K* faisant référence au modèle logistique de croissance des populations. McArthur et Wilson (1967) proposent que des valeurs de *r* ou de *K* peuvent être attribuées à des allèles (interprétation de Roff, 2002). Les génotypes à fort *r* vont être sélectionnés dans un environnement non saturé (par exemple lorsque la mortalité densité-indépendante est importante ou lorsque la densité varie fortement), alors que dans un environnement saturé ceux avec une forte valeur de *K* ont l'avantage. C'est-à-dire, à faible densité, les génotypes permettant une croissance rapide de la population sont sélectionnés, alors qu'à forte densité, la sélection se fait en faveur d'une plus grande capacité de compétition. En terme de traits, les associations suivantes sont donc supposées : un âge précoce de première reproduction, une grande taille de portée ou nichée, durée de génération courte suite à une sélection de type *r*, et les traits opposés pour une sélection *K*.

Cette approche présente certaines limites, soulevées notamment par Stearns (1976; 1977; 1992), Charlesworth (1980) et Boyce (1984). Une critique importante est que ce modèle de sélection, dépendant de la densité, ne considère pas l'action de la densité séparément pour les différentes classes d'âge (ou différents stades) du cycle. L'action de la « densité-dépendance » peut se faire essentiellement sur la survie adulte ou sur la survie juvénile par exemple. Il est alors peu probable d'obtenir les mêmes stratégies dans ces deux situations, les pressions de sélection étant totalement différentes. D'autre part, la « densité-dépendance » n'est qu'un des multiples facteurs agissant sur l'évolution des stratégies démographiques et ne peut probablement pas à elle seule expliquer la totalité des stratégies observées.

La notion de sélection *r*-*K* telle que décrite par McArthur and Wilson (1967) a été utilisée par Pianka (1970) pour décrire, et prédire, certaines associations de traits d'histoire de vie observées chez les êtres vivants, sans faire référence aux effets de la densité. Pianka suppose qu'une reproduction précoce, une petite taille, une vie courte sont associées à une sélection *r*, et les traits opposés à une sélection *K*. Comme argument à ses conclusions, il compare des vertébrés, supposés de type *K* et des invertébrés, de type *r*. Pianka (1970) n'utilise plus les termes sélection *r* et sélection *K* pour décrire des phénomènes de sélection densité-dépendante. Il s'agit alors plutôt de label *r* et *K* (Parry, 1981). De nombreux travaux ont suivi pour tenter de rapprocher les patrons observés en nature à la notion de sélection *r*-*K*, telle que définie par Pianka (1970), sans lien forcément avec la densité. Le travail de Pianka (1970), tout comme l'utilisation erronée du concept de sélection *r*-*K* qui a suivi, a soulevé de nombreuses critiques (voir par exemple Parry, 1981; Boyce, 1984; Stearns, 1992; Roff, 2002), et la notion de sélection *r*-*K* ne devrait pas être utilisée pour représenter la diversité des stratégies démographiques.

Gradient lent-rapide

Le travail de Pianka (1970), même s'il est critiquable, a tout de même permis de mettre en avant l'idée que les stratégies pouvaient se regrouper selon certains gradients. Une fois corrigé pour la masse corporelle et la phylogénie, certaines associations persistent entre les traits d'histoire de vie et se placent sur un gradient lent-rapide (slow-fast continuum, Western, 1979; Stearns, 1983; Gaillard *et al.*, 1989; Promislow & Harvey, 1990). Les espèces lentes sont caractérisées par une durée de génération longue, un âge avancé de première reproduction, une grande longévité, un faible taux de reproduction, et les espèces rapides par les traits opposés. Ce gradient lent-rapide a été confirmé chez différents groupes (Gaillard *et al.*, 1989 pour les mammifères et oiseaux; Shine & Charnov, 1992 pour des résultats concordants chez les reptiles; Rochet *et al.*, 2000 pour des poissons).

La durée de génération, ou simplement l'âge de première reproduction, permettent de situer une espèce ou population sur ce gradient lent-rapide (Gaillard *et al.*, 2005). Dans le cas où les données permettant une analyse démographique détaillée ne sont pas disponibles, la position sur ce gradient permet de déterminer quels sont les traits d'histoire de vie les plus influents sur la dynamique de la population, les espèces rapides ayant une dynamique plus sensible aux paramètres liés à la reproduction, et les lentes ayant une dynamique plutôt influencée par les paramètres de survie (Gaillard *et al.*, 1989; Oli & Dobson, 2003; Gaillard *et al.*, 2005; Oli & Dobson, 2005).

1.1.3 Stratégies d'histoire de vie ou variations des composantes biodémographiques individuelles ?

La notion de stratégie d'histoire de vie fait généralement référence aux stratégies mises en place au cours de l'évolution par sélection naturelle. Ces stratégies peuvent varier entre espèces, mais également au sein d'une même espèce entre populations (Roff, 2002). De mplus, les histoires de vie des individus peuvent aussi varier au sein même d'une population. On parle alors plutôt de tactiques de reproduction ou de variation des composantes biodémographiques individuelles (Danchin *et al.*, 2005), sans forcément supposer l'existence de différentes pressions de sélection à l'origine de cette variabilité. La diversité des tactiques de reproduction au sein d'une population peut en effet s'expliquer par l'hétérogénéité spatiale et/ou temporelle des conditions environnementales, l'hétérogénéité de la qualité des individus, etc. Ces tactiques ne représentent donc pas forcément des stratégies au sens adaptatif du terme.

Ce travail de doctorat s'articule essentiellement autour de cette notion de variation des composantes démographiques individuelles au sein d'une population de petit mammifères. Cependant, le terme « stratégie d'histoire de vie » sera majoritairement employé dans cette thèse. En effet, cette notion est celle généralement employée dans la littérature pour désigner le contexte théorique de l'étude des composantes démographiques. D'autre part, la notion de variation des composantes individuelles reste assez vague. En effet, il est difficile de saisir avec ce terme si le travail s'intéresse à la variation d'un trait en particulier, ou à la variation de l'ensemble des paramètres démographiques, incluant les compromis entre ceux-ci. Mon travail de doctorat a pour principal but de mieux comprendre les co-variations entre les paramètres démographiques au sein d'une population, et non la variation des traits pris séparément. Ainsi, la notion d'histoire de vie, ou de stratégie d'histoire de vie, reste plus proche de l'objectif de cette thèse.

1.1.4 Théorie d’histoire de vie ou théorie des coûts de la reproduction ?

La notion de compromis est centrale à la théorie d’histoire de vie (Bell, 1980; Roff, 2002). Cette théorie suppose en effet que l’énergie disponible (ou utilisable) est limitée, et que les organismes doivent donc faire des compromis entre investir cette énergie dans leur survie (leur *soma*) ou dans leur reproduction (Williams, 1966b, 1966a). La notion de stratégie d’histoire de vie se base sur l’idée que, au cours de l’évolution, se sont mises en place différentes tactiques optimisant cette répartition de l’énergie, en fonction de différentes contraintes (Stearns, 1983; Partridge *et al.*, 1988; Partridge & Sibly, 1991), les tactiques non optimales étant éliminées via la sélection naturelle. Ainsi, la notion de stratégie ou tactique démographique, et la théorie d’histoire de vie, incluant tous les compromis qui en découlent, se basent principalement sur l’existence de coûts de la reproduction (se reproduire demande de l’énergie, énergie qui ne peut donc être utilisée pour son fonctionnement ou sa survie, et donc se reproduire entraîne des coûts en terme de performance future). Si la reproduction était gratuite, et libre de toutes contraintes, une seule stratégie serait optimale : se reproduire aussi vite que possible, tout au long de sa vie et produire un maximum de jeunes. Ainsi, si on limite l’évolution des stratégies démographiques à l’action de la sélection naturelle, la théorie d’histoire de vie pourrait se limiter à une théorie des coûts de la reproduction.

Plusieurs éléments peuvent cependant être avancés afin de nuancer les précédentes affirmations. Tout d’abord, l’évolution ne se fait pas uniquement par sélection naturelle, et d’autres « forces », comme la dérive génétique, doivent aussi être considérées. La dérive génétique correspond au fait que les fréquences alléliques au sein d’une population peuvent fluctuer de manière aléatoire, en l’absence d’autres forces de sélection. Elle peut ainsi permettre à certains caractères (ou plutôt allèles) de se maintenir dans une population, même si ces caractères ne sont pas optimaux (Mayr, 1970). À l’opposé, des allèles codant pour des caractères optimaux (i.e. permettant d’obtenir une fitness maximale) peuvent par ce même processus ne pas se fixer (i.e. ne pas avoir une fréquence égale à 1 dans la population). Ainsi, par la dérive génétique, et donc le hasard, certaines stratégies démographiques non optimales peuvent être observées (Gould & Lewontin, 1979; Tuomi, Hakala & Haukioja, 1983). Cependant, il est difficile d’imaginer que ces stratégies soient très éloignées d’un optimum (en tout cas pour des populations d'effectif assez grand, où l'importance de la dérive serait plus faible, Gouyon, Henry & Arnould, 1997), car cela impliquerait que des traits « optimaux », permettant donc d'obtenir une fitness très supérieure et pour lesquels la force de la sélection serait très grande, n'aient pas été sélectionnés. Il semble plus réaliste de penser que ces stratégies démographiques soient relativement proches de stratégies optimales ("strategies that are satisfactory or good enough", Tuomi *et al.*, 1983, p.33).

Une autre notion permettant de relativiser l'importance des compromis évolutifs dans l'élaboration des stratégies démographiques est l'existence de contraintes phylogénétiques. Les contraintes correspondent à certains traits fixés au sein d'une unité phylogénétique (espèce, famille, genre…), qui déterminent l'intervalle de valeurs que peuvent prendre d'autres traits (Stearns, 1992, chapitre 5) : une mésange ne pourra pas produire un jeune de la taille d'un albatros, quelle que soit l'énergie dont elle dispose; un manchot royal ne pourra pas incuber plus d'un œuf... Le fait que certains traits ne puissent varier que dans un intervalle particulier, quelles que soient les conditions environnementales, implique que les compromis liant ce trait à d'autres sont aussi contraints à un certain intervalle de valeurs. Ainsi, l'évolution des stratégies démographiques est-elle déterminée en partie par l'existence de ces contraintes (Stearns, 1977; Gould *et al.*, 1979; 1980; Tuomi *et al.*, 1983).

Même si l'évolution des stratégies d'histoire de vie n'est pas seulement due à la sélection naturelle, mais que d'autres « forces » doivent être prises en considération, la notion de coûts de la reproduction reste centrale. Il est difficile de penser qu'une stratégie reproductive ne puisse s'expliquer que par l'action de la dérive génétique, ou par l'existence de contraintes, et les compromis évolutifs sont probablement, dans la majorité des cas, le principal facteur à l'origine des stratégies démographiques. Ainsi, les coûts de la reproduction restent à la base de la théorie d'histoire de vie, théorie faisant la prédiction que l'effort reproducteur, et sa variation au cours de la vie de l'organisme, optimisent la valeur reproductive de l'organisme (Fisher, 1930; Williams, 1966b; Charlesworth, 1994, voir cependant Tuomi et al., 1983 pour une vision alternative). La théorie d'histoire de vie pose le cadre théorique permettant de répondre à une des questions fondamentales en écologie : pourquoi les organismes ne se reproduisent-ils pas plus ?

1.2 Age et théorie d’histoire de vie

L’un des principes majeurs de la sélection naturelle en tant que force motrice de l’évolution est que ses effets diminuent avec l’âge de l’individu (Medawar, 1952; Williams, 1957; Hamilton, 1966) : un allèle ayant un effet bénéfique tôt dans la vie de l’organisme aura beaucoup plus de chance d’être sélectionné et de voir sa fréquence augmentée au sein de la population que si son effet n’apparaît que tard dans la vie. Ainsi, la théorie d’histoire de vie, et l’évolution des stratégies démographiques, sont intimement liées à la variation des traits en fonction de l’âge (tout du moins pour les populations structurées en âge ou stade).

Cette diminution des effets de la sélection avec un âge croissant est à la base des hypothèses permettant d’expliquer l’existence de sénescence au sein des populations d’êtres vivants. La sénescence se définit par une détérioration des capacités physiologiques d’un organisme au fur et à mesure qu’il vieillit, conduisant à une diminution de sa performance démographique (Rose, 1991). La sénescence a donc des effets apparents négatifs sur la *fitness* de l’organisme, de par une diminution de sa survie et/ou de sa reproduction. La sénescence étant, au moins en partie, déterminée génétiquement (Kirkwood & Austad, 2000), son existence semble ne pas supporter la théorie darwinienne de l’évolution. Cependant, plusieurs hypothèses permettent d’expliquer son existence dans un contexte évolutionniste. L’action de la sélection naturelle étant faible ou nulle pour des traits s’exprimant à des âges avancés, des mutations néfastes ne s’exprimant qu’en fin de vie peuvent être apparues et s’être accumulées au cours de l’évolution (mutation accumulation hypothesis, Medawar, 1952). Des gènes ayant des effets positifs en début de vie peuvent également avoir été sélectionnés, même s’ils entraînent une diminution de la performance en fin de vie (antagonistic pleiotropy hypothesis, Williams, 1957). Enfin, de par l’existence de coûts de la reproduction, des compromis peuvent exister entre reproduction tôt dans la vie et survie ou reproduction en fin de vie, pouvant ainsi également expliquer la sénescence (disposable soma hypothesis, Kirkwood, 1977).

Le fait que l’énergie disponible et assimilable par les organismes soit limitée, et donc que la reproduction soit coûteuse, suppose dans un contexte évolutif que l’allocation de l’énergie pour la reproduction (ou effort reproducteur) soit optimisée à chaque âge ou stade maximisant ainsi la valeur reproductive des individus (Charlesworth, 1994). Ainsi, l’âge de première reproduction devrait maximiser la *fitness* de l’individu (Cole, 1954), et son effort reproducteur devrait augmenter au fur et à mesure que sa valeur reproductive résiduelle (i.e. la contribution relative d'un individu à la population au cours de tous les stades de son cycle à partir du moment présent) diminue (Fisher, 1930; Charlesworth & Leòn, 1976).

Les liens entre âge et traits d'histoire de vie sont donc au centre de la théorie d'histoire de vie, et les prendre en compte est essentiel pour comprendre l'évolution des stratégies démographiques et la dynamique des populations (Charlesworth, 1994; Caswell, 2001).

1.3 Hétérogénéité individuelle et théorie d'histoire de vie

La majorité des modèles utilisés pour comprendre l'évolution des stratégies d'histoire de vie ou la dynamique des populations se basent sur des données moyennes de traits pour une population donnée, données issues de table de vie ou de suivi longitudinal (Caswell, 2001; Roff, 2002). Cependant, l'hétérogénéité de la qualité des individus au sein même d'une population peut être extrêmement importante et c'est elle qui permet la sélection naturelle. Pour citer Stearns (1992, p.10), "variation in fitness among individuals *is* natural selection". Dans l'ensemble de cette thèse, la notion de qualité individuelle sera utilisée selon la définition de McNamara et Houston (1996), et correspondra donc à « l'ensemble des conditions physiologiques et environnementales qui déterminent la survie et la reproduction de l'individu ». Cette définition pose certains problèmes. Il rend notamment la nuance entre condition, état et qualité difficile à saisir. La condition, qu'on peut considérer synonyme de l'état, d'un individu peut varier au cours de la vie. Par exemple, un individu sera moins performant âgé que jeune dans le cas où la sénescence existe, mais il peut tout de même rester un individu de meilleure qualité que les autres en moyenne. Le fait de ne pas clairement discerner condition et qualité est lié au fait que cette notion de qualité peut être à la fois statique dans le temps et dynamique. Plus précisément, un individu peut posséder certaines caractéristiques (de part un habitat de meilleure qualité, un génome plus performant, certains effets maternels ou certains effets cohortes…) qui le rendent plus performant (d'un point de vue démographique) que les autres. Ces caractéristiques, qu'on peut imaginer statiques (c'est à dire qu'elles ne varient pas dans le temps) peuvent permettre à l'individu en question d'avoir une meilleure survie et/ou reproduction, et finalement une aptitude phénotypique au dessus de la moyenne. Cependant, la condition de cet individu peut quand même varier, et être à un moment donné moins bonne que la condition d'autres individus de la même population. Dans le cas d'une population structurée en âge où la sénescence est marquée, un vieil individu sera par exemple moins performant qu'un plus jeune, mais pourra quand même produire un plus grand nombre de descendants viables au cours de sa vie.

Nous ne discuterons pas plus en détail cette notion de qualité et de condition individuelle dans cette thèse. Dans l'ensemble de ce travail de doctorat, nous considérerons la qualité comme l'ensemble des attributs des individus déterminant leur survie et leur reproduction, sans faire spécifiquement référence à l'aspect statique ou dynamique de ces attributs.

Le fait de ne pas prendre en compte l'hétérogénéité individuelle au sein d'une population peut conduire à une mauvaise interprétation de patrons entre traits (Vaupel & Yashin, 1985; van Noordwijk & de Jong, 1986). En particulier, les effets apparents de l'âge sur la performance démographique, et donc la sénescence, peuvent être fortement biaisés si la variation de la qualité des individus dans la population est grande (Cam *et al.*, 2002). En effet, les individus de mauvaise qualité (i.e. ayant une faible capacité à survivre et/ou se reproduire, sensu McNamara *et al.*, 1996) vont disparaître de la population plus tôt que ceux de meilleure qualité, ce qui a pour conséquence d'augmenter la proportion d'individus de haute qualité dans les classes d'âge avancées (Service, 2000). Cette « sélection intra-cohorte » peut aboutir à une apparente association positive entre âge et performance démographique, malgré l'existence de sénescence.

De même, l'étude des coûts de la reproduction et des compromis entre les paramètres démographiques basée sur des corrélations peut être fortement influencée par l'hétérogénéité individuelle (van Noordwijk *et al.*, 1986). Les individus de haute qualité ayant un potentiel pour la survie et la reproduction supérieur, si la variation de ce potentiel au sein de la population est grande, une corrélation positive sera observée entre intensité de la reproduction et taux de survie par exemple. Ceci met en exergue la nuance qu'il faut apporter entre les questions : « pourquoi les individus ne se reproduisent pas plus? » et « pourquoi certains individus ne se reproduisent-ils pas plus? » (van Noordwijk *et al.*, 1986).

La variation de l'environnement, qu'elle soit temporelle (Lindström, 1999) ou spatiale (Southwood, 1977), peut être un facteur important d'hétérogénéité. Par exemple, les conditions environnementales subies tôt dans la vie peuvent déterminer, au moins en partie, la qualité future des individus (Lindström, 1999; Beckerman *et al.*, 2002). Ces « effets cohortes » (Gaillard *et al.*, 2003c) sont donc une source d'hétérogénéité dans la population, et peuvent clairement influencer la dynamique de la population et les stratégies d'histoire de vie (Uchmanski & Grimm, 1997; Lindström & Kokko, 2002).

Prendre en compte la variation de la qualité des individus au sein d'une population est donc de première importance pour correctement interpréter et comprendre les processus démographiques dans cette population.

1.4 Étude de stratégies d'histoire de vie

Lorsque l'on étudie les stratégies démographiques ou stratégies d'histoire de vie, trois méthodes principales sont utilisées, chacune présentant certains avantages et certaines faiblesses. Il s'agit de la méthode comparative, de la méthode expérimentale et la méthode descriptive. L'approche comparative a pour but généralement de comparer les associations entre traits pour différentes unités taxonomiques (Harvey & Pagel, 1991). Lorsque l´on travaille sur une seule espèce, deux méthodes existent afin d´étudier les paramètres démographiques et leur co-variation: l´expérimentation et la comparaison phénotypique (Reznick, 1992). La méthode expérimentale peut d'autre part se scinder en deux principales approches : la manipulation de traits et la sélection artificielle (Reznick, 1992). Il est souvent difficile de mettre en place des expérimentations au sein de populations animales dans leur milieu naturel, et lorsqu´elles sont possibles, elles ne se font généralement que sur une courte période de temps. De plus, les manipulations peuvent conduire à modifier certains paramètres (e.g. taille de portée) en leur attribuant des valeurs en dehors de celles réalisables en nature (Reznick, 1985), et ainsi ne pas renseigner sur les compromis réels mis en place dans la population. L´avantage de l´expérimentation est qu´elle permet de mettre en évidence des relations de cause à effet entre les variations de différents facteurs, en éliminant les variables confondantes.

Tout comme la méthode expérimentale, la méthode descriptive peut être scindée en deux approches : l'approche par corrélations génétiques et l'approche par corrélations phénotypiques (Reznick, 1985). L'étude des corrélations génétiques repose sur la comparaison d'individus apparentés et renseigne sur la façon dont un gène peut affecté un ou plusieurs traits (notion de gène pleïotropique, Roff, 2002). Par exemple, chez la drosophile, il a été montré que la longévité et la reproduction en début de vie présentaient une corrélation génétique négative (Rose & Charlesworth, 1981), suggérant ainsi que les allèles qui augmentent l'activité de reproduction en début de vie ont des effets négatifs sur la survie (Reznick, 1992). L'autre aspect de la méthode descriptive se base sur la comparaison de phénotypes, et, étant beaucoup plus facile, a été largement utilisé pour étudier les co-variations entre paramètres démographiques. Comparer les phénotypes d´individus de la même population permet de montrer des corrélations entre différents traits et n´apporte pas de réponses toujours claires quant à la causalité des phénomènes observés (Reznick, 1992; Stearns, 1992; Krebs & Davies, 1993). Cependant, ces comparaisons, si elles reposent sur des données à long terme, se basent sur une estimation rigoureuse des paramètres démographiques et de leur variabilité temporelle. Elles peuvent alors permettre de confirmer ou d´infirmer certaines hypothèses d´écologie évolutive, et de préciser les liens entre les paramètres démographiques selon différentes conditions environnementales. L'étude de corrélations phénotypiques basées sur des données longitudinales peut donc être un outil précieux dans la compréhension de la dynamique des populations et l'évolution des stratégies d'histoire de vie (Festa-Bianchet, Gaillard & Jorgenson, 1998). Ainsi de très nombreuses études utilisant des données à long terme et une approche basée sur des corrélations ont permis d'explorer de façon extrêmement rigoureuse les processus démographiques de différents modèles biologiques (Fujiwara & Caswell, 2001; Saether, Engen & Matthysen, 2002; Gaillard & Yoccoz, 2003b pour quelques études qui n'auraient pas été possibles via une approche expérimentale).

1.5 Théorie d'histoire de vie et mammifères

Pour étudier de façon rigoureuse les paramètres démographiques et leur variabilité, un suivi précis à long terme de la population est indispensable (Lebreton *et al.*, 1992). Une alternative est d'utiliser des données transversales, ou tables de vie (e.g. Zammuto & Sherman, 1986; Zammuto, 1987; Oli *et al.*, 2003). Ce type de données, relativement facilement accessibles, pose plusieurs problèmes majeurs (Menkens & Boyce, 1993). Tout d'abord, leur utilisation nécessite de supposer que la population a atteint sa structure stable, ce qui semble rarement réaliste. D'autre part, elle suppose aussi que tous les stades ou toutes les classes d'âge ont la même probabilité de détection. Le suivi longitudinal d'individus marqués permet, avec les méthodes statistiques existant actuellement (analyses des données de capture-recapture, analyses de mesures répétées…) de déterminer rigoureusement les paramètres démographiques et leur variation en fonction de l'âge et/ou de la variation spatiale et temporelle de l'environnement.

Peu de populations de mammifères ont pu faire l´objet d´un tel suivi. La majorité des études sur les stratégies démographiques, basées sur des données à long terme, concernent les grands mammifères (voir entre autres les travaux de T. Clutton-Brock, M. Festa-Bianchet, J.-M. Gaillard sur les ongulés, ou de P. Pistorius et B. LeBoeuf sur des mammifères marins). Plusieurs populations de sciuridés ont tout de même fait l'objet de suivis à long terme et les études des stratégies démographiques chez les sciuridés sont de plus en plus nombreuses (e.g. Wauters & Dhondt, 1995a; Schwartz, Armitage & Van Vuren, 1998; Dobson, Risch & Murie, 1999; Humphries & Boutin, 2000; Dobson & Oli, 2001; Oli, Slade & Dobson, 2001; Broussard *et al.*, 2003; Neuhaus *et al.*, 2004; Broussard *et al.*, 2005). Néanmoins, un rapide survol de la littérature montre clairement un biais de la recherche en écologie vers les espèces de grands herbivores (annexe 1). La taille corporelle étant une variable clé dans l´évolution des stratégies d´histoire de vie (Peters, 1983; Stearns, 1983), il semble important d´améliorer nos connaissances concernant des espèces de taille différente et notamment de petits mammifères, les rongeurs représentant à eux seuls plus de 40% de l´ensemble des espèces de mammifères (Wilson & Reeder, 1993).

1.6 La population d'écureuils roux à Kluane

Le projet de recherche présenté ici se base sur des données à long-terme (1987-2003) récoltées dans une population d'écureuils roux d'Amérique du Nord (*Tamiasciurus hudsonicus,* Figs. 1.1, 1.2) située au Yukon, proche du Parc National de Kluane (Canada, 61°N, 138°W).

Le suivi de cette population a commencé en 1987 dans le cadre d'un projet à grande échelle, initié par Charles Krebs, Stan Boutin et Rudy Boonstra qui visait à comprendre le fonctionnement de la forêt boréale (Krebs, Boutin & Boonstra, 2001). Depuis, chaque année, tous les écureuils roux présents sur 2 sites d'étude d'environ 40 ha (sites témoins) sont marqués et leur activité de reproduction est suivie en détail. Environ 90 femelles (extrêmes : 48 en 1987, première année de suivi et 231 en 1999, année qui suivait une très grande production de cônes) et 100 mâles (extrêmes : 45 en 1987 et 238 en 1999) sont suivis annuellement, et en moyenne, 60 portées (extrêmes : 19 en 1988 et 142 en 1999) ont lieu par an. Tous les jeunes survivant jusqu'à 20-25 jours sont marqués (boucles d'oreille numérotées en métal et système de couleurs permettant une identification individuelle à distance ; Fig. 1.1). Les principales étapes du cycle biologique de l'écureuil roux sont présentées à la figure 1.3.

Figure 1.1 (a) Écureuil roux d’Amérique du Nord adulte en train de manger les graines d’un cône d’épinette blanche. Le système de marquage est visible (boucles d’oreilles métalliques avec des « appendices » bleus, permettant une identification individuelle à distance), ainsi que l’antenne d’un émetteur VHF, fixé autour du coup. **(b)** Écureuil roux d’Amérique du Nord juvénile, âgé d’une vingtaine de jours. Le système de marquage consiste en des boucles d’oreilles métalliques (marquage permanent) et des disques de couleurs (marquage temporaire permettant de reconnaître les jeunes des adultes après l’émancipation des jeunes).

Figure 1.2 Aire de répartition de l’écureuil roux d’Amérique du Nord, *Tamiasciurus hudsonicus* (le cercle représente la population d’étude, région de Kluane, Yukon, Canada)

Les données récoltées au sein de la population d’écureuils de Kluane, et utilisées dans ce travail de doctorat, concernent le statut reproducteur des femelles (reproductrices ou non), les tailles de portée, le nombre et la masse des jeunes pendant l’élevage, la survie des jeunes et des adultes et la masse des adultes. Le système de marquage utilisé permet de marquer les jeunes encore au nid et de les suivre tout au long de leur vie par des recaptures (visuelles ou par piégeage). La dispersion étant faible dans cette population (moyenne <100 m et maximum <600 m, Berteaux & Boutin, 2000), la survie peut-être déterminée de façon relativement certaine, sans biais dû à une émigration importante hors du site d’étude.

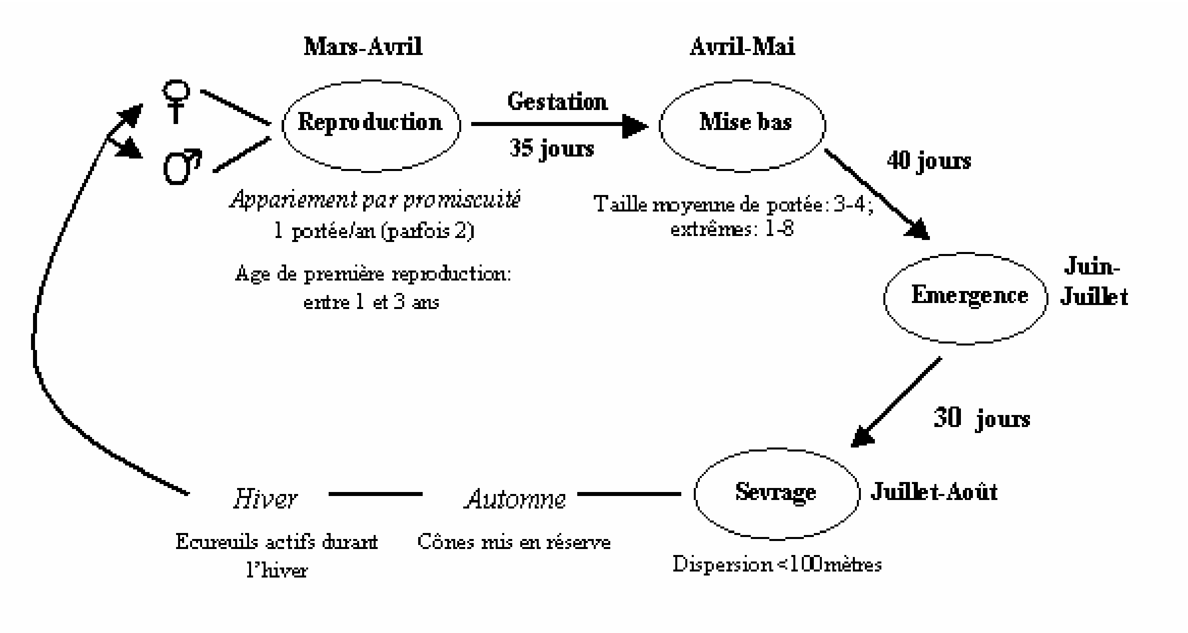

Figure 1.3 Cycle biologique de l'écureuil roux d'Amérique du Nord, *Tamiasciurus hudsonicus*, à Kluane, Yukon, Canada

Cette population se trouve en forêt boréale, caractérisée par la présence d'une unique espèce de conifères, l'épinette blanche (*Picea glauca ;* Figs. 1.4, 1.5). Les écureuils roux d'Amérique du Nord sont des « spécialistes » des cônes de conifères (Gurnell, 1987). La présence d'une unique espèce de conifères et l'extrême variabilité de sa production de cônes conduit à une forte variation inter-annuelle de la disponibilité alimentaire pour cette population (McAdam & Boutin, 2003). Un indice de cette production de cônes est calculé chaque année, en estimant le nombre moyen de cônes produits par arbre (environ 200 arbres sont inventoriés fin juillet chaque année et le nombre total de nouveaux cônes produits est compté). Cet indice de la disponibilité alimentaire permet d'explorer en détail les variations des traits d'histoire de vie et les processus démographiques dans cette population, en lien avec la variation de la principale ressource alimentaire.

Cette population se situe dans un environnement où l'impact direct des activités humaines est très faible (la ville la plus proche compte environ 1000 habitants et se situe à plusieurs dizaines de kilomètres). D'autre part, le comportement des écureuils dans cette population ne semble pas être modifié par les activités de suivi (Price & Boutin, 1993; Stuart-Smith & Boutin, 1995a).

Figure 1.4 Aire d'étude de la population d'écureuil roux d'Amérique du Nord, région de Kluane, Yukon, Canada. Au premier plan, on distingue la forêt boréale, composée majoritairement d'épinettes blanches *Picea glauca* (les parties plus claires correspondent à des zones de trembles) ; à l'arrière plan, on peut voir les premières montagnes du parc national de Kluane.

1.7 Objectifs spécifiques et questions abordées

Ce modèle d'étude et les données à long terme récoltées permettent d'explorer dans le détail certains processus démographiques, en prenant en compte différentes variables environnementales. Ce travail de doctorat a comme but de tester certaines hypothèses issues de la théorie d'histoire de vie, et, dans le cas où elles ne semblent pas supportées, de comprendre pourquoi.

Comme précisé auparavant, la théorie d'histoire de vie repose sur l'hypothèse que la reproduction est coûteuse, en terme de survie ou de performance reproductive future. D'autre part, l'importance de l'âge dans la variation des paramètres démographiques est un thème central en écologie évolutive. Enfin, la variation de la qualité individuelle au sein de la population doit être prise en compte afin de correctement interpréter les patrons mis en évidence via l'analyse de corrélations phénotypiques.

Ainsi, ce travail sera principalement axé sur les liens entre variations environnementales, variation de la qualité individuelle et coûts de la reproduction. Les principales questions abordées dans ce travail peuvent être résumées comme suit :

EFFETS COHORTES ET STRATÉGIES DE REPRODUCTION

Les conditions environnementales subies tôt dans la vie ont-elles des conséquences à court terme sur le recrutement des individus et à long terme sur leur qualité et leur performance démographique (chapitre 2) ? Plus précisément, la disponibilité alimentaire tôt dans la vie affecte-t-elle positivement la performance démographique des individus ? Et comment ces effets cohortes influencent-ils les patrons de survie et de reproduction (chapitre 3) ? Les individus nés les bonnes années sont supposés être de meilleure qualité (effet cohorte à long-terme) et vont donc pouvoir se reproduire de manière intense en début de vie (i.e. grande taille de portée et/ou âge précoce de 1ère reproduction). D'après certaines hypothèses expliquant l'existence de sénescence ("disposable soma theory", Kirkwood & Rose, 1991), une intense activité de reproduction en début de vie doit entraîner une diminution des capacités en fin de vie (i.e. sénescence plus précoce ou marquée). On peut donc faire la prédiction que les individus nés les bonnes années vont se reproduire de manière intense en début de vie, mais subir une sénescence plus précoce et/ou plus intense (chapitre 3).

AGE ET EFFORT REPRODUCTEUR

Comprendre comment les individus répartissent leur énergie entre reproduction, croissance et survie est central en écologie évolutive. Dans ce contexte, il a été proposé que, lorsque la valeur reproductive des individus diminue avec l'âge, la proportion d'énergie investie dans la reproduction augmente. Dans la population d'écureuils roux étudiée dans cette thèse, la valeur reproductive diminue clairement avec l'âge (voir chapitre 3), et on peut faire la prédiction que l'effort reproducteur augmente. Le chapitre 4 concerne cette relation entre effort reproducteur et âge, et discute également la pertinence de certaines mesures souvent utilisées pour quantifier l'effort reproducteur chez les mammifères.

COÛTS DE LA REPRODUCTION, AGE ET HÉTÉROGÉNÉITÉ INDIVIDUELLE

D'après la théorie d'histoire de vie, se reproduire est coûteux et doit donc entraîner une diminution de la performance démographique future. Ainsi, on peut faire la prédiction qu'une première reproduction précoce devrait être associée à une survie plus faible ou une plus faible probabilité de se reproduire dans le futur. Plus généralement, se reproduire devrait associé à une diminution de la survie ou de la reproduction future, comparativement aux individus qui ne se reproduisent pas. Cependant, l'hétérogénéité individuelle peut masquer de tels coûts et, même si ces coûts existent, les résultats opposés aux prédictions peuvent être obtenus. Les chapitres 5 et 6 s'intéressent aux coûts de la reproduction, en prenant en compte cette notion d'hétérogénéité au sein de la population.

Il a été proposé que les coûts de la reproduction sont d'autant plus importants que les conditions pour l'individu sont stressantes. Les travaux à l'origine de cette hypothèse faisaient généralement référence aux conditions environnementales (i.e. densité, disponibilité alimentaire…). Cependant, les coûts de la reproduction ne sont pas seulement fonction de l'environnement et l'âge des individus peut également affecter ces coûts. En effet, au sein d'une population structurée en âge où les jeunes adultes sont encore en croissance et où les plus âgés sont sénescents, la reproduction peut être plus stressante pour ces classes d'âge extrêmes que pour les classes d'âge intermédiaires. Ainsi, dans un telle situation, on peut faire la prédiction que les coûts de la reproduction seront plus importants chez les très jeunes et les très vieux individus que chez les individus d'âge intermédiaire (chapitre 7).

Figure 1.5 Cône d'épinette blanche *Picea glauca*

Partie 1

Effets cohortes et stratégies de reproduction

Chapitre 2 Food resources early in life influence the longevity of red squirrels and the quality of their offspring

Descamps S., Boutin S., Berteaux D., Gaillard J.-M.
(à soumettre, *Ecology Letters*)

Plusieurs travaux (voir références dans le présent manuscrit) ont montré l'importance des conditions subies au début de la vie sur la dynamique de la population, via leurs effets à court et long terme. Ce chapitre s'intéresse aux effets des conditions environnementales subies par les jeunes durant l'année de leur naissance sur leur survie à court terme, donc sur le recrutement dans la population, et sur leur performance démographique à long terme (*fitness*).

Ce travail considère la disponibilité alimentaire à différentes périodes du cycle. Même si l'effet de nombreuses autres variables environnementales reste à être testé, cette étude suggère très fortement l'importance de la disponibilité alimentaire sur les traits d'histoire de vie des écureuils et la dynamique de la population. Il montre que la production de cônes l'année de naissance (i.e. la disponibilité alimentaire entre le sevrage et l'âge de 1 an) a un effet positif sur la survie des jeunes après le sevrage, et donc sur leur recrutement. D'autre part, les individus nés une année de forte abondance de cônes vont vivre plus longtemps et, dans le cas des femelles, élever avec succès un plus grand nombre de jeunes au cours de leur vie que les femelles nées une année de plus faible abondance de cônes. La qualité des jeunes est aussi fonction de la disponibilité alimentaire l'année de naissance de leur mère : une femelle née une année de forte disponibilité en cônes va produire des jeunes ayant une meilleure survie, et donc de plus grande qualité. La disponibilité alimentaire l'année de naissance a donc très probablement une influence à long terme sur la qualité phénotypique des écureuils.

2.1 Abstract

Environmental conditions experienced early in life may have direct numerical effects on recruitment, but also delayed consequences on individual quality and fitness. We used long-term data on a North American red squirrel population to investigate short- and long-term consequences of variation in food availability the first year of life. We measured food availability during rearing, and between weaning and one year of age. We found a positive effect of food availability during rearing on post-weaning survival of both sexes, and consequently on yearly recruitment of weaned red squirrels. Food availability during rearing, and between weaning and one year of age both positively influenced the longevity of squirrels that survived until one year of age. Likewise, female squirrels weaned during a period of high food availability produced best quality offspring. However, yearly breeding success of females was not influenced by food availability early in life. Our study clearly supports the existence of permanent effects of food conditions experienced early in life on individual performance, and points out the importance of considering offspring quality to assess long-term consequences of cohort variations.

Key-words: direct numerical effects; delayed quality effects; cohort variations; cone production; lifetime reproductive success; recruitment; longevity; inter-generational effect; *Tamiasciurus hudsonicus*; North American red squirrel

2.2 Introduction

Environmental conditions experienced early in life may have important consequences on individual fitness and population dynamics (Saether, 1997; Lindström, 1999; Gaillard *et al.*, 2000). Such environmental variations are an important source of heterogeneity in individual quality within a population and influence life history evolution and population dynamics (Lindström *et al.*, 2002).

Previous empirical studies have reported a direct effect of conditions early in life on offspring survival (e.g. Gaillard *et al.*, 1997; Reed *et al.*, 2003; Wauters *et al.*, 2004), and consequently on recruitment. In addition to these short-term numerical effects, conditions during early life may have delayed long-term effects on individual phenotypic quality, and thus on individual fitness (Albon, Clutton-Brock & Guinness, 1987; Metcalfe & Monaghan, 2001;

Beckerman *et al.*, 2002; Gaillard *et al.*, 2003c). Trade-offs between demographic parameters may change according to environmental conditions, so that individuals are expected to allocate variable energy expenditures to reproduction among successive breeding attempts (e.g. Festa-Bianchet, Jorgenson & Réale, 2000; Brommer *et al.*, 2003). For example, females of large herbivores have been selected to trade reproductive effort for survival under harsh conditions (Gaillard *et al.*, 2003b), so that the maternal allocation to reproduction decreases in bad years, leading to a decrease in the offspring birth mass, with cascading effects on their future demographic performance (Gaillard et al., 1997). Effects of environmental conditions on offspring quality are not necessarily driven by changes in body mass. For example, conditions early in life have been reported to influence hormonal environment during prenatal development and thereby reproductive tactics later in life (Clark & Galef, 1995), and to have an effect on telomere shortening through oxidative stress (Hall *et al.*, 2004), and thereby on longevity (Aviv, Levy & Mangel, 2003). In addition, such permanent signatures of environment experienced early in life can be transferred among individuals from successive generations. An individual born during harsh conditions may have a low phenotypic quality, and consequently produce low quality offspring (Albon *et al.*, 1987; Metcalfe *et al.*, 2001).

These long-term consequences of early environment on life-history correspond to what Grafen (1988) called “silver spoon effects”, and can operate through cohort variation (i.e. delayed quality effects, Albon *et al.*, 1987; Gaillard *et al.*, 1997). The study of short- and long-term effects of environmental conditions early in life requires long-term data on individual performance and on variations in environmental quality. Such data may be hard to collect, and even if “silver-spoon effects” have been reported in some birds (Cam, Monnat & Hines, 2003; Reid *et al.*, 2003b), mammals (Albon *et al.*, 1987; Forchhammer *et al.*, 2001; Gaillard *et al.*, 2003c) or reptiles (Madsen & Shine, 2000), empirical evidence of long-term effects of environment and especially food availability experienced early in life remains scarce.

We used long-term data on a northern population of North American red squirrels (Yukon, Canada) to assess both the short- and long-term effects of environmental conditions early in life on individual life history. White spruce (*Picea glauca*) was the dominant tree species in this population, and seeds of spruce cones represented the main food resource to squirrels (McAdam *et al.*, 2003). Yearly production of spruce cones exhibited extreme variations, from years with a quasi-absence of cones to mast years when food was virtually unlimited. Consequently, food available during pre- and post-weaning periods of juveniles varied tremendously among cohorts.

Such variations in cone availability early in life are expected to have long-term effects on individual phenotypic quality of squirrels because their growth is directly linked to cone production (e.g. Humphries *et al.*, 2000). We thus predicted that in our North American red squirrel population, low food availability early in life should decrease recruitment in the population and have long-term negative effects on phenotypic quality and fitness components of squirrels.

2.3 Materials and methods

Study area

We conducted the study in south-western Yukon, Canada (61º N, 138º W). We report results for 15 squirrel cohorts born from 1988 to 2002 in two 40-ha grids separated by the Alaska Highway. All squirrels in the grids were marked with numbered ear tags and a unique color combination of wires for identification at a distance. Fates of squirrels were determined through live-trapping, visual observations and/or radio-telemetry during spring and summer. Yearly reproductive activity of every female was monitored and all young produced were sexed and tagged (see Berteaux *et al.*, 2000; Humphries *et al.*, 2000 for detailed descriptions). Average dispersal distance after weaning (around 70 days of age) is <100 m (Berteaux *et al.*, 2000), so that most young were followed from birth to adulthood. Red squirrels are conifer cone specialists and support winter and spring energy requirements from a larder hoard of cones clipped from trees in late summer (Gurnell, 1987). Food available for reproduction in a given year is a function of cone production the previous season (McAdam *et al.*, 2003). We counted the number of new cones in the top three meters of 170 randomly selected trees to estimate the annual production of spruce cones, when cones are fully formed, but harvesting by squirrels had not yet begun (usually at the end of July).

Study design

We used two variables to describe food availability experienced early in life: cone production the summer preceding the birth of juveniles, which corresponds to the food available during their rearing (called “previous cone production” thereafter), and cone production the year of birth, which corresponds to the food available from weaning to one year of age (called “current cone production” thereafter). These two variables were independent from each other

(Pearson's correlation coefficient: r=-0.10, p=0.71). From 1987 to 2002, food availability estimates varied from an average of 1 to 283 cones per tree (average: 70±24 SE; Fig. 2.1). In the present study, we only considered weaned individuals because a positive effect of previous cone production on survival from birth to weaning has already been demonstrated (Humphries *et al.*, 2000).

In a first step, we investigated the short-term effects of previous and current cone productions on survival from weaning to one year of age to test for direct numerical effects on recruitment. In a second step, we considered potential long-term effects of previous and current cone production on the demographic performance of squirrels that had survived until one year of age. We first tested for an effect of food availability on longevity of males and females, and then, on female lifetime reproductive success (LRS measured as the total number of juveniles successfully weaned during the entire life, Clutton-Brock, 1988). Higher LRS than average can be reached either by having a long lifespan and therefore more breeding attempts (female squirrels only breed once a year every year in most cases) and/or by being more successful at each breeding attempt (i.e. producing more offspring weaned per breeding attempt than average). To account for the influence of longevity on LRS, we used the residuals of the linear regression of females' LRS on their longevity. This variable, hereafter called "residual LRS", corresponds to the part of LRS only related to the yearly breeding success. Finally, in a third step, we considered even longer-term effects of food availability early in life by analyzing how the cone production experienced by females early in life affected the quality of the juveniles they produced during their lifetime. Indeed, variation in demographic performance could occur through variation in the number of offspring produced or through variation in their quality. Assuming that low quality offspring had low survival probability, the number of recruits, adjusted for the number of juveniles a female weaned during its lifetime, provides a relevant measure of the average quality of offspring.

In the second and third steps, we considered only males and females born between 1988 and 1997. As less than 4% of one year old individuals survived until seven years of age (S. Descamps, S. Boutin, D. Berteaux, J. M. Gaillard, unpubl. data, chapter 3), we confidently assumed that most individuals born in 1997 did not survive after 2003 (our last year of data). Consequently, the estimates of longevity and LRS for the most recent cohorts we considered were not underestimated by an over-representation of short-lived individuals.

Confounding effect of cone production during adulthood?

Long-term effects of food availability early in life on subsequent performance can be confounded with cone production available during adulthood when previous and/or current cone production during early life is correlated to average cone production during adulthood. We found a negative correlation between cone production the year of birth and average cone production during adulthood (Pearson's correlation coefficient: -0.31, $p<0.0001$), but there was no correlation between cone production the year before birth and average cone production during adulthood (Pearson's correlation coefficient: -0.03, $p=0.72$). Individuals born in years of large cone production thus experienced on average lower cone production during adulthood, while individuals born in years following a large cone production experienced a similar cone production during adulthood than individuals born in years following a low cone production. Consequently, in this study, any apparent positive demographic effect of current cone production the year of birth, and any apparent positive or negative effect of previous cone production, would result from a conservative test and should safely be interpreted as an actual, delayed long-term cohort effect.

Statistical analyses

The main goal of our study was to investigate short- and long-term demographic effects of food availability experienced early in life. Food availability influences date of birth (Réale *et al.*, 2003b), juvenile mass (Humphries & Boutin, 1996), and bequeathal behaviour of mothers (Berteaux *et al.*, 2000). Therefore, to have a better understanding of consequences of food availability early in life and to identify the factors that shape individual demographic performance in our red squirrel population, we included in our analyses the date of birth, the mass at 25 days (mass when tagged, which was available for most juveniles and was correlated to mass at weaning, S. Boutin, unpubl. data), and the territorial status after weaning (variable with three modalities: owned a territory on natal territory; owned a territory not on natal territory; unknown territorial status). Weaned juveniles with unknown territorial status corresponded to unsettled juveniles and may also include some individuals who were already dead before winter but whose death was unknown. For the mass of juveniles, we considered the residuals from the linear regression of mass over age to remove the effects of age at tagging on mass.

We took into account possible between-sex differences as well as the interaction between the effects of sex and cone productions on survival and longevity. We also included the interaction between the effects of previous and current cone production because the influence of current cone production may depend on previous cone production.

We performed the analyses by fitting mixed models with the MIXED procedure and the GLIMMIX macro of SAS version 8 using the repeated statement and the maximum likelihood method (Littell et al., 1996; SAS Institute, 1999). This allowed us to account for pseudoreplication (sensu Hurlbert, 1984) generated by the occurrence of several individuals per litter. We specified the compound symmetric matrix structure, which assumes that correlation was equivalent for all pairs of individuals within the same litter. Model selection was based on Akaike's Information Criterion (Burnham & Anderson, 2002). A difference of less than two between the AIC of two competing models led us to select the most parsimonious model (Burnham *et al.*, 2002). All parameter estimates are given as mean ± SE.

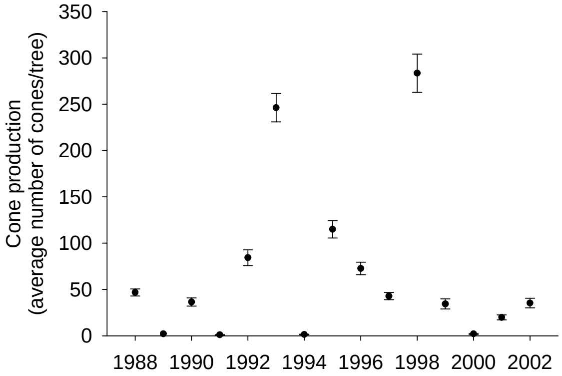

Figure 2.1 Yearly variations of cone production (i.e. average number of cones produced per tree ±SE) at Kluane, Yukon, Canada. 1993 and 1998 correspond to "mast years", where cone production was extremely large, and 1989, 1991, 1994 and 2000 correspond to years of cone crop failure (cone production near 0).

2.4 Results

Short-term effects of food availability experienced early in life

Survival from weaning to one year old varied between cohorts from 8.5 to 88.6% (average: 52.2% ± 6.2 SE) and was higher for females than for males (56.2%±6.5 versus 46.7%±6.2) irrespective of the cone productions (Table 2.1). Survival between weaning and one year of age decreased with increasing previous cone production (estimate of -0.0077±0.0011 on a logit scale; Table 2.1; Fig. 2.2a) and increased with increasing current cone production (estimate of 0.0075±0.0009 on a logit scale; Table 2.1; Fig. 2.2b). In addition, the mass at 25 days of age had a positive effect on juvenile survival (estimate of 0.020±0.006 on a logit scale, Table 2.1), as did territorial status (estimates for juveniles who owned a territory on natal territory of 60.2%±5.8, for juveniles who owned a territory not on natal territory of 57.9%±7.4, and for juveniles with unknown territorial status of 41.5%±7.6).

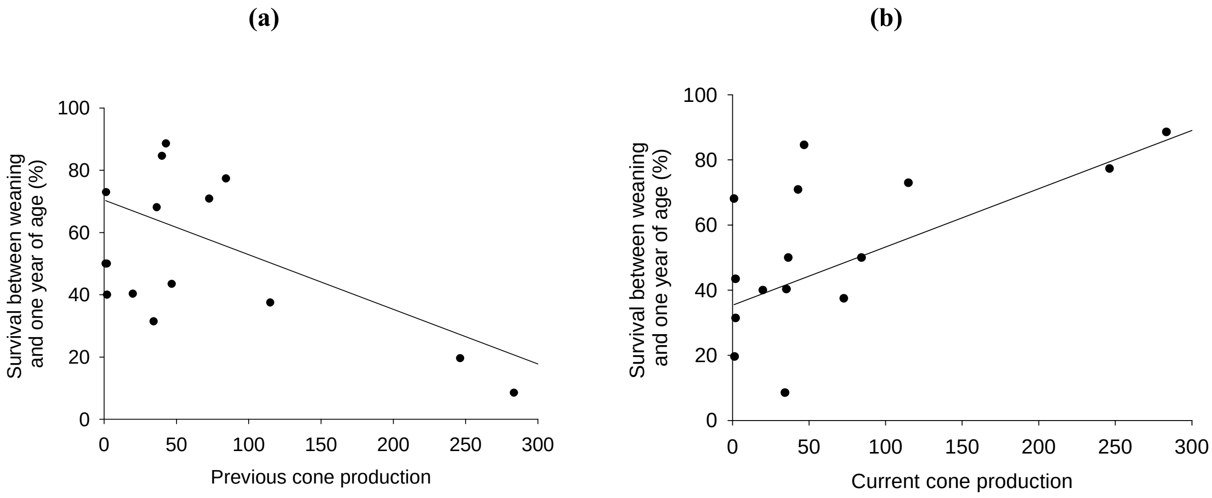

Figure 2.2 Effect of food availability (a) during rearing, and (b) from weaning to one year of age (i.e. previous and current cone productions respectively) on juvenile survival between weaning and one year of age in a North American red squirrel population, Kluane, Yukon, Canada. When excluding the two years of largest cone production, the effect of previous cone production (a) on survival is not significant anymore but the effect of current cone production (b) remains significant.

Table 2.1 Juvenile survival (from weaning to one year of age) in relation to food availability during the first year of life, sex (S), mass at 25 days old (M), date of birth (DB), and territorial status after weaning[a] (T) in a North American red squirrel population, Kluane, Yukon, Canada (n=942 individuals from 543 litters). Previous cone production (PCP) corresponds to the food available during the rearing period, and current cone production (CCP) to the food available from weaning to one year of age. The selected model occurs in bold.

Model	Deviance	np	AIC	ΔAIC
S+M+T+PCP+CCP[b]	**1024.233**	**9**	**1042.233**	**0.000**
S+M+BD+T+PCP+CCP	1023.395	10	1043.395	1.162
S+M+BD+T+PCP+CCP+S × PCP+S × PCP	1022.082	12	1046.082	3.849
S+M+BD+T+PCP+CCP+S × PCP+ CCP × PCP	1022.093	12	1046.093	3.860
S+M+BD+T+PCP+CCP+S × PCP+CCP × PCP	1023.011	12	1047.011	4.778
S+M+BD+T+PCP+CCP+S × PCP+S × PCP+ CCP × PCP	1021.913	13	1047.913	5.680
M+T+PCP+CCP	1035.333	8	1051.333	9.100
S+T+PCP+CCP	1035.873	8	1051.873	9.640
S+BD+T+PCP+CCP	1034.609	9	1052.609	10.376
M+BD+T+PCP+CCP	1034.669	9	1052.669	10.436
S+M+PCP+CCP	1049.370	7	1063.370	21.137
S+M+BD+PCP+CCP	1047.906	8	1063.906	21.673
S+M+BD+T+CCP	1075.265	9	1093.265	51.032
S+M+T+CCP	1086.598	8	1102.598	60.365
S+M+BD+T+PCP	1120.773	9	1138.773	96.540
S+M+T+PCP	1123.755	8	1139.755	97.522
Intercept (null model)	1296.548	3	1302.548	260.315

[a]: this variable had three modalities: owned a territory not on natal territory; owned a territory on natal territory; unknown territorial status, which likely corresponded to unsettled juveniles

[b]: this selected model explained 25% of the total variance (obtained with a GLM that did not take into account the repetition in our dataset)

Table 2.2 Longevity of recruited squirrels (i.e. squirrels that survived until one year of age) in relation to food availability during the first year of life, sex (S), mass at 25 days old (M), date of birth (DB), and territorial status after weaning[a] (T) in a North American red squirrel population, Kluane, Yukon, Canada (n=318 individuals from 207 litters). Previous cone production (PCP) corresponds to the food available during the rearing period, and current cone production (CCP) to the food available from weaning to one year of age. The selected model occurs in bold.

Model	Deviance	np	AIC	ΔAIC
PCP+CCP+ CCP × PCP[b]	**5068.066**	**6**	**5080.066**	**0.000**
M+BD+T+PCP+CCP+ CCP × PCP	5062.338	10	5082.338	2.272
S+BD+T+PCP+CCP+ CCP × PCP	5063.613	10	5083.613	3.547
S+M+BD+PCP+CCP+ CCP × PCP	5066.001	9	5084.001	3.935
S+M+BD+T+PCP+CCP+ CCP × PCP	5062.190	11	5084.190	4.124
S+M+BD+T+PCP+CCP+S × PCP+CCP × PCP	5060.227	12	5084.227	4.161
Intercept (null model)	5078.751	3	5084.751	4.685
S+M+T+PCP+CCP+ CCP × PCP	5064.784	10	5084.784	4.718
S+M+BD+T+PCP+CCP+S × CCP+CCP × PCP	5062.001	12	5086.001	5.935
S+M+BD+T+PCP+CCP+S × CCP+S × PCP+CCP × PCP	5060.221	13	5086.221	6.155
S+M+BD+T+PCP+CCP	5073.540	10	5093.540	13.474
S+M+BD+T+PCP+CCP+S × PCP+S × PCP	5070.870	12	5094.870	14.804

[a]: this variable had three modalities: owned a territory not on natal territory; owned a territory on natal territory; unknown territorial status, which likely corresponded to unsettled juveniles

[b]: this selected model explained 4% of the total variance (obtained with a GLM that did not take into account the repetition in our dataset)

Table 2.3 Lifetime reproductive success of females (for a given longevity) in relation to the food availability during their first year of life, mass at 25 days old (M), date of birth (DB), and territorial status after weaning[a] (T) in a North American red squirrel population, Yukon, Canada. (n=205 individuals for 154 litters). Previous cone production (PCP) corresponds to the food available during the rearing period, and current cone production (CCP) to the food available from weaning to one year of age. The selected model occurs in bold.

Model	Deviance	np	AIC	ΔAIC
Intercept (null model)	**894.565**	**3**	**900.565**	**0.000**
M+T+PCP+CCP	887.369	8	903.369	2.804
BD+T+PCP+CCP	887.429	8	903.429	2.864
M+BD+T+CCP	887.534	8	903.534	2.969
M+BD+T+PCP	889.021	8	905.021	4.456
M+BD+PCP+CCP	891.134	7	905.134	4.569
M+BD+T+PCP+CCP	887.233	9	905.233	4.668
M+BD+T+PCP+CCP+ PCP × CCP	886.607	10	906.607	6.042

[a]: this variable had three modalities: owned a territory not on natal territory; owned a territory on natal territory; unknown territorial status, which likely corresponded to unsettled juveniles

Long-term effects of food availability experienced early in life on longevity and residual LRS

Average longevity per cohort varied between 946 to 1561 days (mean: 1221 ± 61 SE), and average LRS of females varied from 0.6 to 5.6 weaned juveniles (mean: 2.9 ± 0.5 SE). Longevity of squirrels (Fig. 2.3) was influenced by previous and current cone productions (estimate of -0.047 ± 0.015 for the interaction term between previous and current cone production, estimate of 2.30 ± 1.15 for the previous cone production and of 4.25 ± 1.29 for the current cone production, Table 2.2). On the other hand, we did not find any effect of previous or current cone productions on residual LRS (Table 2.3). Thus, the food availability the year of birth had no long-term influence on the breeding success of females for a given longevity. We did not find any difference in longevity between sexes (Table 2.2). Similarly, the juvenile mass, the birth date and the territorial status after weaning did not influence the longevity or residual LRS of squirrels (Tables 2.2 and 2.3).

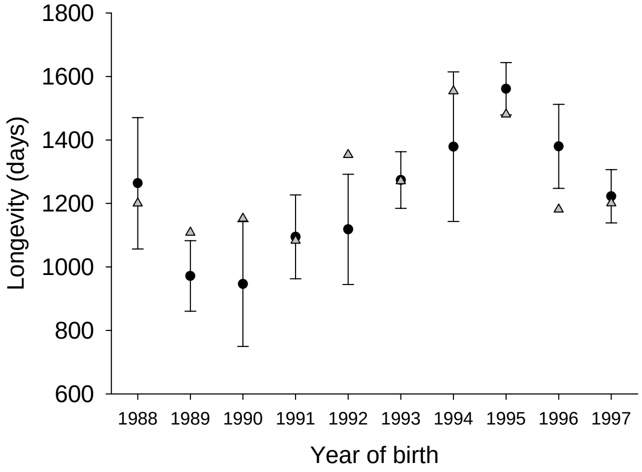

Figure 2.3 Average longevity of North American red squirrels, Kluane, Yukon, Canada. We only considered squirrels that survived ≥1 year. Symbols represent averages per cohort (black circles: actual data; grey triangles: estimated values from the model selected in table 2.2).

Long-term effects of food availability experienced early in life on the number of weaned juveniles recruited in the population

The average number of recruited juveniles varied between cohorts from 0.1 to 4.0 (mean: 1.5 ± 0.3 SE). After adjusting for the number of weaned juveniles (Table 2.4), the previous cone production positively affected the number of juveniles that survived up to one year of age produced over female lifetime (slope of 0.0033 ± 0.0019; Table 2.4; Fig. 2.4). Thus, females raised under high cone availability produced a higher proportion of weaned juveniles that survived to one year of age. Current cone production, birth date, juvenile mass, and territorial status did not affect the proportion of weaned juveniles that reached one year of age (Table 2.4).

Table 2.4 Number of weaned juveniles that survived until one year of age produced by females in relation to the food availability during the first year of life, mass at 25 days old (M), date of birth (DB), territorial status after weaning[a] (T), and number of juveniles weaned (LRS) in a North American red squirrel population, Yukon, Canada. We only considered females whose LRS was ≥1 ($n_{individuals}$=147, $n_{litters}$=113). Previous cone production (PCP) corresponds to the food available during the rearing period, and current cone production (CCP) to the food available from weaning to one year of age. The selected model occurs in bold.

Model	Deviance	np	AIC	ΔAIC
LRS+BD+PCP	454.278	6	466.278	0.000
LRS+PCP [b]	**457.627**	**5**	**467.627**	**1.349**
LRS+M+BD+T+PCP	449.742	9	467.742	1.464
LRS+BD+T+PCP+CCP	450.049	9	468.049	1.771
LRS+M+BD+T+PCP+CCP + PCP × CCP	446.157	11	468.157	1.879
LRS+M+BD+T+PCP+CCP	448.179	10	468.179	1.901
Number recruited~LRS	460.803	4	468.803	2.525
LRS+M+BD+PCP+CCP	452.824	8	468.824	2.546
LRS+BD	460.234	5	470.234	3.956
LRS+M+T+PCP+CCP	453.994	9	471.994	5.716
LRS+M+BD+T+CCP	456.357	9	474.357	8.079
PCP	623.173	4	631.173	164.895
M+BD+T+PCP+CCP	613.475	9	631.475	165.197
BD+PCP	622.959	5	632.959	166.681
Intercept (null model)	631.739	3	637.739	171.461

[a]: this variable had three modalities: owned a territory not on natal territory; owned a territory on natal territory; unknown territorial status, which likely corresponded to unsettled juveniles

[b]: this selected model explained 77% of the total variance (obtained with a GLM that did not take into account the repetition in our dataset)

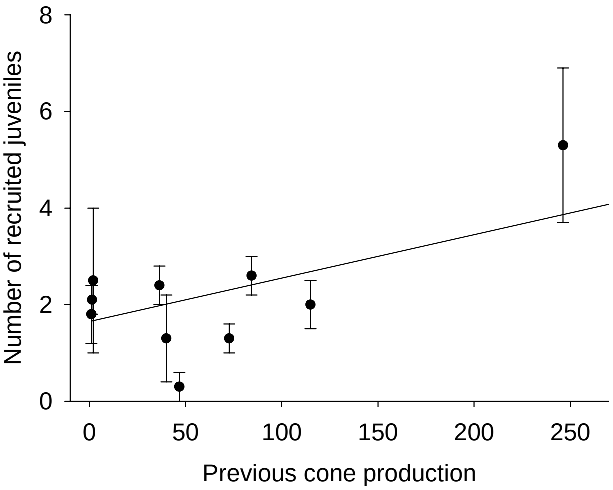

Figure 2.4 Long-term effect of food availability during the rearing period on the total number of juveniles recruited by females during their entire lifespan in a North American red squirrel population, Kluane, Yukon, Canada. Only females that have weaned at least one juvenile during their lifespan have been considered. When excluding the year of largest cone production, the effect of previous cone production was not significant anymore.

2.5 Discussion

Direct numerical effects of conditions early in life

In our North American red squirrel population, food availability experienced during the first year of life by weaned juveniles affected their survival, and consequently, variation in cone production led to direct numerical effects on recruitment. Post-weaning survival increased with current cone production. Squirrels rely on food stored during the previous fall to survive during winter (Kemp & Keith, 1970; Larsen & Boutin, 1994), and it is thus expected that an increase of the food available during winter increases juvenile survival. Similarly, juveniles who owned a territory with certainty at weaning enjoyed a higher survival than juveniles whose territoriality was unknown (i.e. mainly individuals that did not own and defend a territory after weaning).

Surprisingly, an increase of the previous cone production had an apparent negative effect on juvenile survival. This effect was mainly driven by the two mast years with very large cone production (see Figure 2.2a). When excluding these two years from our analyses, the effect of previous cone production did not longer occur (results not shown). A large number of juveniles were weaned during the breeding seasons following these two mast years, and they likely exceeded the number of available territories. This could have led to a higher mortality, as unsettled juveniles are likely to die. Previous studies have reported similar results, with periods of high density followed by high mortality (Clutton-Brock *et al.*, 1991; Rose, Clutton-Brock & Guinness, 1998; Reid *et al.*, 2003b).

Effects of sex, birth date, mass and territorial status on recruitment and individual performance

Females had a higher post-weaning survival than males. As the between-sex differences occurred for any cone availability, the lower male survival does not correspond to a higher susceptibility of males to food shortage. Berteaux and Boutin (2000) found that, after weaning, males dispersed away from the natal territory more often than females. Dispersers may suffer important energetic costs to establish boundaries on a new territory, and do not benefit from mother's resources (Berteaux *et al.*, 2000). In addition, dispersers may be more exposed to predation. The lower post-weaning survival of males could thus be related to their higher propensity to disperse. In a previous 4-year-study (1988-1991) performed in the same area, Boutin and Larsen (1993) did not report any between-sex difference in the post-weaning survival. Their study took place during a period of high snowshoe hare density, so that predation risk of red squirrels was probably low (Stuart-Smith & Boutin, 1995b; Krebs *et al.*, 2001). Higher predation susceptibility of males during dispersal is thus likely to account for our results.

The birth date did not influence post-weaning survival nor demographic performance of squirrels. Previous results in the same population have identified the date of birth of females as an important component of individual quality (Descamps *et al*., 2006, chapter 5) when considered relatively to other females within the same cohort. Consequently, to be born earlier than other females from the same cohort, rather than to be born early, seems to be the cue. Within the same cohort, early born females may have a higher probability to access a high quality territory than late born ones (Price, Boutin & Ydenberg, 1990), and thus a higher survival and/or breeding probabilities. In addition, early born females may be born to high quality females and thereby be themselves high quality individuals (Réale *et al*., 2003a).

Mass when juvenile had a positive effect on post-weaning survival, as observed on Eurasian red squirrels (Wauters, Bijnens & Dhondt, 1993). Heavy juveniles may be more likely to access a good territory after weaning because mass is positively correlated with dominance in our population (Stuart-Smith & Boutin, 1994). However, juvenile mass was not related to longevity in both sexes, nor to breeding success (residual LRS) of females, and was thus not related to individual performance in our North American red squirrel population.

Finally, the territorial status after weaning influenced recruitment in this red squirrel population. Individuals who owned a territory after weaning were more likely to survive and to be recruited than unsettled ones, but we did not observe any difference between individuals that settled on versus outside natal territory after weaning. In addition, the territorial status after weaning did not affect the demographic performance of individuals later in life, which suggests that bequeathal behaviour of mothers (i.e. the behaviour that consists for a female to give part or all of its territory to some of its juveniles at weaning, Price *et al.*, 1993; Berteaux *et al.*, 2000) has only short-term effects on juveniles by increasing their subsequent survival, but not their future performance.

Long-term consequences of conditions experienced early in life

Contrary to studies on Eurasian red squirrels (Wauters *et al.*, 1995a), which did not report any effect of year of birth on individual fitness, we found that the environmental conditions experienced the first year of life had long-term effects on longevity of red squirrels of both sexes. In particular, the previous and current cone productions positively influenced the longevity of squirrels. LRS of females was strongly correlated to their longevity (Pearson's correlation coefficient=0.70, $p<0.0001$) as observed in many other species (Clutton-Brock, 1988). Therefore, it seems likely that long-term effects of cone productions on longevity had consequences on individual fitness, at least for females. We did not find any effect of food availability the first year of life on LRS of females for a given longevity. The yearly breeding success of females was thus not influenced by food conditions experienced early in life.

Cone production the year of birth and the year before birth interacted negatively. The effect of cone production the year of birth was lower when it followed an already high previous cone production. Consequently, juveniles that benefited from high previous and current cone productions had lower longevity than expected if the effects of previous and current cone productions would have been additive. One explanation could be that in years of extreme food availability (i.e. when most trees produce a very large number of cones), many low quality juveniles (e.g. juveniles that own poor territories or no territory at all) are able to survive until one year of age. However, afterwards, when resource availability decreases, these low quality individuals are unlikely to survive, so that the average longevity of their cohort decreases.

Inter-generational consequences of conditions experienced early in life

Mothers raised in years of high previous cone production had a higher proportion of their weaned juveniles surviving until one year of age, and consequently a higher number of juveniles recruited in the population. Females raised under high food availability seem thus able to produce and raise offspring of higher quality than females raised under less favourable conditions. This clearly supports our prediction about long-term effects of food availability experienced during early development on individual life history and fitness, and points out the importance of inter-generational effects of conditions experienced early in life. Cone availability during rearing was likely to affect quality of individuals through an effect on mothers' reproductive output: females that faced low cone availability during their breeding allocated less energy into reproduction and thereby weaned low quality juveniles, which then also produced low quality offspring. Food availability during the breeding season did thus affect three generations of female squirrels.

When excluding individuals born after a mast year (i.e. females born in 1994) from our analyses, the effect of previous cone production on the proportion of recruited juveniles did not occur anymore, meaning that such a relationship was mainly driven by this single year. This suggests that females' performance was affected by food availability during rearing in a threshold manner.

2.6 Conclusion

In our North American red squirrel population, the food availability experienced during the first year of life had permanent effects on demographic performance of males and females, and on phenotypic quality of offspring produced by females. Our results emphasize the importance of considering inter-generational consequences of cohort variation. We did not find any effect of mass around 25 days of age on individual performance, and it seems unlikely that the food availability experienced during the first year of life affects squirrels' quality through effects on early growth. Mechanisms linking environmental conditions to future performance remain to be determined.

Chapitre 3 “Late performance sacrificed for early reproduction”: a study of senescence and cohort effects in a red squirrel population.

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(soumis à *Ecology*)

Peu de populations animales permettent d’examiner de façon relativement exhaustive les effets de l’âge sur les paramètres démographiques, et de faire le lien avec la condition des individus. Ainsi, les patrons liés à la sénescence sont finalement peu connus (à l’exception de certains modèles d’étude), notamment chez les mammifères de petite taille. La façon dont la qualité individuelle influence ces patrons a été également peu étudiée, même s’il est généralement admis que dans une population hétérogène du point de vue de la qualité des individus, la sénescence sera plus difficile à mettre en évidence. Le travail qui suit montre clairement une diminution de la condition et de la performance démographique des écureuils en fin de vie, pour les mâles et les femelles. De plus, il confirme que l’hétérogénéité au sein de la population peut rendre plus complexe l’interprétation des effets de l’âge. Ce travail supporte l’idée proposée au chapitre précédent, selon laquelle les conditions l’année de naissance (effets cohorte) influencent la qualité moyenne des individus qui atteignent l’âge de reproduction, ainsi que leurs stratégies de reproduction. Il suggère clairement un compromis entre reproduction précoce et performance tardive, compromis également supporté par les résultats du chapitre 5.

3.1 Abstract

Individual performance is expected to decrease with age because of senescence, a deterioration of physiological attributes with increasing age. We analyzed long-term data collected on a North American red squirrel population to assess the influence of age on body mass, survival and reproductive performance, and to study the effects of sex and cohort quality on senescence patterns. We found strong evidence of senescence in both sexes with mass and survival decreasing with increasing age. This decrease occurred later for males, which suggests a later onset of senescence, possibly as a result of lower reproductive costs. In females, the number of weaned juveniles also decreased with increasing age as did the number of offspring surviving from weaning to one year of age. The latter suggests that older females may produce juveniles of lower quality providing evidence of an intergenerational effect of mother's age on juveniles' fitness. Finally, our results indicated that females born in a year with good environmental conditions bred more intensely than females born during poor conditions, but paid a cost in terms of an earlier senescence. Our results supported the hypothesis of a trade-off between early reproduction and late performance, and thus the disposable soma theory of senescence.

Key-words: cohort variation; trade-off; *Tamiasciurus hudsonicus*; mass; survival; weaning success; recruitment; intergenerational effect; juvenile quality; disposable soma theory

3.2 Introduction

The assessment of life history changes according to age in animal populations is a key issue in ecology. Most vertebrate populations are strongly age-structured (Charlesworth 1994) so that age-specific estimates of life history traits are required to understand both the evolution of life histories (Partridge *et al.*, 1988; Stearns, 1992) and population dynamics (Tuljapurkar & Caswell, 1996; Caswell, 2001). Life history theory predicts that survival and reproduction should decrease with age because of senescence, a decrease in functional capacities at the end of life (Medawar, 1952; Williams, 1957; Hamilton, 1966; Kirkwood, 1977; Comfort, 1979; Rose, 1991).

The study of senescence in wild populations has proven to be challenging because of the need for long-term datasets on individuals. Initial reports of senescence documented decreases in survival and/or reproduction with age. Although these patterns could have alternative explanations (Abrams, 1991; Blarer, Doebeli & Stearns, 1995; Partridge & Barton, 1996), the case for senescence in the wild has been building. In the case of vertebrates, evidence for senescence has been reviewed by Bennett and Owens (2002) for birds and by Gaillard et al. (2003a) for ungulates. Both studies concluded that senescence in survival or reproductive success is a common feature of the life histories of birds and large herbivores.

Evidence for senescence in natural populations of small mammals has been more elusive (Slade, 1995) but there are now cases of reduced survival (e.g. Millar, 1994; Broussard *et al.*, 2005), and reproduction (e.g. Sherman & Morton, 1984; Morris, 1996; Schwartz *et al.*, 1998; Broussard *et al.*, 2003; Havelka & Millar, 2004) with increasing age. In the most comprehensive studies to date, Broussard et al. (2003; 2005) documented age-specific patterns of somatic investment, survival, and reproduction in two species of ground squirrel. Overall, they concluded that observed decreases in some of these characteristics with age was best explained by senescence. However, in all cases, only females have been studied. The magnitude of senescence may differ between sexes but, in small mammals, age-specific variation in life history traits for males remain undocumented. In polygynous species with sexual dimorphism in body size, performance of males often decreases faster with increasing age than that of females (e.g. Loison *et al.*, 1999), so that males have a lower lifespan than females (Gaillard *et al.*, 2000). However, whether or not the between-sex differences in senescence only depends on the intensity of sexual selection remains largely unknown.

According to the disposable soma theory (Kirkwood, 1977; Kirkwood *et al.*, 1991), a trade-off exists between late performance and early reproduction, and patterns of senescence thus vary as a function of reproductive tactics. Environmental conditions in the year of birth may influence reproductive tactics of individuals so that individuals born in good cohorts reproduce earlier and more intensely than individuals born in poor cohorts. Therefore, environmental conditions in the year of birth are very likely to affect patterns of senescence, and to date, the demographic and evolutionary consequences of such long-term cohort effects remain unknown.

We have been tracking the survival and reproductive performance of individual North American red squirrels in the southwestern Yukon for 15 years in a population where food resources exhibit extreme yearly variations (McAdam *et al.*, 2003). Our objectives in this study were as follows. First we tested the predictions that senescence should be pervasive in life history traits of this iteroparous vertebrate, should occur just after sexual maturity, and should be more pronounced than in larger mammals as predicted by theory (Hamilton, 1966; Charlesworth, 1994). Given the limited dimorphism in squirrels (Boutin *et al.*, 1993) we also predicted that senescence patterns should be similar in males and females. Finally, we examined two aspects not previously considered. First, we measured whether survival of juveniles post-weaning had any relation to age of the mother. Our rationale for this was that females showing signs of senescence may produce offspring of lower quality (Kern *et al.*, 2001), which should be expressed in lower survival of young. Second, we wished to take advantage of the high variability in food supply from year to year to determine if patterns of senescence depend on initial environmental conditions. We predicted that senescence should be more pronounced (i.e. earlier onset and/or higher intensity) in cohorts born during high food years relative to those born during low food years because high-food cohorts should reproduce earlier and more intensely than low-food cohorts, and thereby suffer higher reproductive costs (Kirkwood *et al.*, 1991).

3.3 Materials and methods

Study area and field methods

The study was conducted near Kluane Lake, Yukon, Canada (61° N, 138° W) and began in 1987 (see Price *et al.*, 1986; Boutin *et al.*, 1993; Berteaux *et al.*, 2000 for detailed descriptions). We report results for the years 1987-2003 for two 40 ha grids separated by the Alaska Highway. All squirrels were marked with numbered ear tags and a unique color combination of wires for identification at a distance. Fates of male and female squirrels were determined through live-trapping, visual observations and/or radio-telemetry from April to August. Reproductive females were weighed after parturition, and males and females were weighed each time they were trapped (to the nearest gram with a Pesola scale). Young of the year were counted and sexed soon after birth, tagged at about 20-25 days of age, and weighed within a week of weaning (around 70 days of age). The average dispersal distance after weaning is less than 100 meters (Berteaux *et al.*, 2000), so that most young were followed from birth to adulthood. The habitat was boreal forest with white spruce (*Picea glauca*) as the dominant tree species and spruce cone seeds were the main food resource (McAdam *et al.*, 2003). Red squirrels store unopened cones at hoarding sites (middens) that they defend actively throughout the year (Gurnell, 1987). Food available for reproduction in a given year is a function of cone production the previous year (McAdam *et al.*, 2003). We estimated spruce cone production each year, when cones were fully formed, but harvesting by squirrels had not yet begun (usually at the end of July). We counted the number of new cones in the top three meters of 170 randomly selected trees. Average yearly cone production ranged from about 1 to 283 cones per tree (average 60 ± 20 SE).

Mass and reproduction analyses

Our data set included repeated measurements made on the same individuals at different ages. To account for pseudoreplication problems (sensu Hurlbert, 1984), we fitted linear mixed models with the MIXED procedure of SAS version 8 using the repeated statement and the maximum likelihood method (Littell *et al.*, 1996; SAS Institute, 1999). We specified the compound symmetric matrix structure, which assumes that the correlation of measurements made on the same individual is a function of the individual considered, but does not vary during its lifetime (i.e. same correlation for all pairs of measurements). The use of other matrix structures such as an autoregressive structure of order one led to similar results.

To characterize the functional relationship among mass, reproduction, and age, we tested and compared several continuous and discrete models (table 3.1a). Model selection was based on the Akaike Information Criterion, as recommended when several non-nested models have been fitted (Burnham and Anderson 2002). We selected the model with the lowest AIC, i.e, the model providing the best trade-off between accuracy and precision (Burnham *et al.*, 2002). A difference of less than two units in the AIC of two models indicates that a model cannot be preferred over the other (Burnham *et al.*, 2002). In that latter case, we selected the most parsimonious model (i.e. the model with less parameters).

We first tested for an age effect on the mass of squirrels, used as a proxy of body condition. For females, we considered mass after parturition (taking litter size into account) as these data were available for most females and were standardized for the same breeding period. For males, we used average mass in May because May was a period of high trapping activity, and most males present on the study area were trapped at least once during this period. We then studied the effect of females' age on litter size at birth, number of weaned juveniles and juvenile mass at weaning (mean mass per litter after accounting for variation in litter size at birth). Finally, we investigated the effect of mothers' age on the number of recruited juveniles (i.e. the number of weaned juveniles from a litter surviving to one year of age). For weaning success analyses, we only considered breeding females and for recruitment analyses, we only considered females who weaned at least one juvenile.

To account for possible confounding effects of food availability on mass and reproductive output, we incorporated cone production in the previous year (i.e. main food resource during reproduction, McAdam *et al.*, 2003) to study effect of age on body mass, litter size, weaning success and recruitment. We also used cone production in the current year (i.e. cone production the year of weaning) to study age effects on recruitment, as this reflected the main resource used by juveniles from weaning to one year of age. Berteaux and Boutin (2000) found that old females bequeath all or part of their territory to their young more often than younger ones. This behaviour likely influences survival of young after weaning. To test the effect of mother's age on recruitment, we thus included in our models a factor called *bequeathal* that described mother's behaviour at weaning (with three modalities: female kept her territory, female gave part of her territory to one or several of her juveniles, female gave all her territory to one or more of her juveniles).

Survival analyses

Survival analyses were carried out with capture-mark-recapture methods (Lebreton *et al.*, 1992), using the program SURGE 5.0 (Reboulet *et al.*, 1999). Goodness-of-fit tests were conducted with the bootstrap procedure of program MARK (White & Burnham, 1999, 1000 simulations were performed). As we focused on senescence patterns, we only considered mature squirrels (i.e. $\geq$1 year old). Our dataset consisted of 343 females and 216 males of known age, tagged as juveniles between 1987 and 2001. Male and female data fitted the Cormack-Jolly-Seber model (Bootstrap goodness-of-fit tests: deviance for females=156.74, p=0.16, deviance for males=160.23, p=0.12), which was thus used as a starting point for model selection. Because preliminary analyses indicated that capture probabilities were sex-dependent, we treated sexes separately. To assess the presence/absence of squirrels in the population, and then to estimate survival rates, we used trapping and visual observations from mid-April to mid-June, which corresponded to a period of high trapping intensity (i.e. census of all squirrels in the study area). As survival rates were the parameters of interest in our study, we first modelled capture rates to have more statistical power when modeling survival (Lebreton *et al.*, 1992). We compared among models with constant, time-dependent, age-dependent capture rates and capture rates that were a function of capture effort (defined as the average number of times squirrels are captured every year between mid-April and mid-June). For males, the selected model included capture rates that were a function of capture effort, and for females, the selected model included constant capture rates (appendix 2-a). For survival modelling, we tested different age-dependent models whose notation and biological meaning are reported in table 3.2a. As for analyses of mass and reproduction, model selection was based on AIC (Burnham *et al.*, 2002).

Analyses of cohort effects

As a first step, we tested for different age structures of several traits and selected for the best age-dependent model. Then, to investigate how cohort quality influenced patterns of age-specific variation, we included in the previously retained models a variable describing food conditions in the year of birth (i.e. food availability during rearing, which corresponds to the cone production one year before). For each trait, we compared a model with no cohort effect, a model with an additive cohort effect, and a model with an interaction between age and cohort quality, based on AIC. Following McAdam and Boutin (2003), we considered as high quality cohorts, squirrels born in years when previous cone production was >50 cones per tree (range: 73-283 cones per tree), and as low quality cohorts, squirrels born in years when previous cone production was <50 cones per tree (range: 1-47 cones per tree). All results are reported as mean ± SE.

3.4 Results

Age effects on mass

Average mass of females after parturition was 258.7 g ± 1.3. After taking into account the potential confounding effects of food availability and litter size, the best age-dependent model for female mass after parturition included a quadratic effect of age (Table 3.1b; see appendix 2-b for complete results of model selection). According to this model, female mass decreased significantly from five years of age onwards (Fig. 3.1a), and this decrease corresponded to 2% of females' mass (about 5 g). When testing for cohort effects, the best model we found included neither additive nor interactive cohort effects (Table 3.1c).

Average mass of males in May was 257.3 g ± 0.9. When taking into account the effect of food availability, the best model included a quadratic effect of age (Table 3.1b; see appendix 2-b for complete results of model selection), and showed a decrease of male mass from six years of age onwards (Fig. 3.1b). Again, this decrease corresponded to 2% of males' mass (about 5g). As for females, we did not find any significant cohort effect on mass of males (Table 3.1c).

Table 3.1 Relation of mass and reproductive performance to age and cohort quality in a population of North American red squirrels, Kluane, Yukon, Canada.

(a) Variables describing age effect used to test the shape of the relationship between life-history traits and age.

Age effect
linear regression: Age
quadratic regression: Age+Age^2
inverse regression: 1/Age
1 juvenile class (1 yr) and 1 adult class (≥2 yr)
1 prime-age class (1-6 yrs) and 1 senescent class (≥7 yrs)
1 prime-age class (1-5 yrs) and 1 senescent class (≥6 yrs)
1 prime-age class (1-4 yrs) and 1 senescent class (≥5 yrs)
1 juvenile class (1 yr), 1 prime-age class (2-6 yrs), 1 senescent class (≥7 yrs)
1 juvenile class (1 yr), 1 prime-age class (2-5 yrs), 1 senescent class (≥6 yrs)
1juvenile class (1 yr), 1 prime-age class (2-4 yrs), 1 senescent class (≥5 yrs)

(b) Results of the model selection for mass of males and females, and reproductive parameters of females.

Life history trait	**Initial model**	**Selected model**
Mass of females	*Age effect* + Food availability + Litter size	Age + Age^2 + Food availability + Litter size
Mass of males	*Age effect* + Food availability	Age+Age^2+ Food availability
Litter size	*Age effect* + Food availability	Age+Age^2
Number of weaned juveniles	*Age effect* + Food availability + Litter size	Age+Age^2 + Food availability + Litter size
Average mass of juveniles at weaning	*Age effect* + Food availability + Litter size	Food availability + Litter size
Number of recruited juveniles	*Age effect* + Food availability + Number of weaned juveniles + Bequeathal	(Yearling, Prime Age 2-5, Old ≥6) + Food availability + Number of weaned juveniles + Bequeathal

(c) Cohort quality effects on mass and reproductive parameters.

Life history trait	**Model**	**Deviance**	**np**	**AIC**	**ΔAIC**
Mass of females	*Previously selected model*	3863.286	7	3877.286	0.000
	Previously selected model + Cohort quality	3862.542	8	3878.542	1.256
	Previously selected model + Cohort quality + Cohort quality×age	3861.509	9	3879.509	2.223
Mass of males	*Previously selected model*	4017.123	6	4029.123	0.325
	Previously selected model + Cohort quality	4017.123	7	4031.123	2.325
	Previously selected model + Cohort quality + Cohort quality×age	4012.798	8	4028.798	0.000
Litter size	*Previously selected model*	1429.921	5	1439.921	5.844
	Previously selected model + Cohort quality	1428.215	6	1440.215	6.138
	Previously selected model + Cohort quality + Cohort quality×age	1420.077	7	1434.077	0.000
Number of weaned juveniles	*Previously selected model*	1716.928	6	1728.928	1.801
	Previously selected model + Cohort quality	1713.127	7	1727.127	0.000
	Previously selected model + Cohort quality + Cohort quality×age	1712.636	8	1728.636	1.509
Average mass of juveniles at weaning	*Previously selected model (no age effect)*	2306.226	5	2316.226	0.000
	Previously selected model (no age effect) + Cohort quality	2306.070	6	2318.070	1.844
Number of recruited juveniles	*Previously selected model*	553.667	9	571.667	2.458
	Previously selected model + Cohort quality	549.509	10	569.209	0.000
	Previously selected model + Cohort quality + Cohort quality×age	549.316	12	573.316	4.107

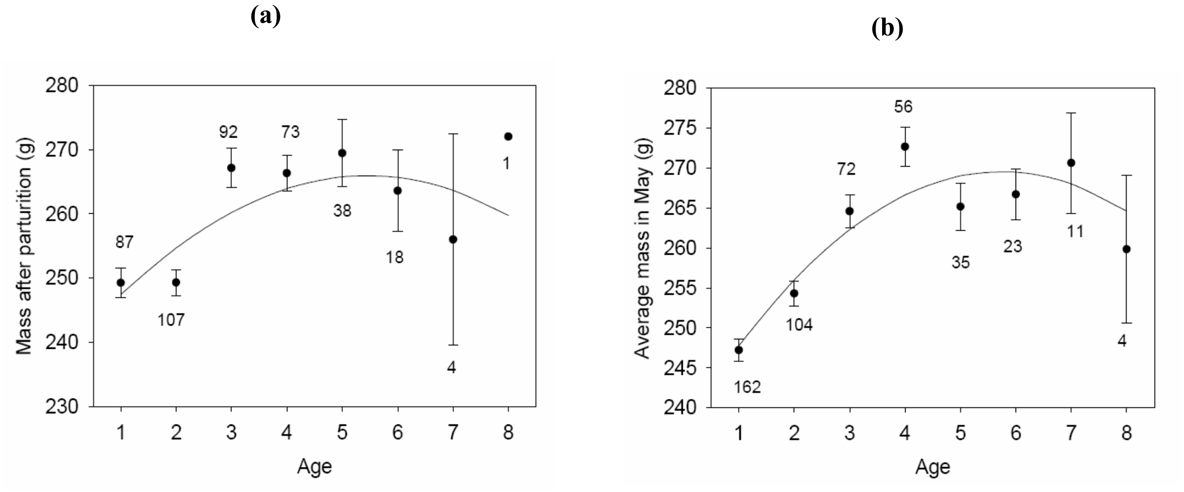

Figure 3.1 Average mass according to age in a North American red squirrel population, Kluane, Yukon, Canada: (a) mass of females after parturition and (b) mass of males in May. Numbers correspond to sample-sizes for each age category, and lines represent quadratic regressions.

Age effets on survival

Survival of females – For females, the model with lowest AIC included a quadratic effect of age and an additive effect of time (Table 3.2b) and showed that survival of females decreased after four years of age (Fig. 3.2). The additive effect of time means that survival varied among years but that the relation of survival to age remained constant. The model with three age classes (1-4, 4-6, >6 years old) provided a better fit than models with two age classes and showed an initial decrease in survival of about 19% after four years of age and 56% after 6 years of age (Table 3.2b; average survival from 1 to 4 years old: 0.73 ± 0.02; average survival from 4 to 6 years old: 0.59 ± 0.04; average survival after 6 years old: 0.26 ± 0.07). When testing for cohort effects, we found that survival of females was independent of cohort quality (Table 3.1c).

Survival of males – For males, the model with two age classes (1-7 and >7 years old) without any effect of time provided the best fit to data (Table 3.2b). Survival of prime-age males was 46% higher than that of old males (average survival for 1-7 years old males: 0.71 ± 0.02; average survival for >7 years old males: 0.38 ± 0.12; Fig. 3.2). As for females, we found no cohort quality effect on males' survival (Table 3.1c).

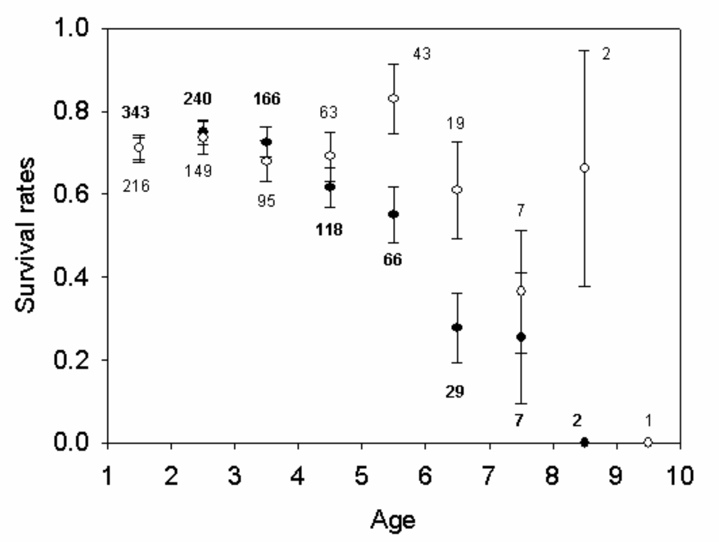

Figure 3.2 Male (open circles) and female (filled circles) survival according to age (results from the full-age dependent models) in a North American red squirrel population, Kluane, Yukon, Canada. Numbers correspond to sample sizes for each age and sex category (bold numbers correspond to female sample sizes).

Age effects on reproduction of females

Litter size – Litter size at birth varied from one to six in our population, with an average of 3.00 ± 0.04, and was age-dependent. The best model of litter size variations included a quadratic effect of mother's age, after accounting for changes in food availability during reproduction (Table 3.1b; see appendix 2-c for complete results of model selection). Litter size increased from one to four years of age, and then decreased 17% between four and eight years old (Fig. 3.3a). The model including an inverse effect of age (appendix 2-c) provided an adequate fit to data (ΔAIC=1.5) and showed a very slight increase (<2%) in litter size with increasing age. The good fit of this model compared to that of the quadratic model is likely to be due to the first four age classes where litter size increased and sample sizes were high. When testing for cohort quality effects, the model with the lowest AIC included an interactive cohort effect (Table 3.1c), indicating that females born in good years produced larger litters at the beginning of their life (between one and three years of age) than females born in poor years, but not after (Fig. 3.3b). Moreover, for females born in good years, litter size slightly increased between one and three years of age and markedly decreased after (increase of 4% from one to three years of age followed by a decrease of 20% between three and eight years of age; Fig. 3.3b), whereas for females born in poor years, litter size markedly increased until six years of age and then slightly decreased (increase of 21% from one to six years of age followed by a decrease of 4% between six and eight years of age; Fig. 3.3b).

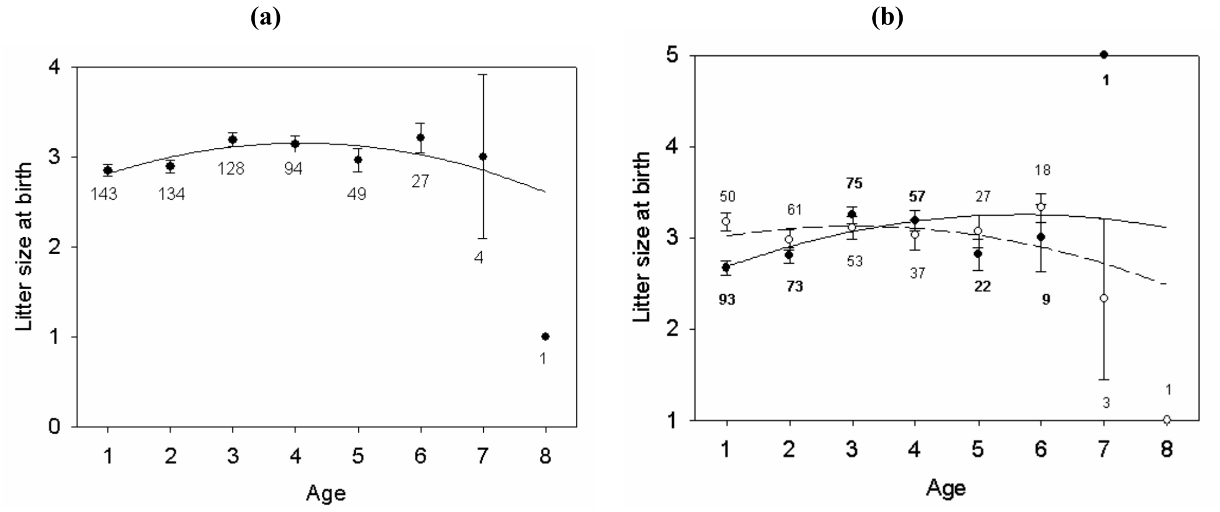

Figure 3.3 Average litter size at birth according to mother's age (a), and mother's age and cohort quality (b) in a North American red squirrel population, Kluane, Yukon, Canada. Lines represent quadratic regressions. In b, good (dotted line/white symbols) and poor (solid line/black symbols) quality cohorts are represented. Numbers correspond to sample-sizes for each age and cohort category (bold numbers correspond to low quality cohorts).

Weaning success – Female red squirrels weaned on average 1.11 ± 0.05 juveniles per breeding attempt, but this varied according to litter size at birth. The best age-dependent model describing the number of juveniles reared successfully to weaning included a quadratic effect of age (Table 3.1b; see appendix 2-d for complete results of model selection). This model was adjusted for the litter size at birth and indicated a decline in the number of weaned juveniles after three years of age (decline from 1.26 to 0 between three and eight years of age; Fig. 3.4). When testing for cohort effects, we found that the model with the lowest AIC included an additive effect of cohort quality (Table 3.1c; ΔAIC=1.8 with the model including no cohort effect) and suggested that females from high quality cohorts tended to wean a higher proportion of juveniles than females from low quality cohorts (difference of 0.18 ± 0.09 weaned juveniles per litter).

Table 3.2 Model selection for the survival rates in a population of North American red squirrels, Kluane, Yukon, Canada.

(a) Model notation for survival analyses.

Notation	Biological meaning
ϕ	Constant survival
ϕ(t)	Year effect
ϕ(a.t)	Complete age dependence + year effect + interaction
ϕ(a+t)	Additive model: complete age dependence + year effect
ϕ(a)	Complete age dependence
ϕ(yearling (t), ad_{2-4} (t), $ad_{>4}$ (t))	3 age-classes model (1, 2-4, >4) + year effect for the 3 classes
ϕ(yearling (t), ad (t))	2 age-classes model (1-2, >2) + year effect for the 2 classes
ϕ(ad_{1-3} (t), $ad_{>3}$ (t))	2 age-classes model (1-3, >3) + year effect for the 2 classes
ϕ(ad_{1-5}(t), $ad_{>5}$)	2 age-classes model (1-5 >5) + year effect for the prime-age class
ϕ((ad_{1-5}, $ad_{>5}$)+t)	Additive model: 2 age-classes model (1-5, >5) + year effect (no interaction age×time)
ϕ(ad_{1-5}, $ad_{>5}$)	2 age-classes model (1-5, >5) + no year effect
ϕ(ad_{1-4} (t), ad_{4-6} (t), $ad_{>6}$ (t))	3 age-classes model (1-4, 4-6, >6) + year effect for the 3 classes
ϕ((ad_{1-4}, ad_{4-6}, $ad_{>6}$)+t)	Additive model: 3 age-classes model (1-4, 4-6, >6) + year effect (no interaction age×time)
ϕ(linear)	Linear relationship between age and survival
ϕ(quadratic)	Quadratic relationship between age and survival
ϕ(linear+time)	Linear relationship between age and survival and additive effect of time
ϕ(quadratic+time)	Quadratic relationship between age and survival and additive effect of time
ϕ(quadratic+time+cohort quality [a])	Quadratic relationship between age and survival, additive effects of time and cohort quality
ϕ(quadratic+time+cohort quality + cohort quality×age)	Quadratic relationship between age and survival, additive effect of time and interactive effect of cohort quality
ϕ((ad_{1-7}, $ad_{>7}$)+cohort quality)	2 age-classes model (1-7, >7) and additive effect of cohort quality
ϕ((ad_{1-7}, $ad_{>7}$)+cohort quality + cohort quality×age)	2 age-classes model (1-7, >7) and interactive effect of cohort quality

[a]: cohort quality is based on the food availability during rearing (i.e. cone production the year before birth)

(b) Results of the model selection for survival rates for males and females. Models in bold represent the selected models. Capture rates were considered constant for females and function of capture effort for males.

	Females (n=343)				Males (n=216)			
Model	Deviance	np	AIC	ΔAIC	Deviance	np	AIC	ΔAIC
ϕ	1360.334	2	1364.334	58.686	888.769	3	894.769	5.836
ϕ(t)	1307.952	16	1339.952	34.304	872.393	17	906.393	17.460
ϕ(a×t)	1223.805	71	1365.805	60.157	813.155	70	953.155	64.222
ϕ(a+t)	1268.390	25	1318.390	12.742	868.015	21	910.015	21.082
ϕ(a)	1315.311	9	1333.311	27.663	875.509	11	897.509	8.576
ϕ(yearling(t), ad$_{2\text{-}4}$(t), ad$_{>4}$(t))	1262.586	41	1344.586	38.938	846.588	41	928.588	39.655
ϕ(yearling(t), ad$_{2\text{-}5}$(t), ad$_{>5}$(t))	1269.249	40	1349.249	43.601	846.612	40	926.612	37.679
ϕ(yearling(t), ad$_{2\text{-}6}$(t), ad$_{>6}$(t))	1268.096	39	1346.096	40.448	844.338	39	922.338	33.405
ϕ(yearling(t), ad(t))	1300.492	29	1358.492	52.844	857.409	29	915.409	26.476
ϕ(ad$_{1\text{-}3}$ (t), ad$_{>3}$ (t))	1284.224	29	1342.224	36.576	856.200	30	916.200	27.267
ϕ(ad$_{1\text{-}4}$ (t), ad$_{>4}$ (t))	1272.476	28	1328.476	22.828	858.121	29	916.121	27.188
ϕ(ad$_{1\text{-}5}$ (t), ad$_{>5}$ (t))	1275.363	27	1329.363	23.715	858.708	28	914.708	25.775
ϕ(ad$_{1\text{-}6}$ (t), ad$_{>6}$ (t))	1273.404	26	1325.404	19.756	858.940	27	912.940	24.007
ϕ(ad$_{1\text{-}7}$ (t), ad$_{>7}$ (t))	1295.488	25	1345.488	39.840	860.273	26	912.273	23.340
ϕ(ad$_{1\text{-}8}$ (t), ad$_{>8}$ (t))	1303.604	24	1351.604	45.956	865.880	25	915.880	26.947
ϕ(ad$_{1\text{-}4}$ (t), ad$_{4\text{-}6}$ (t), ad$_{>6}$ (t))	1250.856	37	1324.856	19.208				
ϕ((ad$_{1\text{-}4}$, ad$_{4\text{-}6}$, ad$_{>6}$)+t)	1271.820	18	1307.820	2.172				
ϕ(ad$_{1\text{-}4}$, ad$_{4\text{-}6}$, ad$_{>6}$)	1318.085	4	1326.085	20.437				
ϕ((ad$_{1\text{-}7}$, ad$_{>7}$)+t)					865.491	18	901.491	12.558
ϕ(ad$_{1\text{-}7}$, ad$_{>7}$)					**881.391**	**4**	**889.391**	**0.458**
ϕ(linear)	1331.587	3	1337.587	31.939	885.690	4	893.690	4.757
ϕ(quadratic)	1317.260	4	1325.260	19.612	882.308	5	892.308	3.375
ϕ(linear+time)	1281.912	17	1315.912	10.264	869.337	18	905.337	16.404
ϕ(quadratic+time)	**1269.618**	**18**	**1305.618**	**0.000**	866.235	19	904.235	15.302
ϕ(quadratic+time+cohort quality)	1269.427	19	1307.427	1.809				
ϕ(quadratic+time+cohort quality+cohort quality×age)	1269.342	20	1309.342	3.724				
ϕ((ad$_{1\text{-}7}$, ad $_{>7}$)+cohort quality)					878.933	5	888.933	0.000
ϕ((ad$_{1\text{-}7}$, ad $_{>7}$)+cohort quality + cohort quality×age)					878.056	6	890.056	1.123

Mass of juveniles at weaning – The average mass of juveniles at weaning (mean mass per litter) was 155.5g ± 1.4 (n=258), and was not dependent on mother's age. The best model accounting for variation in the average mass of juveniles at weaning only included food availability and litter size effects (Table 3.1b; see appendix 2-e for complete results of model selection). In addition, we did not find any effect of cohort quality on the mass of juveniles at weaning (Table 3.1c).

Age effects on survival from weaning to one year of age

The best model describing the number of recruited juveniles included three age-classes (yearlings, 2-5 years old females, ≥6 years old ; Table 3.1b and appendix 2-f for complete results of model selection), with the highest number of recruited juveniles for prime-age females (average number of recruited juveniles for 2-5 years old females: 0.89 ± 0.065 [n=215]) followed by 1 year old females (0.51 ± 0.11 [n=61]), and >5 years old females (0.30 ± 0.21 [n=10]). This model took into account the number of weaned juveniles, the food available for juveniles from weaning to one year of age, and the bequeathal behaviour of the mother. When testing for cohort quality, we found a significant additive effect (Table 3.1c). Females born in a high quality cohort had a higher number of recruited juveniles than females born in a low quality cohort (difference of 0.16 ± 0.08 recruited juveniles).

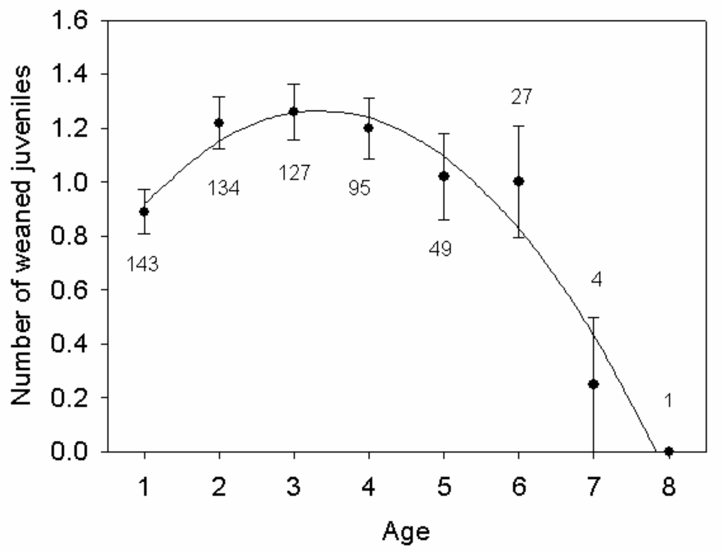

Figure 3.4 Number of weaned juveniles according to mother's age in a North American red squirrel population, Kluane, Yukon, Canada. Lines represent quadratic regressions and numbers correspond to sample-sizes for each age category.

3.5 Discussion

Pervasiveness of senescence in life history traits

An observed decrease in survival or fecundity with increasing age is often described as evidence for senescence in the wild (e.g. Promislow, 1991; McElligott, Altwegg & Hayden, 2002; Orell & Belda, 2002). However, selection acts on the covariation of survival and reproduction rather than on individual fitness components, so that a given trait alone could improve with age, even if the overall performance declines as individuals senesce (Partridge *et al.*, 1996). Moreover, a decrease in survival or reproductive performance may be attributable to senescence only if it is caused by a decline in physiological performance (Abrams, 1991). A link between lower survival and/or fecundity and a decrease in physiological condition may sometimes be lacking (Blarer *et al.*, 1995; Packer, Tatar & Collins, 1998). Consequently, an integrated study of age-specific changes of body condition, survival and reproduction is required to reliably assess senescence in a free-living animal population. We show that in a population of North American red squirrels, body mass, survival and reproductive success of females (including offspring quality) all decrease with increasing age, and that body mass and survival of males also do. These results clearly indicate a decrease of demographic performance with increasing age in this North American red squirrel population, at least for females and suggest a decrease in body condition. Therefore, our study gave strong support to the existence of senescence in this population of North American red squirrels.

It is often argued that senescence will affect few individuals in free-living populations characterized by high extrinsic mortality rates (e.g. Hayflick, 2000). Our study on red squirrels clearly shows that a substantial proportion of individuals will be at risk when senescence occurs. Female survival decreased by 19% at four years of age and by 56% at six years of age. According to our data, an average of 35% and 10% of one year old females were still alive at four and six years, respectively. In a population of Richardson's ground squirrels, survival of females decreased by about 40% after four years old, and 7% of one year old females survived until that age (Broussard *et al.*, 2005). The impact of senescence on the population demography could thus be higher in small mammals such as squirrels than in large mammals such as ungulates. For instance, the female survival of roe deer only decreased by 7.5% when the individuals reached eight years, and by 24% when they reached 12 years, although the proportion of one year-olds still at risk when eight and 12 years of age was higher (60% and 37 % respectively). Such results suggest that the higher intensity of senescence in short-lived organisms compared to large ones predicted by the theory (Hamilton, 1966) might be supported by empirical data.

Onset of senescence

According to theory (Hamilton, 1966; Charlesworth, 1994), senescence should begin at the onset of breeding because sensitivity of fitness to age-specific changes in survival and reproduction decreases with age after physiological maturation. Our results indicate that senescence begins later than the age of first reproduction (maturity begins at one year old, Becker, Boutin & Larsen, 1998) in red squirrels. Several non exclusive hypotheses for delayed senescence can be proposed. First, a decrease in mass and performance might be too subtle to be detected right after maturity (Promislow, 1991). In our red squirrel population, the full-age dependent model did suggest that survival started to decrease after two years of age for females, but this decrease was not marked before four years of age. Observed trends thus conform to the prediction that senescence begins right after the first reproduction, as observed for many species of birds (Bennett *et al.*, 2002; Saino *et al.*, 2002), but that the decline in life history traits are too subtle to be detected at that time. Second, the idea that senescence started after maturity does not necessarily mean that mass, survival and reproductive performance should all decrease from that age. Deterioration of some but not all traits may start after the first reproduction. When variation in prime-age survival is the main determinant of fitness, strong selection pressures may operate to maintain low risk of mortality well after the age at first breeding (Gaillard *et al.*, 2003b). The consequences would be a decoupling among life history traits in the onset of senescence. Somatic senescence occurred in a population of Richardson’s ground squirrels without any decline in reproductive performance (Broussard *et al.*, 2005), whereas reproductive senescence, but not somatic senescence, was reported in a population of Columbian ground squirrels (Broussard *et al.*, 2003). Somatic and reproductive senescence could thus have been shaped by different selective pressures (Packer *et al.*, 1998), and consequently physiological deterioration, survival decline and reproductive decline could occur at different ages.

Between-sex differences in the magnitude of senescence

A lower adult survival and thereby a lower lifespan in males often occurs in populations of large herbivores (Gaillard *et al.*, 2000). In these polygynous and/or sexually dimorphic species, males are larger than females, have much larger energy expenditures during the mating period, do not eat during the rut period, and may therefore be subject to greater mortality, especially during periods of resource shortage (Toigo & Gaillard, 2003). In the North American red squirrel population studied here, male squirrels are about the same size as females (males are 5 to 10% heavier than females, Boutin *et al.*, 1993). We thus predicted similar patterns of senescence for both sexes. Although age-specific variations in survival and mass were similar for both sexes, males exhibited slightly higher survival rates than females, and the decline in survival and mass appeared later in life for males. Our results thus suggest that the intensity of senescence was greater in females than in males. One potential explanation in this polytocous species could involve greater costs of reproduction for females, leading to an earlier onset of senescence (Kirkwood, 1977; Kirkwood *et al.*, 1991). In support of this interpretation, we observed that males feed more often on cones than females in early spring (Descamps and Boutin, unpubl. data), which suggests that more cones (i.e. the main food resource) are available for males than for females at the beginning of the breeding season. As costs of reproduction are expected to be more pronounced when food availability is low (Reznick, 1985; Roff, 2002), we suggest that, contrary to what has been reported in most studies focusing on large herbivores, male red squirrels incur lower fitness costs of reproduction than females, and thereby enjoy lower mortality and later onset of senescence.

Intergenerational effects of senescence: age of mother and quality of juveniles

Weaned juveniles born to old females (≥ 6 years old) had a lower probability of surviving until one year of age than weaned juveniles born to prime-age females, and were thus of lower phenotypic quality. This supports the hypothesis of a lower breeding performance of old females, and thus of senescence. We did not find any difference in mass of juveniles according to mother's age. The absence of effect of mothers' age on the weaning mass of juveniles may be explained by the lack of data for mothers >6 years old.

Previous similar maternal effects on offspring quality have been reported in insects (e.g. Kern *et al.*, 2001; Priest, Mackowiak & Promislow, 2002; Yanagi & Miyatake, 2002; Nikola, Darka & Vesna, 2004), rodents in laboratory (Wang & vom Saal, 2000; Tarìn *et al.*, 2003), cattle (Fuerst-Waltl *et al.*, 2004), humans (Parsons, 1964), and birds (Saino *et al.*, 2002), where offspring quality decreases as mothers age. Nevertheless, evidence of intergenerational effects of mother’s age in free-living populations of vertebrates is still scarce despite its evolutionary and demographic importance (Kern *et al.*, 2001).

Cohort quality and senescence patterns

Senescence is expected to involve a trade-off between early and late demographic performance (Kirkwood, 1977; Kirkwood *et al.*, 1991), so that the magnitude of senescence should be higher (i. e. earlier onset and/or higher intensity) in high quality cohorts than in poor quality ones. Individuals from good cohorts should reproduce earlier and more intensely than individuals born from poor cohorts, and should thus suffer higher reproductive costs. As expected, female red squirrels born in high quality cohorts produced larger litters early in life than females born in low quality cohorts, and the litter size of females born in good cohorts decreased earlier in life and more intensely than the litter size of females born in poor cohorts. A more intense breeding activity early in life is thus associated with an earlier decline in reproductive performance. Such results strongly support our prediction and the disposable soma theory of senescence (Kirkwood, 1977). In addition, females born in high quality cohorts tended to breed more successfully throughout their life and produced juveniles that were more likely to survive from weaning to recruitment. This supports the idea that females born a year with high cone availability (i.e. high quality cohort) were high quality females, and that environmental conditions the year of birth may have long-term effects on individual life-history (Lindström, 1999).

Partie 2

Âge et effort reproducteur

Chapitre 4 Increase of reproductive effort with age in mammals: the evidence may not lie where it is expected

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(soumis à *Journal of Animal Ecology*)

Le chapitre précédent a clairement montré une diminution de la valeur reproductive résiduelle avec l'âge. Dans une telle population, il est prédit que l'effort reproducteur augmente au cours de la vie. Cette prédiction a été peu testée au sein des mammifères, et lorsqu'elle l'a été, les résultats restent souvent peu concluants. Le présent chapitre a d'une part permis de montrer clairement l'augmentation de l'effort reproducteur avec l'âge dans cette population d'écureuils, et d'autre part discute la pertinence des variables généralement utilisées dans ce contexte. Il suggère que l'utilisation de mesures dites « directes » de l'effort reproducteur (changements de masse au cours de la saison de reproduction et masse totale des jeunes produits) n'est pas valable dans tous les systèmes d'étude. La sénescence (qui est souvent une des conditions initiales pour supposer une augmentation de l'effort avec l'âge) peut notamment biaiser l'interprétation des résultats basés sur de telles mesures.

4.1 Abstract

Life history theory predicts that reproductive effort should increase with age as residual reproductive value decreases but in mammals, empirical evidence for this prediction is rare. We investigated age-specific variation in reproductive effort in female North American red squirrels, using both direct and indirect (or behavioural) measures of effort from the onset of breeding to the weaning of juveniles. Indirect measures such as the probability of breeding, the probability of attempting a second reproduction within the same season, and the propensity to bequeath the territory to juveniles all indicate an increase in reproductive effort with age. Direct measures such as the proportion of mass change during reproduction and the litter mass at weaning did not show any age-specific variation. A full assessment of all forms of reproductive effort reflecting various stages of the entire parental investment period may be necessary to reveal increases with age as predicted by theory. When senescence occurs and/or individual heterogeneity is important, direct measures of effort may not be suitable to assess the relation of reproductive effort to age, and indirect measures may be needed.

Key-words: North American red squirrel, *Tamiasciurus hudsonicus,* individual heterogeneity, senescence, life history theory

4.2 Introduction

The general life history problem as defined by Schaffer (1983) and Stearns (1992) is how to optimize resource allocation to growth, survival and reproduction. According to the principle of energy allocation (Cody, 1966; Williams, 1966a) trade-offs among growth, survival and reproduction should occur when the amount of energy that is available to individuals becomes limited. Reproductive effort corresponds to the parental input into reproduction, and is defined as the amount of energy allocated to reproduction regardless of fitness costs (Evans, 1990). According to evolutionary theories, reproductive effort should increase from the first breeding attempt to the end of life, since residual reproductive value decreases with age (Fisher, 1930; Williams, 1966b; Charlesworth *et al.*, 1976; Stearns, 1976, 1992).

Mammals are unique among living organisms in that parental input into reproduction involves a two-stage, highly sophisticated strategy combining viviparity and lactation. This complex strategy engages the full metabolic machinery of females during reproduction, since most of the energy allowing offspring growth is first processed by mothers. Female mammals thus offer critical tests for evolutionary theories dealing with parental effort, especially now that long-term field data have accumulated for a few decades in a number of free-living populations. Unfortunately, more than 75 years after Fisher's theories were formulated (1930), it is becoming clear that empirical data are contradictory.

For instance, an increase of reproductive effort with age followed by a decrease has been reported for female polar bears (*Ursus maritimus*, Derocher & Stirling, 1994), and female Columbian ground squirrels (*Spermophilus columbianus*, Broussard *et al.*, 2003). Reproductive effort of females was not related to age in Northern elephant seals (*Mirounga angustirostris*, Crocker *et al.*, 2001), Richardson's ground squirrels (*Spermophilus richardsonii*, Broussard *et al.*, 2005) and European ground squirrels (*Spermophilus citellus*, Millesi *et al.*, 1999a), and did increase with age in moose (*Alces alces*, Ericsson *et al.*, 2001). Patterns of age-specific variation in reproductive effort among mammals are thus clouded by contradictory results.

A first necessary step in resolving this conflict between theory and data is to better understand the nature of the evidence for and against the theory. Reproductive effort has been measured in different ways and these measures tend to capture only a subset of the potential ways energetic input into reproduction could occur. Clutton-Brock (1984) found that variables describing reproductive effort at parturition (such as the offspring birth mass) decreased with age, whereas variables describing reproductive effort of females around weaning (such as offspring mass in early winter) increased with age. Such results point out that an increase in effort with age may be expressed in only some of the variables describing parental input into reproduction (Cameron *et al.*, 2000). A full assessment of all forms of reproductive effort reflecting various stages of the entire parental investment period may be necessary to reveal increases with age as predicted by theory.

Using long-term data (>16 years), we investigated age-specific reproductive effort in a North American red squirrel *Tamiasciurus hudsonicus* population studied in Canada. In addition to litter mass and mass changes of adults during reproduction, which are often used as direct measures of the reproductive effort reflecting parental input during gestation and lactation (e.g. Michener & Locklear, 1990; Kojola, 1991; Bowen *et al.*, 1994; Millesi *et al.*, 1999a; Ericsson *et al.*, 2001; Weladji *et al.*, 2002; Yoccoz *et al.*, 2002; Broussard *et al.*, 2005; Mysterud, Solberg & Yoccoz, 2005), we used two indirect measures of reproductive effort. We used the breeding propensity, a measure of reproductive effort preceding gestation, and territory bequeathal, a measure of effort following lactation. Bequeathal indicates whether a female gives part or all of her territory to one or several of her juveniles at weaning (Price *et al.*, 1993; Berteaux *et al.*, 2000; Boutin, Larsen & Berteaux, 2000). These two indirect measures of reproductive effort reflect substantial energy input into reproduction. Indeed, mating chases in promiscuous red squirrels (Smith 1968; Boutin & Larsen 1993) occur at the end of winter (from February to April), when snow cover is still high and temperatures are still low. Thus, energy expended to find a mate and reproduce is likely to be high. In the same way, females who bequeath their territory need to establish a new territory, which requires considerable energy (Larsen *et al.*, 1994).

Survival rates and the probability of breeding successfully clearly decrease with increasing age in this red squirrel population (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3), and consequently, reproductive values also decrease with age. According to life history theory, we thus predicted that reproductive effort should increase with increasing age in this population.

4.3 Materials and methods

Study area and red squirrel population

Our work was conducted in the South Yukon, Canada (61º N, 138º W) and we report results for the years 1988-2003 for two 40 ha control grids. All squirrels were marked with numbered ear tags and a unique colour combination of wires for identification at a distance. Fates of female squirrels were determined through live-trapping (Tomahawk traps) and visual observations from April to August. The breeding status of females was determined through nipple condition, changes in mass and/or lactation. The nest of each breeding female was visited soon after birth to count and sex the young. Juveniles were tagged at about 20-25 days of age and weighed within a week of weaning (around 70 days of age). Females were weighed soon after parturition and within a week of weaning their juveniles. Females were also trapped and weighed regularly throughout the breeding season, which allowed us to weigh females around the emergence of their juveniles (between 35 and 45 days after parturition, Humphries *et al.*, 1996). Weights were determined to the nearest gram with a Pesola scale.

Habitat is boreal forest with white spruce *Picea glauca* as the dominant tree species. Spruce cone seeds represent the main food resource for red squirrels in this population (McAdam *et al.*, 2003). At the end of summer, red squirrels store unopened cones on hoarding sites (middens) that they defend year round (Humphries *et al.*, 2005). Food available for reproduction one year is determined by cone production the previous year (McAdam *et al.*, 2003). We estimated spruce cone production each year when cones were fully formed but harvesting by squirrels had not yet begun (usually at the end of July). We counted the number of new cones in the top three meters of 170 trees randomly distributed on the study area.

Study design

We assessed age effects on reproductive effort in females using a suite of dependent variables reflecting the diversity of physiological and behavioural processes involved in reproduction. Our choice of variables indicative of reproductive effort thus encompassed key parameters hereafter organized chronologically from the propensity to breed to the weaning of juveniles.

We first investigated the effect of mother's age on the breeding propensity (i.e. the probability to breed or not). We considered that a female was breeding when she gave birth to at least one juvenile. In 1993 and 1998, the two years with the highest cone production (mast years), some females that were successful in their first breeding attempt bred a second time. We also investigated the effect of mother's age on the probability to breed twice in a year, considering only females that had weaned ≥ 1 juvenile at the first breeding attempt.

Second, we considered mass change between parturition and emergence of juveniles, and then between emergence and weaning. Humphries and Boutin (1996) suggested that in our red squirrel population, females adjust the energy stored during the early lactation period (from parturition to emergence) to the future reproductive demands of late lactation. Thus, early lactation mass gain is an important component of reproductive effort, so that an increased effort should correspond to a higher mass gain between parturition and emergence. Furthermore, as this energy storage is used during late lactation (from emergence to weaning), mass change during the late lactation period should also be a relevant indicator of mother's energetic input into reproduction: a high reproductive effort should translate in a high mass loss.

In a third step, we studied the effects of mother's age on litter mass at weaning. As we did not get mass at weaning for every weaned juvenile, mass of a given litter was approximated as the product of the number of weaned juveniles from this litter times the average mass of juveniles from this litter whose weaning mass was known.

Finally, we investigated the relationship between female's age and the probability to bequeath the territory at weaning (Price *et al.*, 1993; Berteaux *et al.*, 2000). Territory bequeathal was measured as a binary variable: the female keeps her territory vs. gives part or all of her territory to one or several of her juveniles. Berteaux and Boutin (2000) showed that females bequeathing their territory are older on average than females keeping it. However, it was unclear whether this age effect was simply due to a difference between yearling and older mothers, or whether it resulted from a more progressive effect of age on the probability to bequeath a territory.

Statistical analyses

Our data set included repeated measurements of the same individuals at different ages. To analyse the variation in the proportion of mass change and in the litter mass, we fitted generalized linear mixed models with the MIXED procedure in SAS version 8 (SAS Institute, 1999). For the binary dependent variables (breeding propensity and territory bequeathal), we fitted mixed models with the GLIMMIX macro of SAS version 8 with a binomial distribution and a *logit* link function (SAS Institute, 1999). For both types of responses, we used the repeated statement and the maximum likelihood method. This allowed us to take into account the non independence in our data set (Littell *et al.*, 1996) and to avoid pseudo-replication problems (Hurlbert, 1984). We specified the compound symmetric matrix structure, which assumes that the correlation of measurements made on the same individual is a function of the individual considered but does not vary throughout its life.

To test for an age effect on the probability to breed a second time within the same season, we performed logistic regressions with the LOGISTIC procedure in SAS version 8 (SAS Institute, 1999) because only one individual appeared twice in our data set.

To characterize the functional relationship between reproductive effort and age, we tested and compared different continuous (linear, quadratic, inverse regressions) and discrete (2 or 3 age classes) models (Table 4.1a). Our model selection was based on the Akaike Information Criterion (Burnham *et al.*, 2002). When the difference of AIC between two models was <2, both models were equally competitive and we retained the most parsimonious one (Burnham *et al.*, 2002).

As food availability could strongly influence reproductive effort, we included in our models the variable *Previous Cone Production*, which corresponds to cone production one year before reproduction (i.e. food available for the current reproduction). To study the probability to breed a second time within the same season, we did not incorporate *Previous cone production* because this variable did not show any variation between the two years when the dependent variable was measured (1993 and 1998). To analyse mass changes, we included litter size in our models, as litter size influences reproductive effort of females (Humphries *et al.*, 1996). To analyse litter mass, we included mass of the mother (mass after parturition) in our models as mass decreases at old ages in this red squirrel population (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3). Territory bequeathal occurs at the end of summer, when new cones of the year are fully formed. As this new cone production influences bequeathal behaviour (Berteaux *et al.*, 2000), cone production year of reproduction (hereafter named *Current cone production*) was also included in the modeling of the bequeathal probability. Results are reported as means ± SE.

4.4 Results

Breeding propensity

According to AIC values and the parsimony principle, the best model involved a breeding probability that increased with age (linear effect of age on a logit scale; Table 4.1a; Fig. 4.1a; see appendix 3-a for complete results of model selection). The effect of the previous cone production was not significant (Table 4.1a). When we modeled the probability to breed a second time in a given breeding season, the best model included an inverse effect of age (1/age, Table 4.1b). The model with a linear effect of age (on a logit scale) provided a similar fit (ΔAIC=0.312). The two models indicated that the probability to breed twice within the season increased with age (Fig. 4.1b).

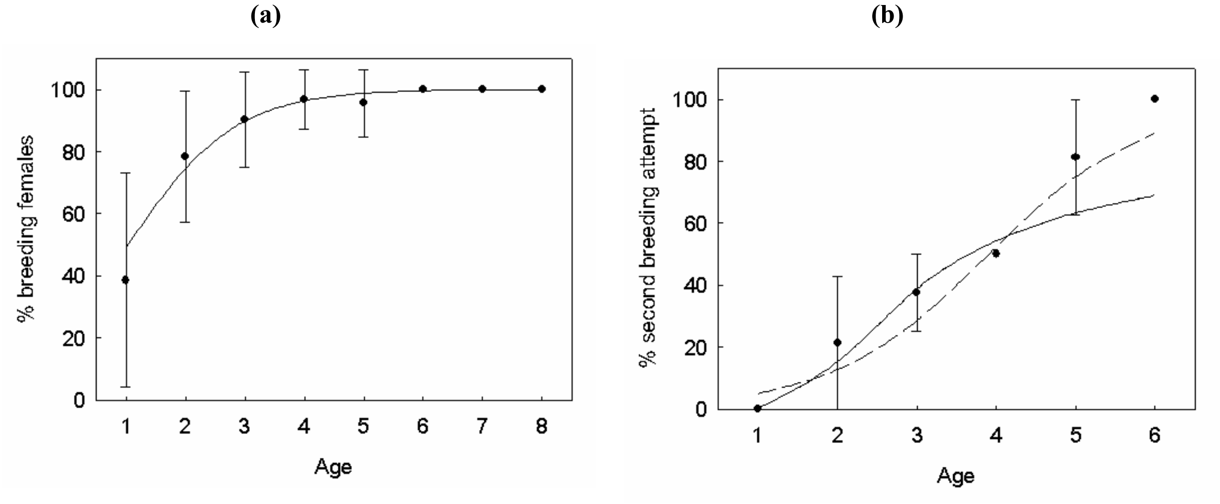

Figure 4.1 Age and breeding propensity in a population of North American red squirrels, studied at Kluane, Yukon, Canada (means ± se). (a) Proportion of reproductive females according to age. The line corresponds to the logistic regression curve: logit(Probability to breed)=1.1-1.1×Age (see table 4.1a); (b) Proportion of 2nd reproduction attempts according to age in two years when second reproductions were observed in the population (1993 and 1998; means ± se). The solid line corresponds to the model logit(Probability to breed twice)=2.1-7.5/Age and the dashed line to the model logit(Probability to breed twice)=3.9-1.0×Age (see table 4.1b).

Female mass change during reproduction

Previous cone production, litter size, and mother's age had no detectable effect on mass gain of mothers between parturition and emergence (Table 4.1b; Fig. 4.2a; see appendix 3-b for complete results of model selection). The proportion of mass loss between emergence and weaning decreased with increasing previous cone production, but increased with increasing litter size (Table 4.1b; slope of 0.007 ± 0.003 for litter sizes varying from 1 to 6; slope of $-10^{-4} \pm 3.10^{-5}$ for cone productions varying from 1 to 280). Age did not influence the proportion of mass change in females (Table 4.1b; Fig. 4.2b).

Litter mass at weaning

Four models provided an equivalent fit to the data (ΔAIC<2, Table 4.3; see appendix 3-c for complete results of model selection). Two models indicated a decrease in litter mass for old mothers (model including a quadratic effect of age, and model including three age-classes: yearlings, females 2-4 years old and females >4 years old) while the others (model including an inverse effect of age, and model including two age-classes: yearlings, females >1 year old) indicated a constant litter mass after one year of age (Table 4.1b). These two latter models had one parameter less than the two former ones. Consequently, the most parsimonious conclusion is that litter mass at weaning did not change with mother's age after one year of age (Fig. 4.2c). These two models also included positive effects of the previous cone production and of the mass of the mother (Table 4.1b, model 2: slope of 0.40 ± 0.08 for cone productions varying from 1 to 280; slope of 0.83 ± 0.36 for mother masses varying from 213g to 345g).

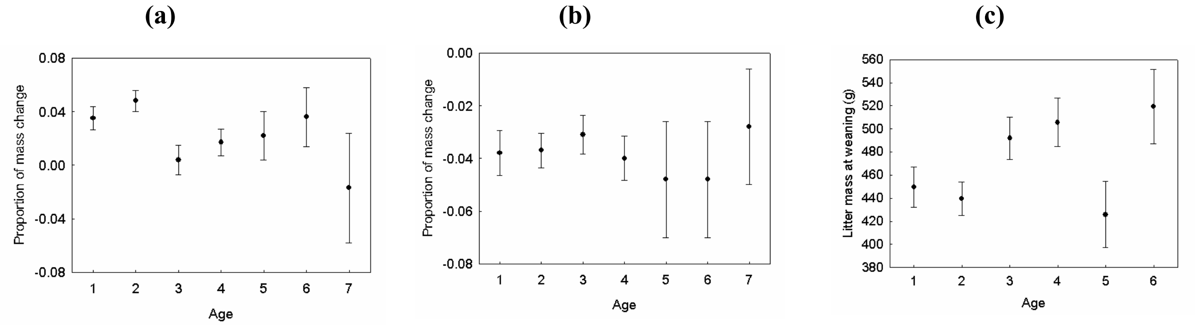

Figure 4.2 Age and direct measures of reproductive effort (proportion of mass change in reproductive females and litter mass at weaning) in a population of North American red squirrels, studied at Kluane, Yukon, Canada (means ± se). (a) Mass change between parturition and emergence of the juveniles, (b) mass change between emergence and weaning of the juveniles, (c) litter mass at weaning.

Territory bequeathal

The best model was a discrete model with three age classes: yearlings, females between 2 and 5 years of age, and females >5 years of age (Table 4.1b; see appendix 3-d for complete results of model selection). The probability to bequeath the territory at weaning was a function of the current and previous cone productions, and increased from yearlings to prime-age females, and from prime-age to senescent females (estimated probabilities to bequeath a territory at weaning for the years 1991-2003: 0.39 ± 0.049 for yearlings; 0.57 ± 0.053 for 2-5 years old females; 0.83 ± 0.036 for females >5 years of age). Two other models provided similar fits (inverse regression and model with three age classes: yearlings, females 2-4 years old and females >4 years old; ΔAIC<2), and indicated an increase in the probability of bequeathal as females got older. In all of the best models, the probability to bequeath the territory at weaning increased with current cone production, but decreased with previous cone production (slope of 0.006 ± 0.002 for current cone production; slope of -0.007 ± 0.001 for previous cone production).

4.5 Discussion

Reproductive effort and age

Variation in reproductive effort according to age may be expressed only in some variables and at particular stages of breeding (Clutton-Brock, 1984). In particular, an increase in reproductive effort may only occur when the chances that offspring will survive are reasonably high. Thus, to study the relationship between reproductive effort and age, the entire breeding period has to be considered. We used four variables describing parental input into reproduction from the onset of reproduction to juvenile emancipation. Interestingly, the two variables reflecting female reproductive effort during the most physiologically demanding stages of reproduction (gestation and lactation) were not affected by mother’s age, whereas the two variables more remotely connected to energy investment into reproduction did vary with age, in the direction predicted by theory. Contrary to findings on European red squirrels where the proportion of females that produced a litter decreased after four years of age (Wauters *et al.*, 1995a), the probability to breed once or twice within the same season increased with age in our North American red squirrel population. In addition, the probability to bequeath part or all of the territory at weaning also increased with age as previously suggested (Berteaux *et al.*, 2000). Our study thus strongly supports an increase of female reproductive effort with age, despite the absence of any age effect on direct measures of effort such as mass of juveniles or female mass change. The increase in bequeathal probability with age also supports the idea that effort increases essentially when chances that offspring survive are high (that is at weaning).

Table 4.1 Relation of reproductive effort to age in a population of North American red squirrels, Kluane, Yukon, Canada.

(a) Variables describing age effect used to test the shape of the relationship of reproductive effort to age.

Age effect	**Notation**
linear regression	A_{linear}
quadratic regression	$A_{quadratic}$
inverse regression	A^{-1}
1 juvenile class (1 yr) and 1 adult class (≥2 yr)	$A_{1,>1}$
1 prime-age class (1-6 yrs) and 1 senescent class (≥7 yrs)	$A_{1-6,>6}$
1 prime-age class (1-5 yrs) and 1 senescent class (≥6 yrs)	$A_{1-5,>5}$
1 prime-age class (1-4 yrs) and 1 senescent class (≥5 yrs)	$A_{1-4,>4}$
1 juvenile class (1 yr), 1 prime-age class (2-6 yrs), 1 senescent class (≥7 yrs)	$A_{1,2-6,>6}$
1 juvenile class (1 yr), 1 prime-age class (2-5 yrs), 1 senescent class (≥6 yrs)	$A_{1,2-5,>5}$
1juvenile class (1 yr), 1 prime-age class (2-4 yrs), 1 senescent class (≥5 yrs)	$A_{1,2-4,>4}$

(b) Results of the model selection for breeding propensity of females, proportion of mass changes of females during reproduction, litter mass at weaning and bequeathal probability. More than one model are selected when ΔAIC<2 and when the number of parameters is equivalent. PCP represents the previous cone production (i.e. cone production one year before reproduction, which corresponds to food available for reproduction), and CCP the current cone production (i.e. cone production of the year, which corresponds to food available after weaning of juveniles). LS corresponds to litter size, and MM to mother mass (after parturition).

Life history trait	**Sample sizes**[§]	**Initial model**	**Selected models**
Probability to breed	n_{obs}=782, n_{ind}=322	*Age effect* + PCP	Logit (Probability to breed)~A_{linear}
Probability to breed a second time in the same season	n_{obs}=67, n_{ind}=66	*Age effect*	Logit (Probability to breed a 2nd time)~A_{linear} Logit (Probability to breed a 2nd time)~A^{-1}
Mass change between parturition and emergence of juveniles	n_{obs}=265, n_{ind}=165	*Age effect* + PCP +LS	Mass change~Constant
Mass change between emergence and weaning of juveniles	n_{obs}=265, n_{ind}=165	*Age effect* + PCP +LS	Mass Change~PCP+LS
Litter mass at weaning	n_{obs}=180, n_{ind}=133	*Age effect* + PCP + MM	Litter mass~A^{-1} + PCP + MM Litter mass~$A_{1,>1}$ + PCP + MM
Probability to bequeath territory	n_{obs}=336, n_{ind}=186	*Age effect* + PCP+ CCP	Logit (Bequeathal)~$A_{1,2-5,>5}$+PCP+CCP

[§]: n_{obs} corresponds to the number of measurements, and n_{ind} to the number of individuals

Reproductive effort, senescence and individual heterogeneity

We found 26 studies of reproductive effort in female mammals (Table 4.2) and in 19 of these (73%), reproductive effort was measured, at least in part, by changes in female mass during the breeding season or total litter mass produced. Only six of these studies (32%) reported an increase in reproductive effort with increasing age. Among these six studies, one only compared yearlings versus adults (Millesi *et al.*, 1999b), and one only considered young individuals (Mongolian gerbils <4 month old, Clark, Moghaddas & Galef, 2002). Two others did not check for a possible decrease in effort at the end of life (whereas such a decrease might have occurred, see fig. 4 in Lunn, Boyd & Croxall, 1994; fig. 1 in Gendreau, Côté & Festa-Bianchet, 2005), and the effects of mothers' age and mass were confounded in the other two (Birgersson & Ekvall, 1996; Ericsson *et al.*, 2001). Thus, results of our study and a survey of the current literature strongly indicate that the evidence for an increase in reproductive effort as measured by female mass change or litter mass is weak.

Two non-exclusive hypotheses may explain such a discrepancy between empirical results and predictions from life history theory. The first one involves the aging process. Senescence can be defined as a deterioration of functional capacities at the end of life, leading to a lower survival and reproductive performance (Rose, 1991). Senescence can confound the assessment of reproductive effort with age when effort is defined in terms of mass change during reproduction or litter mass. A lower breeding efficiency at the end of life could result in a mass change or litter mass apparently equivalent or lower for senescent individuals than for prime-age ones, even if their energetic input into reproduction is higher. For example, old individuals may spend more time acquiring energy (e.g. more time foraging) but may be less efficient at converting energy into milk production (as suggested in Ericsson *et al.*, 2001). The result may be an apparent lower reproductive effort, in terms of litter mass and female mass change, despite a higher energetic input from the parent. Among the 19 studies reporting analyses of female mass change or litter mass to measure reproductive effort, eight (42%) reported an increase in mass change or litter mass at intermediate ages followed by a decrease at old ages (Clutton-Brock, 1984; Derocher *et al.*, 1994; Dobson *et al.*, 1999; Boltnev *et al.*, 2001; Hood *et al.*, 2002; Weladji *et al.*, 2002; Broussard *et al.*, 2003; Adams, 2005). In our red squirrel population, we found that performance of females decreased at old ages (Descamps, Berteaux, Gaillard, Boutin, unpubl. data, chapter 3), in the absence of age specific mass changes during lactation or age specific litter mass at weaning.

Table 4.2 Review of the literature studying age effect on reproductive effort in mammals. "*Max. age*" corresponds to the maximum age (in years) of individuals in the study. "*Variables*" indicates variables used to estimate reproductive effort. When several measures of effort were used, only those indicating an increase of effort with age have been shown in the table, and a footnote has been added. In the "*Variables*" column, "*mass loss*" corresponds to mass loss of mothers during reproduction (reproductive periods may vary between studies), and "*litter mass*" corresponds to mass of the litter (usually at birth or at weaning).

Species	**Sex**	**Max. age**	**Variables**	**Variation in reproductive effort with age**	**Reference**
Richardson's ground squirrel	F	6	Litter mass	No effect	Broussard *et al.*, 2005
Caribou	F	16	Litter mass	Increase then constant	Adams, 2005
Mountain goat	F	15	Litter mass	Increase for male offspring, no effect for females	Gendreau *et al.*, 2005
European rabbit	F	7	Litter size	Increase then decrease	Rödel *et al.*, 2004
Columbian ground squirrel	F	9	Litter mass	Increase then decrease	Broussard *et al.*, 2003
Mongolian gerbil	F	0.3	Mass loss, maternal care	Increase	Clark *et al.*, 2002 [*]
Reindeer	F	12	Litter mass	Increase then decrease	Weladji *et al.*, 2002
Big brown bat	F	?	Litter mass	Increase then decrease	Hood, Bloss & Kunz, 2002 [†]
Northern elephant seal	F	13	Energy expenditure	No effect	Crocker *et al.*, 2001
Moose	F	19	Litter mass	Increase	Ericsson *et al.*, 2001 [‡]
Northern fur seal	F	23	Litter mass	Increase then decrease	Boltnev & York, 2001
Horse	F	>9	Breeding propensity	Increase	Cameron *et al.*, 2000 [§]
Columbian ground squirrel	F	8	Litter mass	Increase then constant after 1 year old	Dobson *et al.*, 1999 [‡]
European ground squirrel	F	>2	Mass loss	Increase (between yearlings and adults	Millesi *et al.*, 1999b
European ground squirrel	F	4	Breeding propensity	No effect	Millesi *et al.*, 1999a
Fallow deer	F,	?	Litter mass, growth rate	Increase	Birgersson *et al.*, 1996 [‡]
Domestic swine	F	6	Litter size	Increase	Meikle *et al.*, 1996
Eurasian red squirrel	F	≥5	Breeding propensity	Increase then decrease	Wauters *et al.*, 1995a
Polar bear	F	27	Litter mass	Increase then decrease	Derocher *et al.*, 1994
Antarctic fur seal	F	20	Litter mass	Increase	Lunn *et al.*, 1994 [¶]
Antarctic fur seal	F	14	Litter mass, growth rate	No effect	Lunn *et al.*, 1993
Nothern elephant seal	F	15	Indirect evidence	Increase	Sydeman *et al.*, 1991 [*†]
Bison	F	18	Nursing time	Increase	Green, 1990 [*‡]
Harp seal	F	16	Nursing and aggressive behaviours	No effect	Stewart, 1987
Harp seal	F	25	Mass loss	No effect	Stewart, 1986
Red deer	F	14	Litter mass, breeding propensity, neonatal survival	Increase then decrease	Clutton-Brock, 1984 [*§]

(Suite du tableau 4.2)

Moose	M	21	Mass loss	Increase then constant or decrease	Mysterud *et al.*, 2005
Brushtail possum	M	7	Mass loss	Decrease	Isaac, 2005
Reindeer	M	5	Mass loss	Increase	Mysterud *et al.*, 2003
Red deer	M	19	Mass loss	Increase then decrease	Yoccoz *et al.*, 2002
Laboratory house mouse	M	1	Aggressiveness/Pup defence	Increase (between 6 and 12 month old females	Pflanz, 2002
Reindeer	M	6	Mass loss	Increase	Kojola, 1991
Bison	M	12	Rutting behaviour	Increase then decrease	Maher & Byers, 1987
Northern elephant seal	M	14	Mass loss	No effect (between sub-adults and adults	Deutsch, Haley & Le Boeuf, 1990
Wood bison	M	16	Rutting behaviour	Increase	Komers, Messier & Gates, 1992

[*]: study that concerns only 1st reproduction of females; also, decrease in breeding propensity and litter size

[†]: age of individuals based on tooth wear

[‡]: not adjusted for mothers' mass

[§]: also, no effect on mass loss; investment by old individuals seemed to be better targeted at the most critical period for offspring survival

[¶]: also, increase then decrease for the breeding propensity

[*†]: conclusion based on the increase of the probability to breed successfully with age despite senescence

[*‡]: also, no effect of age on mass loss

[*§]: also, decrease then increase for suckling bout duration, calves survival and condition

An alternative hypothesis to account for the absence of an age effect on female mass change or litter mass is based on individual heterogeneity. When individuals differ in quality within a population, the proportion of high quality individuals for each age-class should increase with age (because low quality individuals die first, Service, 2000; Cam *et al.*, 2002). Therefore, an absence of age-specific variation in mass loss during reproduction or a decrease in mass loss during reproduction for old females does not necessarily mean that reproductive effort does not vary with age, but could be the result of an apparent increase in average quality with age. For example, when females differ in the quality of their territory, a female with a high quality territory could easily gain mass, whereas a female in a poor territory could gain very little mass despite an intense foraging activity. If the proportion of high quality females (i.e. females that own a high quality territory) among each age-class increases with age, the result would be an apparent lower mass loss during reproduction as female get older, and thus an apparent decrease in reproductive effort.

Mass change during reproduction depends on mother's foraging activity, which itself is related to reproductive effort of females in mammals, except for the most extreme capital breeders (Jonsson 1997), and to habitat quality. Thereby, when individual heterogeneity within a population is important and mainly determined by territory or habitat quality, resource availability and foraging activity of females are likely to be more influential to shape the relationship between reproductive effort and age than mass change of females or litter mass (see Tuomi *et al.*, 1983 for a similar viewpoint).

Our study focused on reproductive effort in female mammals, but the same interpretations could be applied to male mammals, and other taxonomic groups. In male mammals, reproductive effort has also often been studied through mass loss during reproduction (Table 4.2). As for females, senescence and individual heterogeneity may affect our interpretation of mass loss in terms of reproductive effort. For example, mass loss of old senescent ungulates during the rut may be important because of a low foraging efficiency, and not because of a high rutting activity (i.e. reproductive effort). On the opposite, mass loss among old individuals may be very limited despite an intense rutting activity when individual heterogeneity is important and old individuals are of above-average quality.

4.6 Conclusion

Life history theory predicts an increase of reproductive effort with age, but in mammals, where energy input into reproduction is usually high, empirical evidence for this prediction is rare. Two reasons can be proposed to explain why empirical studies of reproductive effort rarely supported evolutionary theory. First, reproductive effort may not necessarily increase at all the steps of the breeding cycle, and old individuals may invest more only at some points of the cycle (when offspring' chance of survival is high). Therefore, measures of reproductive effort from the onset of breeding to the weaning of juveniles may be necessary. Second, direct measures of parental input into reproduction (such as litter mass or mass loss) may be irrelevant to analyse variation in reproductive effort with age in free-living animal populations when senescence occurs or individual heterogeneity is important. As a consequence, evidence for an increase of reproductive effort may not necessarily lie where it is expected and several measures of effort are needed to reliably study variation of effort with age. Indirect behavioural measures of effort may be less affected by senescence or individual quality and may thereby be more relevant to assess the relation of reproductive effort to age. The detailed long-term data on female red squirrels we used in the present study allowed testing for an increase of reproductive effort with age at different periods of the breeding cycle, from the onset of breeding to the weaning of juveniles, based on direct and indirect (i.e. behavioural) measures of effort. Whereas direct measures did not show any age-specific variation in reproductive effort, behavioural measures clearly indicate that reproductive effort in female squirrels increased with age as predicted by evolutionary theory.

Partie 3

Coûts de la reproduction, âge et hétérogénéité individuelle

Chapitre 5 Best squirrels trade a long life for an early reproduction

Descamps S., Boutin S., Berteaux D., Gaillard J.-M.
(*Proceedings of the Royal Society of London-B,* 2006. 273: 2369-2374)

Après s'être intéressé aux effets de l'âge sur la performance démographique et l'effort reproducteur, la suite de ce travail traite des coûts de la reproduction à différents âges. Plus particulièrement, le présent chapitre s'intéresse aux coûts liés à une reproduction précoce ou non. Les femelles écureuils roux de cette population se reproduisent pour la première fois à 1 ou 2 ans, voire exceptionnellement 3 ou 4 ans. Ce travail teste, et supporte, la prédiction que se reproduire tôt entraîne des coûts en terme de performance future. Un compromis clair apparaît entre reproduction précoce et longévité, les individus se reproduisant à un an vivant moins longtemps que les autres. Ce chapitre montre aussi un lien entre qualité individuelle, âge de première reproduction et conséquences de cette première reproduction. Les individus de haute qualité se reproduisent plus tôt que les autres, et malgré une moins bonne survie, tendent à avoir une meilleure *fitness* (i.e. produisent plus de jeunes avec succès tout au long de leur vie).

5.1 Abstract

Age at primiparity plays a crucial role in population dynamics and life history evolution. Long-term data on female North American red squirrels were analysed to study the fitness consequences of delaying first reproduction. Early breeders were born earlier, had a higher breeding success and achieved a higher lifetime reproductive success (LRS) than females who delayed their first reproduction, which suggests a higher quality of early breeders. However, early breeders had similar mass when tagged, and similar number of food caches available at one year of age as late breeders. Nevertheless, we found evidence of survival costs of early primiparity. Early breeders had a lower survival between one and two years of age than late breeders and a lower lifespan. Our study points out that two reproductive tactics co-occurred in this population: a tactic based on early maturity at the cost of a lower survival versus a tactic based on delayed maturity and long lifespan. High quality individuals express the most profitable tactic by breeding early whereas low quality individuals do the best of a bad job by delaying their first reproduction.

Key words: survival cost of reproduction**,** phenotypic quality, lifetime reproductive success, *Tamiasciurus hudsonicus*

5.2 Introduction

The age at which females first reproduce can greatly affect individual fitness and population dynamics (Cole, 1954; Stearns, 1992). Early primiparity should be selected for because it reduces the period during which animals risk dying before reproducing (Cole, 1954; Bell, 1980). Nevertheless, females often delay their first reproduction well after physiological maturity in a large number of species, suggesting that reproducing early in life may be costly (Williams, 1966b; Gadgil & Bossert, 1970; Bell, 1980; Stearns, 1992). Delaying the first reproduction could be compensated for by increased survival and/or future reproductive success which should offset the lost benefits of reproducing early (Curio, 1983).

In mammals, few studies have addressed the demographic consequences of changing age at first reproduction, and most of these have focused on large iteroparous mammals (see for examples Reiter & Le Boeuf, 1991 on elephant seal; Saether & Heim, 1993 on moose; Festa-

Bianchet *et al.*, 1995 on bighorn sheep; but see Neuhaus *et al.*, 2004 on Columbian ground squirrels). In natural populations of small mammals (<5kg, sensu Bourlière, 1975), the breeding status of females is difficult to assess and nests are hard to find (Slade, 1995). However, the population growth rate of small mammal populations is highly sensitive to changes in age at primiparity (Dobson *et al.*, 2001; Oli *et al.*, 2001).

Physiological and environmental conditions determining survival and reproductive success of individuals may vary a lot within a population (McNamara *et al.*, 1996). Such heterogeneity among phenotypic quality can mask the costs of early breeding when the probability to breed early is skewed toward high quality individuals (van Noordwijk *et al.*, 1986). The idea that individual heterogeneity plays a crucial role in the detection of some trade-offs has recently gained importance (e.g. Forslund & Pärt, 1995; Pärt, 1995; Dobson *et al.*, 1999; Cam & Monnat, 2000a; Cam *et al.*, 2002; 2004; Golet *et al.*, 2004). It is now becoming clear that controlling for potential phenotypic differences between early and late breeders is required to interpret reliably the fitness consequences of age at primiparity.

We used long-term data (16 years) collected on a North American red squirrel population to study the fitness consequences of delaying the first reproduction. Red squirrels are physiologically capable of giving birth at one year old (Rusch & Reeder, 1978; Becker *et al.*, 1998) but less than 50% of females do so at Kluane, Yukon (this study). Such variations of the age at primiparity and the detailed knowledge of individual life histories of squirrels in this population gave us a unique opportunity to study the consequences of early reproduction on fitness in a small mammal population.

5.3 Materials and methods

Study area

We conducted the study in the South of the Yukon territory, Canada (61°N, 138°W) from 1987 to 2003 (for a detailed description of the study, see Berteaux *et al.*, 2000). All squirrels on two contiguous control grids (~40 ha each) separated by a major road were marked with numbered ear tags and a unique color combination for identification at a distance. We trapped female squirrels weekly (Tomahawk traps) from April to August every year to determine their fate and reproductive status, through changes in mass, palpation, and nipples condition. Most of the births occur from March to May, and as soon as we trapped lactating females, we found their nest by monitoring them through visual observations or telemetry. We counted and sexed pups soon after birth, tagged and weighed them at about 20-25 days of age and trapped them around weaning (70 days of age). The average dispersal distance of North American red squirrels is very low (<100 m, Larsen *et al.*, 1994; Berteaux *et al.*, 2000), and we followed most individuals from birth to death.

Study design and statistical analyses

We considered only individuals surviving to one year of age. We called "early breeders" the females who bred (i.e. gave birth to at least one juvenile) for the first time at one year of age (early primiparity), and "late breeders" the females who postponed their first reproduction (delayed primiparity). Age at primiparity was known for 313 females (143 females bred at 1 year of age, 170 did not). Sixty-seven percent of late breeders bred for the first time at two years of age, 28% at three years of age, and 5% at four years of age. The LRS was measured on 279 females (134 early breeders and 145 late breeders). Analyses were carried out with SAS version 8.0 (SAS Institute, 1999).

Individuals born in a year of high food availability may experience fitness benefits throughout their lives (Lindström, 1999). Such cohort variation may also influence the reproductive decisions of individuals, with high food availability or favourable weather conditions promoting early reproduction (Boutin, 1990; Becker *et al.*, 1998). Thus, to account for such cohort effects that may confound the interpretation of results, we included in all analyses the year of birth as a categorical variable.

In a first step, we studied the apparent short-term effects of age at primiparity on survival between one and two years of age, and on the reproductive success at two years of age. We thus performed logistic regressions with age at primiparity and year of birth as independent variables, and survival or breeding probability at two years of age as dependent variables.

In a second step, we analysed the fitness consequences of variation in age at primiparity. Based on recent work (Brommer *et al.*, 2004), we used the lifetime reproductive success (LRS) as a reliable proxy for individual fitness. We defined LRS as the total number of juveniles successfully weaned during the entire life of the individual. A female can reach a higher than average LRS either by having more breeding attempts (i.e. early primiparity and/or long lifespan) and/or by being more successful at each breeding attempt (i.e. more offspring weaned per breeding attempt). We therefore looked for differences in LRS according to age at primiparity both in absolute terms (ANOVAs with age at primiparity and year of birth as independent variables) and relative to longevity and average number of juveniles weaned per breeding attempt (ANCOVAs with age at primiparity, year of birth, and longevity or average number of juveniles weaned per breeding attempt as independent variables).

In a third step, to investigate the differences in phenotypic quality between early and late breeders, we compared their date of birth, their mass around 25 days of age (i.e. mass when tagged) and the number of hoarding sites (hereafter called "middens") they owned at one year old at the onset of the breeding season. We thus performed ANOVAs with age at primiparity and year of birth as independent variables, and date of birth, mass or number of middens as dependent variables. For date of birth, we considered the difference (in days) between the date of birth of each female and the average date of birth for all females of the same cohort. As early born squirrels have access to more vacant territories than their later-born counterparts (Price *et al.*, 1990), date of birth is likely to influence the quality of the territory obtained by weaned juveniles, and thereby their survival and reproductive success. Mass at weaning has been reported as a critical factor for juvenile survival in a European red squirrel population (Wauters *et al.*, 1993). In our North American red squirrel population, mass at weaning (i.e. mass around 70 days of age) was available for relatively few squirrels. We thus used the mass when tagged (i.e. mass around 25 days of age), which was available for 302 out of our 312 females, and was correlated to the mass at weaning (Stan Boutin, unpubl. data). As females were not tagged exactly at the same age, we considered in our analyses the residuals of the linear regression of mass when tagged on age ($n=302$, $R^2=0.70$, $t=26.4$, $p<0.0001$). As mass and phenotypic quality of squirrels were likely to be linked to territory characteristics, we also analysed the number of middens owned by squirrels at one year of age at the beginning of the breeding season, with the assumption that it measures the quantity of cones produced per territory. Finally, to confirm the relevance of these variables (date of birth, mass and number of middens) as proxies of quality for squirrels (sensu McNamara *et al.*, 1996), we tested their effect on the lifetime reproductive success of females using ANCOVAs (with age at primiparity and year of birth included in the model as categorical variables).

All the results are reported as means±SE and correspond to predicted values from models.

5.4 Results

Year of birth was included in all our analyses, and was significant in most of them.

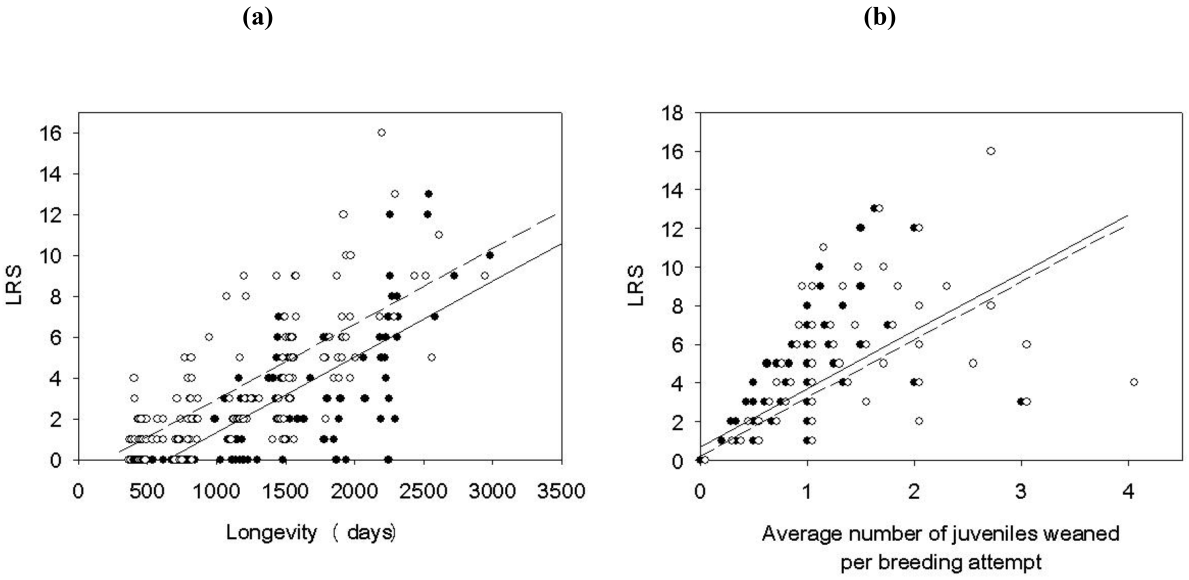

Figure 5.1 Lifetime reproductive success (number of weaned juveniles during the entire life) for females of a North American red squirrel population, Kluane, Yukon, Canada according to age at first reproduction and (a) longevity or (b) average number of juveniles weaned per breeding attempt (white circles and dashed lines: early breeders ; black circles and solid lines: late breeders).

Short term effects of early primiparity on individual performance

Early breeders had a lower probability to survive until two years of age than late breeders (77.6% ± 5.2 versus 83.5% ± 4.2, p=0.0056). Early breeders who survived to two years of age had a higher probability to breed the next season than late breeders (71.6% ± 6.3 versus 65.1% ± 7.3, p=0.029). When we restricted the analysis to individuals that survived to and bred at two years old, we did not find any effect of age at primiparity on the probability to breed successfully (i.e. to wean at least one juvenile) at two years of age (77.8% ± 7.9 versus 81.1% ± 7.6, p=0.12).

Fitness consequences of delaying the first reproduction

Early breeders had a shorter longevity than late breeders (1035 days ± 89 versus 1245 days ± 89; $F_{1, 263}=6.35$, $p=0.012$). The average number of juveniles weaned per breeding attempt was higher for early breeders (0.97 ± 0.059 versus 0.50 ± 0.059; $F_{1, 263}=24.33$, $p<0.0001$). If we considered only females who bred at least once (*i.e.* who gave birth to at least one juvenile), the average number of juveniles weaned per breeding attempt was still higher for early than for late breeders (1.00 ± 0.058 versus 0.76 ± 0.058; $F_{1, 218}=4.95$, $p=0.027$). This difference can be partly accounted for by the larger proportion of late breeders that did not succeed in weaning one offspring compared to early breeders (19% vs. 15%, respectively).

Early breeders tended to have a higher LRS than late breeders (3.0 ± 0.4 versus 2.3 ± 0.4; $F_{1, 263}=3.05$, $p=0.082$), but when we considered only females who survived until two years of age, LRS of early breeders was much higher than that of late breeders (4.6 ± 0.3 versus 2.9 ± 0.3; $F_{1, 187}=7.14$, $p=0.0082$). When we controlled for the positive effect of longevity ($F_{1, 262}=341.70$, $p<0.0001$) on LRS, the difference between early and late breeders ($F_{1, 262}=29.71$, $p<0.0001$) increased to 1.5 ± 0.3 (Fig. 5.1a). On the other hand, when we controlled for the positive effect on LRS of the mean number of juveniles weaned per breeding attempt ($F_{1, 262}=211.32$, $p<0.0001$), late breeders had higher LRS than early breeders (difference of 0.6 ± 0.3, $F_{1, 262}=3.96$, $p=0.048$; Fig. 5.1b). Thus, the higher LRS of early breeders resulted from a much higher yearly weaning success (in terms of number of weaned juveniles) than late breeders, and this overcompensated for their shorter longevity.

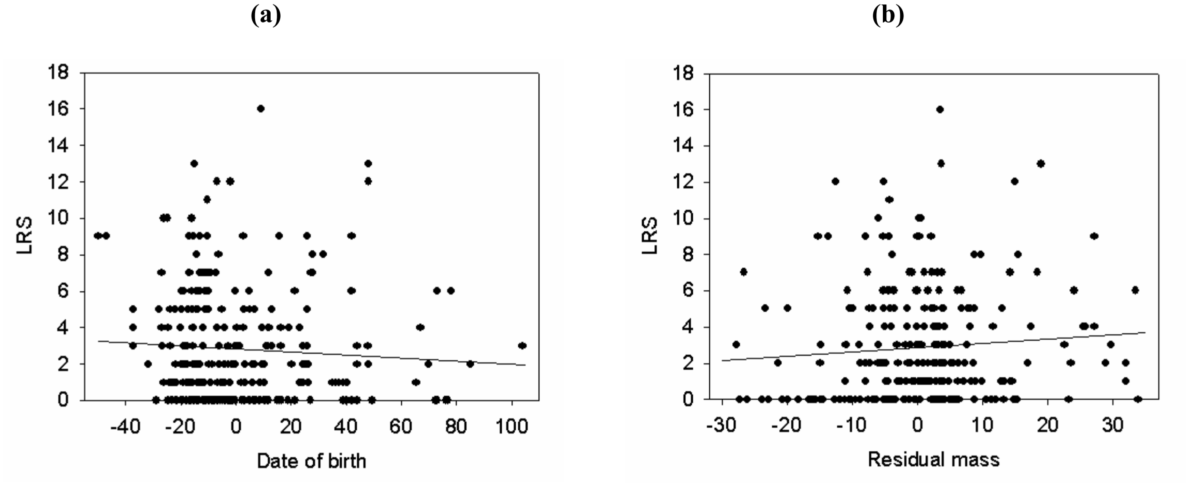

Figure 5.2 Lifetime reproductive success (number of weaned juveniles during the entire life) for females of a North American red squirrel population, Kluane, Yukon, Canada according to (a) their date of birth (i.e. difference in days with the average date of birth of their cohort) and (b) their mass when juvenile (i.e. residuals of the linear regression of mass when tagged on age).

Tracking the confounding influence of individual heterogeneity

Early breeders were born 12.7 ± 2.9 days earlier than late breeders ($F_{1,\,296}$=19.29, p<0.0001). We found no difference in the mass when tagged (at about 25 days of age) between early and late breeders (residual values: 0.1 ± 2.1 versus –1.2 ± 2.1; $F_{1,\,286}$=1.72, p=0.19). The number of middens on females' territory at one year old was not different between early and late breeders (1.4 ± 0.1 versus 1.3 ± 0.1; $F_{1,\,205}$=0.51, p=0.48).

After controlling for the effects of age at primiparity ($F_{1,\,262}$=1.53, p=0.22), females born late tended to have a lower LRS than females born early (Fig. 5.2a; $F_{1,\,262}$=3.77, p=0.053). Similarly, mass around 25 days of age tended to have a positive effect on LRS (Fig. 5.2b; $F_{1,\,253}$=3.09, p=0.080) after controlling for the effects of age at primiparity ($F_{1,\,253}$=2.16, p=0.14). We found no effect of number of middens ($F_{1,\,181}$=0.65, p=0.42) on LRS.

5.5 Discussion

Costs of early primiparity and individual heterogeneity

Measuring the cost of early reproduction by comparing early and late breeders is based on a comparison between two groups in which individuals have been allocated based on unknown factors. This could potentially confound the interpretation of our results (van Noordwijk *et al.*, 1986), and the most likely confounding factor is individual heterogeneity (McNamara *et al.*, 1996). Heterogeneity among individuals may be a consequence of cohort variation. Early primiparity is influenced significantly by year of birth, and year of birth may have long term effects on individual life history (Lindström, 1999; Beckerman *et al.*, 2002). Consequently, apparent differences between early and late breeders could be a consequence of long-term or delayed cohort effects and not of costs of early primiparity. Early breeders could have a lower longevity or survival than late breeders because they were born during unfavourable years and not because of reproductive costs. In this study, all analyses included year of birth of individuals to take into account the confounding effects of cohort variation, and the differences we observed between early and late breeders were thus unlikely to represent consequences of cohort variation.

Moreover, breeding early may be a reproductive tactic used by low quality individuals with low survival probability. Such a tactic would ascertain at least some reproductive success for these low quality squirrels. The observed difference between early and late breeders would then be a consequence of the lower quality of early breeders, and not of the costs of early reproduction. In this population of North American red squirrels, our results suggest a higher quality of early breeders (see discussion below), and consequently, the difference we report on longevity between early and late breeders is likely to represent actual costs of early primiparity.

Age at primiparity and individual quality

Early breeders were born earlier than late breeders (after correcting for cohort variation) and those who survived until two years of age achieved a higher LRS. Similar results have been found in microtines, where early born females are early breeders (Prevot-Julliard *et al.*, 1999; Lambin & Yoccoz, 2001) and early breeders achieve higher LRS (Ribble, 1992). However, such results contrast with those found on Eurasian red squirrels for which early and late females achieved similar LRS (Wauters *et al.*, 1995a). North American and Eurasian red squirrels could thus have different reproductive tactics. In Eurasian red squirrel, females rarely defend a territory at one year of age, and often behave like floaters for one or two years (Wauters & Dhondt, 1989, 1992). Consequently, the proportion of one year old breeding females is very low. This difference in the spacing behaviour between Eurasian and North American red squirrels may explain the difference we report in reproductive tactics.

In our red squirrel population, in addition to an earlier date of birth, early breeders who survived until two years of age had a higher probability to breed when two years old. They also had a higher LRS and better breeding success than late breeders. These results support the idea of heterogeneity between early and late breeders, and of a higher quality of early breeders. As females born earlier in the season may have a higher probability to access a good vacant territory (Price *et al.*, 1990), their higher quality was likely to be the consequence of higher territory quality. It has been observed in North American red squirrels that a low territory quality may prevent females to reach the physiological condition required to start follicular development, and thus to breed (Becker, 1993). This supports the idea that early breeders benefited from a high quality territory, thanks to an early date of birth. Similar results have been found in a Eurasian red squirrel population (Wauters *et al.*, 2001), where females who bred as yearlings had higher territory quality than females who delayed their first reproduction. Such benefits early in life (i.e. a good first territory) may also have long-term effects and give fitness advantages throughout the life (i.e., "silver spoon" effect, Grafen, 1988; Wauters *et al.*, 1995a).

In our study, mass when juvenile tended to affect positively fitness of females, as observed in Eurasian red squirrels (Wauters *et al.*, 1989), but we found no difference between mass of early and late breeders. This may appear surprising since body mass is an important determinant of oestrus in Eurasian and North American red squirrels (Wauters *et al.*, 1989; Becker *et al.*, 1998). However, these studies considered mass of squirrels when territorial and before the onset of reproduction, which is dependent on the quality of the territory owned by females. Such data were not available in our study and we thus used mass during the juvenile stage (around 25 days of age). Juvenile mass does not reflect the quality of the territory that females got at one year of age, which may account for the absence of difference between early and late breeders that we report. If early and late primiparous females differ essentially in the quality of the territory they got after weaning (which is itself dependent of their date of birth), it is not surprising that juvenile mass was similar for early and late breeders.

As in previous studies on North American red squirrels (e.g. Berteaux & Boutin 2000), we used the number of middens per territory as a surrogate of territory quality regarding resource availability. The number of middens per territory at one year of age was similar for early and late breeders. As this measure does not take into account the quantity of cones stored per midden, the number of middens may be a poor measure of territory quality. Moreover, even if the number of middens was correlated to the quantity of cones produced per territory, the quality of a territory is likely to be a function of other factors. Quality of the food produced (e.g. McAdam & Millar, 1999) or distribution of trees (e.g. Becker *et al.*, 1998) within the territory may also be important determinants of territory quality and age at primiparity. We can conclude from our results that early breeders were not inferior individuals to late breeders, but detailed field measures (such as the quantity and quality of cones produced per territory) would be needed to conclude more confidently that territories of early breeders were of higher quality than territories of late ones.

Variation in age at primiparity: life history tactic or constraint?

Early breeders had a shorter lifespan than late breeders. Such survival costs of early primiparity have been observed in other mammals (e.g. Reiter *et al.*, 1991; Lambin *et al.*, 2001). In our North American red squirrel population, this shorter lifespan was overcompensated by a higher reproductive activity in terms of a higher number of weaned juveniles, and early breeders who survived after their first reproduction enjoyed higher fitness than late breeders. In our squirrel population, it thus pays to breed as one year-olds.

The coexistence of early and late breeders can be interpreted as the occurrence of two reproductive tactics in our population. Individuals born early in the season have the possibility to reproduce early and exhibit a high risk-high benefit tactic based on intense breeding at the costs of a shorter lifespan. On the other hand, individuals born late in the season cannot reproduce as one year-olds and show a low risk-low benefit tactic based on a lower breeding intensity over a long lifespan. An alternative hypothesis explaining the existence of a delayed first reproduction despite the advantage of breeding early could be that late breeders experience a lower variability of their reproductive success or survival as observed in deer mice (Fairbairn, 1977). Late breeding would thus be an alternative tactic based on a lower risk of producing no offspring at the cost of a lower average fitness. However, the variability of LRS was lower for early breeders than for late breeders (coefficients of variation: 0.9 vs. 1.3), which does not support this alternative hypothesis.

Differences in quality between early and late breeders indicate that passive constraints rather than active tactics drive the decision to delay primiparity (constraint hypothesis, Curio, 1983), as suggested for bank voles (Prevot-Julliard *et al.*, 1999). To the question "is a particular life-history as expressed by a given individual the optimal fitness solution for that individual or evidence of an individual doing the best it can" (Cooch, Cam & Link, 2002), our study showed that both answers may hold depending on the birth date. Early born squirrels express the most profitable tactic by breeding early, whereas late born squirrels do the best of a bad job by delaying their first reproduction.

Chapitre 6 Non-breeding in a North American red squirrel population: restraint or constraint?

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(à soumettre, *Journal of Animal Ecology*)

Le chapitre précédant se concentrait sur les coûts liés à la reproduction à 1 an. Le présent chapitre concerne les coûts de la reproduction pour les femelles de plus de 1 an, et compare les probabilités de survivre et se reproduire dans le futur en fonction du statut reproducteur actuel. Deux statuts reproducteurs ont été considérés : femelles reproductrices (i.e. femelles qui ont donné naissance à au moins un jeune) et femelles non-reproductrices. Ne pas se reproduire une année donnée peut être une stratégie adaptative permettant d'augmenter ses chances de survivre ou de se reproduire dans le futur, mais peut aussi être du à des contraintes phénotypiques. Dans ce cas ci, les individus non-reproducteurs seraient des individus de moindre qualité. Nos résultats montrent qu'une femelle non-reproductrice une année donnée a une plus grande probabilité d'être encore non-reproductrice l'année suivante. De plus, la masse des femelles non-reproductrices est inférieure à celle des femelles reproductrices. Ces résultats suggèrent fortement que les femelles non-reproductrices sont des individus de faible qualité, et que ne pas se reproduire est la conséquence de contraintes phénotypiques, quelle que soit la classe d'âge considérée.

6.1 Abstract

According to life history theory, breeding induces fitness costs, and non-breeding should be an adaptive strategy allowing individuals to increase their residual reproductive value. However, in populations where individuals differ in quality, non-breeders may be low quality individuals, and non-breeding would be the result of phenotypic constraints. Whether non-breeding is an adaptive strategy or the result of constraints leads to opposite predictions, that we examined in female North American red squirrels in northern Canada using multi-state modelling. We found that non-breeding females had a lower probability to breed in the future than breeding ones, and equivalent survival rates. The difference in future breeding probability between breeders and non-breeders was a function of food availability, and our results suggest a higher susceptibility of non-breeders to environmental conditions. In addition, non-breeding females had a lower mass than breeding ones, and mass was repeatable over time. Our study clearly supports the hypothesis that non-breeders were low quality individuals and that non-breeding was driven by phenotypic constraints in this North American red squirrel population.

Key-words: intermittent breeding; adaptive strategy; phenotypic constraints; restraint; cone production; survival; breeding probability; *Tamiasciurus hudsonicus*

6.2 Introduction

According to life history theory, reproduction induces fitness costs and trade-offs exist between survival and reproduction, or between current and future reproduction (Williams, 1966b; Stearns, 1992; Roff, 2002). To understand these trade-offs, and consequently costs of reproduction, is one of the main goal of evolutionary ecology.

With the assumption that breeding is costly for individuals, non breeders are expected to avoid a subsequent decrease in their survival or reproductive success. Non-breeding would thus be a tactic allowing individuals to increase their residual reproductive value (i.e. the number of offspring that individuals can expect to have after the current breeding season) and consequently their fitness (Cam *et al.*, 1998). For example, reproduction can be more costly at high population density (Festa-Bianchet *et al.*, 1998) and non-breeding during periods of high density could thereby enhance individuals' chance to survive and breed in the future. In such circumstances, non-breeders would be "prudent parents" (Drent & Daan, 1980; Cam *et al.*, 1998), that restraint their reproduction (the restraint hypothesis, Curio, 1983).

However, in populations where individuals differ in quality, the measurement of trade-offs, and thus costs of reproduction may be confounded by such individual heterogeneity (van Noordwijk *et al.*, 1986; McNamara *et al.*, 1996), so that fitness components are positively correlated (Reznick, 1992). Low quality individuals exhibit low survival and breeding probability, whereas high quality individuals exhibit high survival and breeding probability (e.g. Harris & Wanless, 1995; Cam *et al.*, 1998; Beauplet *et al.*, 2006). In such a situation, non-breeding would be related to individual quality, and be the consequence of phenotypic constraints (the constraint hypothesis, Curio, 1983).

In a population of North American red squirrels monitored since 1987 in Northern Canada (see Berteaux *et al.*, 2000; and Humphries *et al.*, 2000 for details), it has been suggested that early reproduction by yearlings (i.e. at one year of age) is constrained by individual quality (Descamps *et al.*, 2006, chapter 5). However, whether non-breeding is also the consequence of constraint among all age-classes remains unknown. To explain non breeding in natural populations as a result of a reproductive tactic (i.e. restraint) or of phenotypic constraints leads to different predictions. If non-breeding decision is the consequence of reproductive restraint, non-breeders should be of similar phenotypic quality, and exhibit higher survival and/or future breeding probability the next season than breeders as they avoid some reproductive costs. If non-breeding decision is the consequence of constraints, non-breeders should be of lower phenotypic quality, and exhibit lower survival and/or future breeding probability the subsequent season than breeders. The purpose of this paper was to determine which of this prediction is the most suitable for adult females in this North American red squirrel population, using long-term data (16 years) on mass (used as a proxy of condition), reproduction and survival.

6.3 Materials and methods

Red squirrel population

The study was conducted on a 80-ha site of white spruce forest in southern Yukon, Canada (61º N, 138º W), near Kluane lake. All squirrels were permanently marked with metal ear tags and an individual colour combination of wires for identification at a distance. Fates of squirrels were determined through visual observations, live-trapping and/or radio-telemetry from early spring to late summer every year since 1987 (see Price *et al.*, 1986; Boutin *et al.*, 1993; Berteaux *et al.*, 2000 for detailed descriptions of the study). Breeding status of females and parturition dates were determined through nipple condition, mass changes and/or lactation. For each breeding female, nest was visited soon after birth to count and sex the young, and juveniles were tagged at about 20-25 days old. Offspring are weaned around 70 days of age and dispersal distance after weaning is less than 100 meters (Berteaux *et al.*, 2000). Spruce cone seeds represent the main food resource to red squirrels in this population (McAdam *et al.*, 2003) and red squirrels store unopened cones on hoarding sites that they defend year round. We estimated spruce cone production every year (usually end of July) when cones were fully formed but harvesting by squirrels had not yet begun. We counted the number of new cones in the top three meters of 170 trees randomly distributed on the study area. Food available for reproduction year t is determined by the cone production year t-1 (what we called previous cone production) and food available between reproductive seasons year t and t+1 is determined by the cone production year t, or “current cone production” (McAdam et al., 2003).

Study design

In North American red squirrels, oestrus of females lasts for only one or two days (Gurnell, 1987; Becker, 1993), and occurs in late winter (February-April) at Kluane (Réale *et al.*, 2003a), when monitoring of females is difficult because of weather conditions. Consequently, to assess whether a female attempts to breed or not is extremely difficult. We thereby considered non-breeding females as females that did not give birth. Consequently, our sample of non-breeders may have included some individuals who attempted to breed but failed before giving birth. In mammals, the highest costs of reproduction generally occur during lactation (Gittleman & Thompson, 1988), so that females that attempted to breed but failed before giving birth probably suffered negligible costs of reproduction. In that sense, such females may be considered as non breeders and their inclusion in the “non-breeder” group does not change our predictions.

As consequences of non-breeding at one year of age (age at maturity) have already been studied (Descamps *et al*, 2006, chapter 5), we only considered in this study adult females ≥2 years old. Yearly proportion of non-breeding females (≥2 years old) varied from 9 to 54% (calculated from 1993 to 2003, where all age classes were present) and averaged 19%±4 SE.

In a first step, we compared the subsequent survival and breeding probabilities of breeding and non breeding females. In a second step, we compared the mass (average mass between

August 15th-30th) of breeding and non-breeding females to test for a difference in their phenotypic quality. The relevance of this measure of mass to describe females' condition will be discussed. We also calculated the repeatability of females' mass over time to determine if phenotypic quality of females (relatively to other females) varied over their life. If low quality females one particular year were likely to be of low quality the following season, this would give support to the constraint hypothesis.

Survival and breeding probabilities analyses

Analyses were carried out using multistate capture-recapture models (Lebreton & Pradel, 2002) to test for an effect of breeding status on future survival and breeding probabilities (Nichols *et al.*, 1994; Viallefont, Cooch & Cooke, 1995). In such models, individuals can move within a set of states between occasions of capture. Three kinds of parameters are estimated: the recapture probabilities p^{i}_{t} defined as the probability of resight of an individual in state *i* at time *t*; the survival probabilities ϕ^{i}_{t} defined as the probability for an individual in state *i* at time *t* to survive until time *t+1*; and the transition probabilities ψ^{ij}_{t} defined as the probability that an individual in state *i* at time *t* is in state *j* at time *t+1* given that it survived from *t* to *t+1*. Such methodology is relevant to develop tests of hypotheses about reproductive costs (Nichols *et al.*, 1994; Tavecchia *et al.*, 2005) where transition probabilities correspond to breeding probabilities. In our study, states were defined as breeder (i.e. females that gave birth to ≥1 juvenile) and non breeder.

We started our model selection with the Arnason-Schwarz model (Lebreton et al., 2002; Choquet et al., 2004) where recapture was function of time and arrival state (i.e. state at time t+1), survival was function of time and departure state (i.e. state at time t) and transition was function of time, departure and arrival states. Ideally, the most general model we should start with should be an age-dependent version of the Arnason-Schwarz model. However, no goodness-of-fit (GOF) test exists for such a model. Thus, following recommendation of Lebreton et al. (2002), we started from a simple model for which the GOF can be assessed (that is the Arnason-Schwarz model) and then moved to more complex models (including age effects). The GOF of the Arnason-Schwarz model was assessed using a procedure recently developed for multi-state capture-mark-recapture models (Pradel, Wintrebert & Gimenez, 2003) implemented in the software U-CARE (Choquet *et al.*, 2003). After assessing the GOF of the Arnason- Schwarz model, we modelled recapture rates first, then transition probabilities and finally survival rates.

Age influences survival rates in our red squirrel population (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3), and was thus included in our analyses. Based on previous results (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3), we considered age as a quadratic function for survival modelling.

As food availability is likely to affect survival and breeding probabilities, we tested for cone productions effect. We considered the food available for reproduction at time t (i.e. previous cone production), and the food available for survival between t and t+1 and for reproduction at time t+1 (i.e. current cone production).

We used software M-SURGE 1.4 (Choquet *et al.*, 2004) for model selection and parameter estimation, with a *logit* link function (Choquet *et al.*, 2004). Our model selection was based on AICc (Burnham *et al.*, 2002), a variant of AIC (Akaike's Information Criterion) which accounts for the bias introduced when sample size is small relative to the number of parameters in models. A difference of less than two units of AICc between two models means that they are competitive to explain the data (Burnham *et al.*, 2002).

Mass analyses

Our data corresponded to repeated measurements of mass made on the same females at different ages (n=375 measures of mass made on 222 females). To account for pseudoreplication problems (sensu Hurlbert, 1984), we fitted linear mixed models with the MIXED procedure of SAS version 8.0 using the repeated statement, the maximum likelihood method and the compound symmetric matrix structure (Littell *et al.*, 1996; SAS Institute, 1999). Age and age^2 were included in our model as mass varies as a quadratic function of age (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3). Year was also included in our model as a categorical variable to take into account yearly environmental fluctuations.

We calculated the repeatability (or intra-class correlation coefficient) of females' mass following Lessells and Boag (1987). Repeatability was calculated using variance components (between-individual variation versus within-individual variation) obtained from the mean-squares of one-way ANOVAs and corresponds to the proportion of variance that is due to permanent differences between individuals.

6.4 Results

Survival and breeding probability of breeders and non-breeders

The Arnason-Schwarz model provided a good fit to our data (χ^2_{31}=31.845, p=0.424) and was used as a starting point for our model selection. The best selected model was a model with constant recapture rates, breeding probabilities function of current breeding status and previous cone production, and survival function of age and current cone production (Table 6.1).

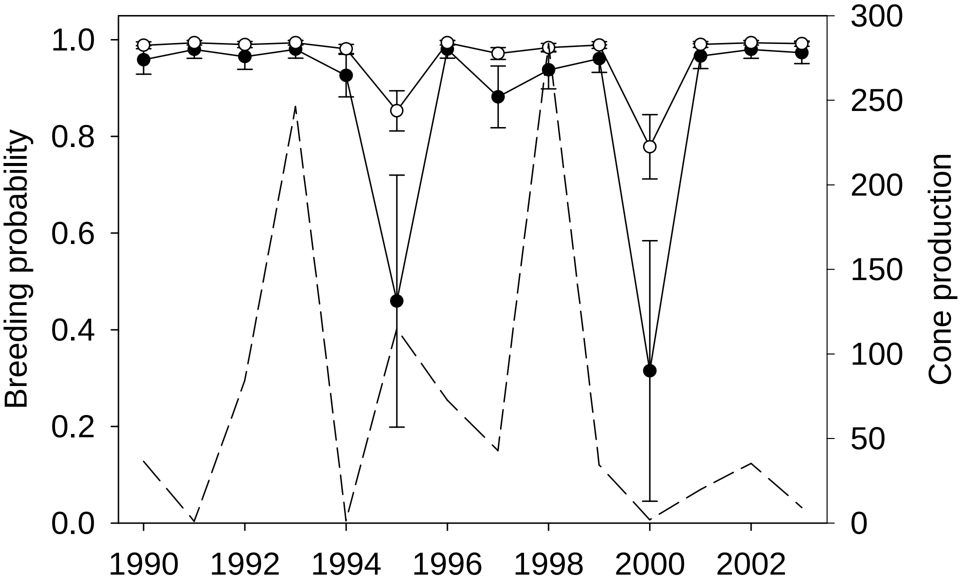

Figure 6.1 Probability to breed year *t+1* for breeding (white symbols) and non-breeding (black symbols) females at year *t* according to year in a North American red squirrel population, Kluane, Yukon, Canada. Results correspond to estimated values (means ± SE) from model selected in table 6.1. Dashed line corresponds to cone production of the current year.

This model showed that breeders had a higher probability to breed the following year (year t+1) than non breeders (Fig. 6.1) This difference in breeding probability varied according to food abundance (interaction between breeding status and previous cone production, Table 6.1), and is more pronounced following a year of high food abundance (that is two years after a mast years, Table 6.1; Fig. 6.1). There was thus a time lag of two years between cone production and its effect on breeding probability (or more precisely a time lag of one year and a half, as cone production occurs at the end of summer and breeding at the end of winter). This model also indicates that survival of females were equivalent for breeders and non-breeders, decreased with age and increased with current cone production (Table 6.1; Fig. 6.2).

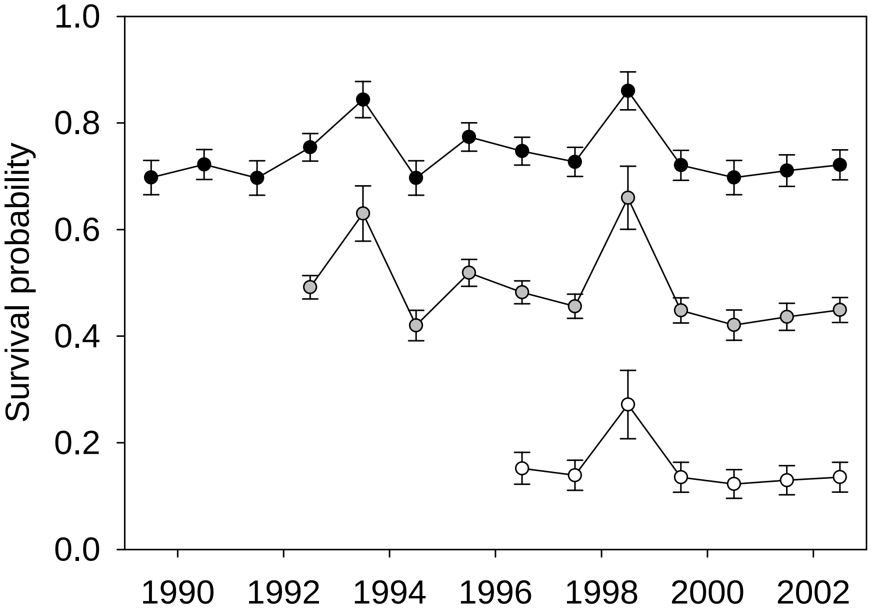

Figure 6.2 Probability to survive between year *t* and *t+1* according to age (black symbols: 2 years old females; grey symbols: 5 years old females; white symbols: 8 years old females) and year in a North American red squirrel population, Kluane, Yukon, Canada. Results correspond to estimated values from model selected in table 6.1. Survival of females decreased with age from 2 to 8 years old and survival curves for each age class are parallel.

Mass of breeders and non-breeders

Mass of breeders at the end of August was significantly higher than mass of non-breeders (observed masses for breeders and non-breeders, respectively: 254.0 g ± 1.3 SE and 240.5 g ± 1.4 SE; $F_{1,53}$=4.73; p=0.034), after accounting for age (age: $F_{1,137}$=24.81; p<0.0001, age^2: $F_{1,137}$=8.32; p=0.0046) and year ($F_{1,137}$=5.88; p<0.0001) effects. We found significant repeatability for the mass of females at the end of August (n=100 females with at least 2 measures of mass, n=253 measures of mass; $F_{99,153}$=3.21, p<0.001; repeatability: r=0.45).

Table 6.1 Modelling of recapture rates (p), breeding probabilities (ψ) and survival (ϕ) of female North American red squirrels, Kluane, Yukon, Canada (n=204). *t* refers to year effect (14 modalities), *i* to breeding status (non breeder and breeder), *a* to age (quadratic function), *CCP* to food available for survival between t and t+1 and for reproduction at time t+1 (current cone production), and *PCP* to food available for reproduction at time t (previous cone production).

Recapture	**Transition**	**Survival**	**np**[1]	**Deviance**	**AICc**	**ΔAICc**
p	$\boldsymbol{\psi^{i}_{PCP}}$	$\boldsymbol{\phi_{CCP+a}}$	**8**	**770.102**	**786.840**	**0.000**
p	ψ^{i}_{PCP}	ϕ_{t+a}	21	743.960	791.037	4.197
p	ψ^{i}_{PCP}	ϕ_{PCP+a}	8	777.484	794.222	7.382
p	ψ^{i}_{PCP}	ϕ_{a}	7	779.969	794.540	7.700
p	ψ^{i}_{PCP}	ϕ^{i}_{t+a}	37	723.870	814.810	27.970
p	ψ^{i}_{PCP}	ϕ_{t}	19	772.719	814.849	28.009
p	ψ^{i}_{PCP}	ϕ^{i}	7	810.964	825.535	38.695
p	ψ^{i}_{PCP}	ϕ^{i}_{t}	33	750.741	829.941	43.101
p	ψ^{i}	ϕ^{i}_{t}	31	781.090	854.625	67.785
p	ψ^{i}_{t}	ϕ^{i}_{t}	47	733.926	856.849	70.009
p^{i}	ψ^{i}_{t}	ϕ^{i}_{t}	47	733.926	856.849	70.009
p	ψ^{i}_{CCP}	ϕ^{i}_{t}	33	779.208	858.408	71.568
p_{t}	ψ^{i}_{t}	ϕ^{i}_{t}	52	726.819	867.322	80.482
p^{i}_{t}	ψ^{i}_{t}	ϕ^{i}_{t}	54	725.622	873.488	86.648
p	ψ^{i}_{PCP}	ϕ^{i}_{t*a}	77	689.297	938.630	151.790
p	ψ_{t}	ϕ^{i}_{t}	42	873.131	979.566	192.726

[1]: number of parameters

6.5 Discussion

Non-breeding by female red squirrels : restraint or constraint?

The constraint hypothesis requires "the demonstration of a lack of some skill instrumental for successful breeding" (Curio, 1983). A causal relationship has been shown between body fat and reproduction in human (Frisch & McArthur, 1974) and rat (Frisch, Hegsted & Yoshinaga, 1977) for examples. Correlations have also been found between body mass and breeding probability in numerous mammalian species, such as North American (Becker *et al.*, 1998) and European red squirrel (Wauters *et al.*, 1989), roe deer (Gaillard *et al.*, 1992; Hewison, 1996), red deer (Albon, Mitchell & Staines, 1983), caribou (Gerhart *et al.*, 1997) and black bear (Elowe & Dodge, 1989). More generally, there seems to be no doubt that the whole-body energy balance regulates ovulation (Bronson & Manning, 1991).

In our red squirrel population, non-breeding females had a lower mass at the end of August than breeding females. Weaning generally occurs in July in this population, so one month before our mass measurements. Furthermore, during the last part of the lactation period (from emergence of juveniles to their weaning), mass of mothers is expected to decrease (Humphries *et al.*, 1996). It thus seems very unlikely that the higher mass of breeding females at the end of the summer compared to non-breeding ones was the consequence of their breeding status, and the most relevant explanation is that breeding females were larger females or females in better condition than non breeding ones. In addition, mass of females was repeatable over time, which suggests consistency in body condition (relatively to other females), and thus in phenotypic quality.

Finally, non-breeding adult females had a lower probability to breed the following year than breeding females and the same probability to survive until the next breeding season. All these results strongly suggest that non breeding females were low quality individuals, that did not breed because they did not reach the condition required to enter into oestrus. It thus seems very likely that non-breeding was driven by phenotypic constraints in female North American red squirrels at Kluane.

Survival cost of reproduction and age

Similar conclusions have been drawn for yearlings in this red squirrel population, where females that bred at one year of age (i.e. early breeders) were of higher quality than females that delayed their first reproduction (Descamps *et al*, 2006, chapter 5). However, such early primiparity was associated to high survival costs, whereas reproduction in older females did not lead to any apparent cost. To detect cost of reproduction within a free-living population without any experiment is often difficult because individuals differ in quality and such heterogeneity may hide costs of reproduction (van Noordwijk *et al.*, 1986; Reznick, 1992; McNamara *et al.*, 1996).

Two non-exclusive explanations can explain the absence of apparent fitness cost of reproduction among females ≥2 years old whereas such costs were apparent among yearlings. First, the difference in quality between breeders and non-breeders may be higher for females ≥2 years old than for yearlings. In such a case, survival rates of breeders may be too high compared to those of non-breeders to detect any survival cost of reproduction. However, it seems unlikely that heterogeneity within the population increases with age. Indeed, the average quality of individuals should increase with age as low quality individuals die first (Service, 2000). In particular, first reproduction may act as a filter, selecting for individuals of high quality (Barbraud & Weimerskirch, 2005). Therefore, the hypothesis of increasing heterogeneity with increasing age does not seem relevant.

The second explanation is that survival costs of reproduction were higher for yearlings than for older females. As young individuals are still growing, it may be harder for them to deal with all the energetic costs of reproduction, which would lead to higher survival costs.

Non-breeding and environmental conditions

Food available during reproduction (that is previous cone production) influenced the probability to breed the subsequent year. In particular, breeding probability at year t+1 decreased when food available during reproduction at year t was extremely large (i.e. when year t-1 was a mast year). One mechanism explaining this time-lag between cone production and its effect on breeding probability could involve population density. In our red squirrel population, a very large number of juveniles were successfully weaned in years of large cone availability. As dispersal is very limited after weaning in our population (Berteaux *et al.*, 2000), this large number led to a high density the following season, which may have negative effects on breeding probabilities, as observed in Eurasian red squirrel (Wauters & Lens, 1995b). However, densities following years of high cone abundance were not the highest density recorded over the 15 years of monitoring. Density alone is unlikely to explain the lowest breeding probabilities we observed, and may have interacted with weather conditions and/or cone production of the next year.

Furthermore, the decline in breeding probability following years of high cone abundance was higher for non-breeders than for breeders. This indicates that non-breeders were more sensitive to environmental conditions than breeders, and supports the idea of non-breeders being low quality individuals. Territory quality, in terms of food availability, is very likely to play a role in determining individual quality and reproductive strategies (Southwood, 1977), through effects on energy acquisition (van Noordwijk *et al.*, 1986; Glazier, 2000). Therefore, breeders may have benefited from more resources, and thus from high quality territories and larger hoarding sites than non-breeders. However, to clearly determine how density and environmental conditions affect breeding probability in our North American red squirrel population in relation to individual quality, further investigations are needed.

Chapitre 7 Survival costs of reproduction in a North American red squirrel population: youngest and oldest females pay the bill

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(à soumettre, *The American Naturalist*)

L'étude des coûts de la reproduction à partir de corrélations phénotypiques peut-être problématique lorsque l'hétérogénéité de la qualité des individus est importante au sein de la population. Il a été proposé que de tels coûts soient plus facilement détectables lorsque les conditions sont stressantes pour les reproducteurs. Ces conditions stressantes peuvent correspondre à un environnement non favorable à la reproduction à une période donnée, mais également à un état physiologique non favorable. En particulier, on peut faire l'hypothèse que se reproduire est plus exigeant pour les individus qui n'ont pas fini leur croissance, et également pour les individus sénescents. Nous avons vérifié cette hypothèse dans la population d'écureuils roux de Kluane, où la masse des jeunes femelles augmente jusqu'à 3 ans, et où les vieilles femelles deviennent sénescentes après 4 ans. Nos résultats confirment notre hypothèse de départ, et montrent clairement des coûts de la reproduction plus importants pour les femelles <3 ans et ≥5 ans, malgré l'hétérogénéité individuelle au sein de notre population.

7.1 Abstract

Costs of reproduction are expected to be more pronounced under stressful conditions, so that reproduction for young growing and old senescent individuals should be more costly than for prime-age ones. We tested this prediction by investigating costs of reproduction as a function of age in female North American red squirrels in northern Canada (Yukon Territory) through the use of long-term data on survival and reproduction. We found that one and two year old females that bequeathed their territory at weaning to their offspring tended to have a lower survival than those who kept it, whereas no such cost was detected after two years old. In addition, survival of females>5 years of age decreased with increasing litter size at weaning, and this decline was more pronounced as females got older. Furthermore, this decrease in survival tended to be more pronounced for females that bequeathed their territory at weaning. No cost of reproduction was apparent for prime-age females. These results clearly support our prediction and costs of reproduction were more pronounced in young growing and old senescent females than in prime-age ones. The importance of age-specific variation in costs of reproduction in evolutionary ecology is discussed.

Key-words: survival; reproduction; trade-off; territory bequeathal; age-structured population; *Tamiasciurus hudsonicus*

7.2 Introduction

The assumption that trade-offs exist between demographic components is at the core of evolutionary ecology (Roff, 2002). Trade-offs are supposed to exist because reproduction is energetically costly and energy available to individuals is limited (Cody, 1966; Williams, 1966b). One of the main goals of evolutionary ecology is to study and understand these trade-offs, and thus the fitness costs of reproduction (Stearns, 1992). When studying costs of reproduction, two questions are of primary importance (Barbraud *et al.*, 2005). (1) Does current reproduction entail future survival and/or reproduction? (2) How do reproductive costs vary according to individual quality?

Trade-offs may be apparent only when the organism is subjected to particular conditions (Roff, 2002). As reproduction is an energetically expensive activity, it has been suggested that under conditions of stress, fitness costs of reproduction may be more pronounced (Reznick, 1985; Festa-Bianchet *et al.*, 1998). In age-structured populations, individual quality (i.e. the physiological and environmental conditions that determine its survival and reproduction, McNamara *et al.*, 1996) may be strongly related to individual's age. First, young individuals may still be growing and, consequently, to invest energy into reproduction can have greater consequences on future survival and/or reproduction for young than for adult individuals. Second, physiological condition decreases with age when senescence occurs (Rose, 1991) and it may be harder for senescent individuals to meet all the energetic demands of reproduction. Consequently, in age-structured populations where young breeders are still growing and senescence occurs, reproduction is expected to be more stressful for young and old individuals than for prime-age ones. In humans, for example, to breed as a teenager or an elder has important fitness costs for women (e.g. Newcomb, Rodriguez & Johnson, 1991; Mayor, 2004), whereas cost of reproduction in prime-age women are limited. In female ungulates, it has also been shown that reproduction had survival costs that were greatest at one year of age, and/or increased in old females (e.g. Clutton-Brock, Guinness & Albon, 1982 on red deer; Tavecchia *et al.*, 2005 on Soay sheep).

Variation in reproductive costs with age can have very important evolutionary consequences, but has received little attention. The study of reproductive investment into reproduction is central to the understanding of life history evolution (Schaffer, 1983; Stearns, 1992), and age-specific variation in costs of reproduction may strongly affect our understanding of variation in reproductive investment. Reproductive investment corresponds to investment made in offspring that increases offspring' fitness potential at the cost of the parent's ability to invest in future offspring (Trivers, 1972; Evans, 1990). In contrast, reproductive effort represents input provided to offspring irrespective of its costs to the parent (Evans, 1990). Thus, if costs of reproduction do increase with age for a given reproductive effort, a reproductive effort invariant with age would lead to an increase in reproductive investment with increasing age, and would thus support life history theory and the terminal investment hypothesis (Fisher, 1930; Williams, 1966b; Charlesworth *et al.*, 1976; Clutton-Brock, 1984). The study of age-specific variation in costs of reproduction is crucial to the understanding of relationship between reproductive effort and reproductive investment (sensu Evans, 1990), and thereby of life-history evolution.

The main purpose of this paper was to analyse how costs of reproduction vary with individuals' age in a free-living small mammal population. We used long-term data on female

North American red squirrels in northern Canada (Yukon Territory) whose reproduction and survival have been monitored since 1987. In this population, females are physiologically able to breed at one year old but are still growing at that age, and a clear senescence occurs after four years old for females (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3). Consequently, this age-structured North American red squirrel population gave us a unique opportunity to investigate costs of reproduction as a function of age, with the prediction that costs of reproduction should be higher for young growing and senescent females than for prime-age ones.

7.3 Materials and methods

Red squirrel population

The study was conducted in southern Yukon, Canada (61º N, 138º W) on two 40-ha grids of white spruce forest separated by the Alaska highway. All squirrels were marked with numbered ear tags and an individual colour combination of wires for identification at a distance. Fates of squirrels were determined through live-trapping (Tomahawk traps), visual observations and/or radio-telemetry from April to August every year since 1987 (see Price *et al.*, 1986; Boutin *et al.*, 1993; Berteaux *et al.*, 2000 for detailed descriptions of the study). Breeding status of females and parturition dates were determined through nipple condition, mass changes and/or lactation. For each breeding female, nest was visited soon after birth to count and sex the young, and juveniles were tagged at about 20-25 days old. Weaning occurs around 70 days of age and average dispersal distance of weaned juveniles is less than 100 meters (Berteaux *et al.*, 2000), so that most young are followed from birth to death. Spruce cone seeds represent the main food resource to red squirrels in this population (McAdam *et al.*, 2003). Red squirrels store unopened cones on hoarding sites that they defend year round. We estimated spruce cone production every year (usually end of July) when cones were fully formed but harvesting by squirrels had not yet begun. We counted the number of new cones in the top three meters of 170 trees randomly distributed on the study area. Food available for reproduction one year is determined by cone production of previous summer (McAdam *et al.*, 2003).

Study design

It has been shown that non-breeding females in this North American red squirrel population are individuals in a low condition (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapters 5-6). As individual heterogeneity within a population may bias the study of reproductive costs (van Noordwijk *et al.*, 1986; Reznick, 1992; McNamara *et al.*, 1996), we excluded these low-quality females from our sample and considered only breeding females (i.e. females that gave birth to at least one juvenile) to keep a more homogeneous group of individuals. Our study focuses on fitness consequences of variation in reproductive intensity of females in relation to age, with reproductive intensity characterized by litter size at weaning (i.e. number of juveniles successfully weaned; range 0-5) and bequeathal behaviour (i.e. behaviour that consists of females giving part or all of their territory to their offspring at weaning, Price *et al.*, 1993; Berteaux *et al.*, 2000). Bequeathal behaviour was characterized by a categorical variable with two modalities (modality 0: females kept their territory at weaning of their juveniles; modality 1: females gave away part or all of their territory at weaning to their juveniles). We made the assumption that producing a large litter and bequeathing territory were more costly than producing a small litter and keeping a territory. To test for the prediction that costs of reproduction are higher for young and old females than for prime-age ones, we included the first-order interactions between litter size at weaning or bequeathal, age and age^2 (that is litter size×age, litter size×age^2, bequeathal×age, and bequeathal×age^2). We first analysed survival costs of reproduction and tested for an effect of breeding intensity in year *t* on survival between year *t* and *t+1*. We then considered costs on future reproduction and tested for an effect of breeding intensity year t on litter size at weaning year t+1.

Yearly environmental variations may influence the reproductive output of females and confound our interpretations (if large litters were produced only in years of favourable conditions for example). We thus included in our models food available during reproduction at year t (that is cone production year t-1 or “previous cone production”) and food available between t and t+1 and at t+1 (that is cone production of the current year, or “current cone production”). As survival and reproductive performance are quadratic functions of age in our population (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3), age and age^2 were included in our analyses. Parturition date of females may also affect reproductive performance of females and costs of reproduction (Berteaux *et al.*, 2000; Réale *et al.*, 2003a), and was included in our analyses. We considered the difference (in days) between the parturition date of each female and the average parturition date of all females the same year.

Statistical analyses

Our data set included repeated measurements on the same females at different ages. To account for pseudoreplication problems (sensu Hurlbert, 1984), we fitted generalized linear mixed models with the MIXED procedure and the GLIMMIX macro in SAS version 8.0 (SAS Institute, 1999). We used the repeated statement and the maximum likelihood method, which allowed us to take into account the non independence in our data set (Littell *et al.*, 1996). We specified the compound symmetric matrix structure, which assumes that the correlation of measurements was identical for all pairs of measurements made on the same individual. Recapture rates of females were close to one (>0.95) and constant through time (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3). In this case, the use of mixed models for survival analyses is appropriate (Cam & Monnat, 2000b) and such statistical procedure allowed easily incorporating into our analyses the variables described earlier that may have confounding effects on the interpretation of reproductive costs.

Our model selection was based on AICc (Burnham *et al.*, 2002), a variant of AIC (Akaike's Information Criterion) which accounts for the bias introduced when sample size is relatively small compared to the number of parameters in tested models. From AICc, we calculated the difference between each AICc value and the best model AICc value (ΔAICc). A difference of less than two units of AICc between two models means that they are competitive to explain the data (Burnham *et al.*, 2002). Results are reported as means ± SE.

7.4 Results

Effects of current reproduction on future survival

Survival of females from one breeding season to the next was a quadratic function of age (Table 7.1; age effect: 1.55 ± 0.50 and age^2 effect: -0.18 ± 0.05 on a logit scale), and survival decreased after four years of age (increase from one to four years of age, and then decrease until eight years of age, the maximum age for females in our population). In addition, cone production the year of reproduction had a positive effect on subsequent survival (Table 7.1; cone production effect: 0.0049 ± 0.0015 on a logit scale with cone production varying from 1 to 283 cones/tree).

Litter size at weaning alone had a positive effect on females' survival (Table 7.1; effect of litter size at weaning: 0.96 ± 0.29 on a logit scale with litter size varying from 0 to 5) but it interacted negatively with age of females (Table 7.1; interaction effect: -0.20 ± 0.09 on a logit scale). An increase of litter size at weaning affected positively females <5 years old, but negatively females ≥5 years old (Fig. 7.1). In addition, the decrease in survival with increasing litter size accelerated with increasing age from five years of age onwards (Fig. 7.1).

Similarly, the effect of bequeathal and the interaction term between bequeathal behaviour and age of females affected survival of females (Table 7.1; estimated survival difference between females bequeathing and keeping their territory at weaning: 1.44 ± 0.63 on a logit scale; estimated effect of the interaction term with age: -0.44 ± 0.20 on a logit scale). Model with lowest AICc showed that females ≤3 years old who kept their territory after weaning had a higher survival than females ≤3 years old that bequeathed it, and the reverse relationship was true for females >3 years old (Table 7.1; Fig 7.2). In addition, the decrease in survival with increasing litter size was slower for old females (≥5 years old) that kept their territory after weaning than for old females bequeathing their territory after weaning (Table 7.2; Fig. 7.2). However, the difference in AICc between this model and model including no effect of bequeathal and no interaction between bequeathal and age was <2 (ΔAICc=1.2; Table 7.1). Therefore, the effects of bequeathal and bequeathal×age can reasonably be interpreted as marginally significant based on AICc. If model selection had been based on *p*-values, these effects would also have been selected (*p*-values for the bequeathal and bequeathal×age effects were respectively 0.024 and 0.030).

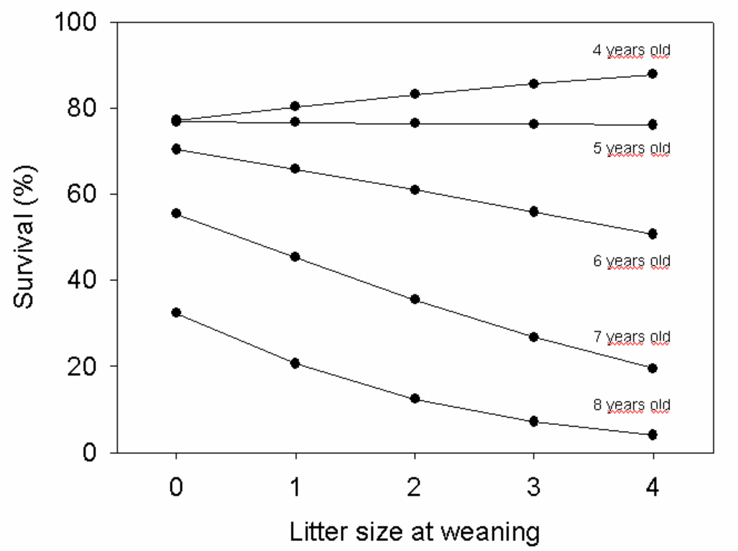

Figure 7.1 Predicted survival of females from year *t* to *t+1* according to their breeding outcome (litter size at weaning) and age at year *t* in a North American red squirrel population, Kluane, Yukon, Canada. Each curve corresponds to females of a particular age and for clarity, we present only curves for females 4 to 8 years old. Values correspond to estimates from model selected in table 7.1 (example of females bequeathing their territory).

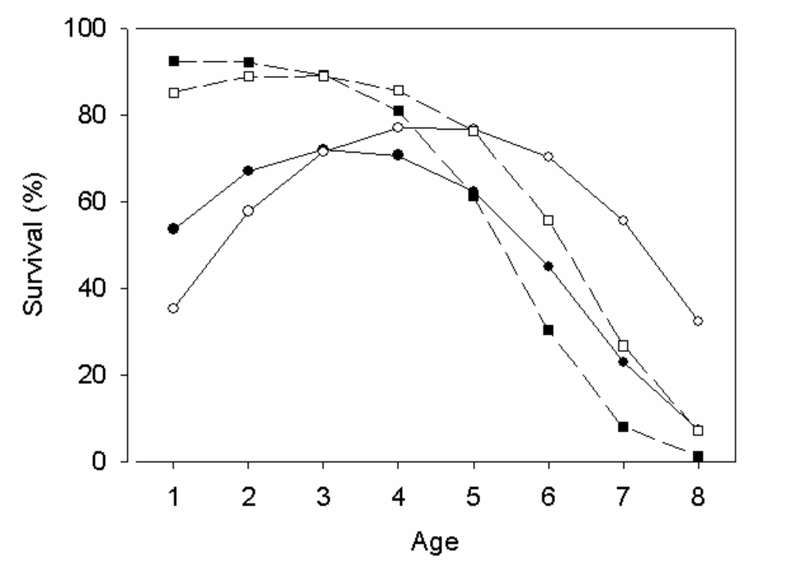

Figure 7.2 Predicted survival of females from year *t* to *t+1* according to age and bequeathal behaviour in year *t* in a North American red squirrel population, Kluane, Yukon, Canada. White symbols represent survival of females who bequeathed their territory at weaning, and black ones survival of females who kept their territory at weaning. Circles correspond to a litter size at weaning of 0, and squares to a litter size of 3. Values correspond to estimates from model selected in table 7.1.

Effects of current reproduction on future reproduction

Breeding outcome (i.e. litter size at weaning) at year t+1 was not affected by breeding outcome at year t (Table 7.3). We found significant negative effects of age (Table 7.3, age effect: -0.18 ± 0.06), previous cone production (i.e. cone production at t-1, which corresponds to food available during reproduction at year t; Table 7.3; estimated effect: -0.0027 ± 0.0008), and date of parturition at year t (Table 7.3; effect of parturition date: -0.0091 ± 0.0047) on litter size at weaning at year t+1. Consequently, old or late breeding females at year t raised successfully less juveniles at year t+1 than females younger or breeding earlier at year t. Also, females breeding a year of high food availability produced a lower number of juveniles the subsequent year.

Table 7.1 Survival (from t to t+1) of breeding females according to their breeding outcome at time t (i.e. litter size at weaning at time t or LSIZE) in a North American red squirrel population, Kluane, Yukon,Canada. Current cone production (CCP) corresponds to food available for females after reproduction at time t, and previous cone production (PCP) to food available during reproduction at time t. The bequeathal variable (B) had two modalities: females gave part of or all their territory to their juveniles at weaning or females kept their territory at weaning. Date of parturition (PD) corresponds to the difference (in days) between the date of parturition for a particular female and the average date of parturition of the current year. Age of females is indicated as A in models. 431 observations have been made on 219 females.

Model	Deviance	np	AICc	ΔAICc
A+A^2+CP+LSIZE+B+A×LSIZE+A×B	**461.381**	**10**	**481.905**	**0.000**
A+A^2+CP+PCP+LSIZE+B+A×LSIZE+A×B	459.602	11	482.232	0.327
A+A^2+CP+LSIZE+B+PD+A×LSIZE+A×B	459.779	11	482.409	0.504
A+A^2+CP+PCP+LSIZE+B+PD+A×LSIZE+A×B	458.080	12	482.826	0.921
A+A^2+CP+LSIZE+A×LSIZE	**466.769**	**8**	**483.110**	**1.205**
A+A^2+CP+PCP+LSIZE+B+PD+A×LSIZE+A×B+A^2×B	456.281	13	483.154	1.249
A+A^2+CP+PCP+LSIZE+A×LSIZE	463.167	10	483.691	1.786
A+A^2+CP+LSIZE+B+A×B	466.156	9	484.584	2.679
A+A^2+CP+LSIZE+B+A×LSIZE	466.464	9	484.892	2.987
A+A^2+CP+PCP+LSIZE+B+PD+A×LSIZE+A^2×LSIZE+A×B	458.114	13	484.987	3.082
A+A^2+CP+PCP+LSIZE+B+PD+A×LSIZE+A^2×LSIZE+A×B+A^2×B	456.244	14	485.254	3.349
A+A^2+CP+PCP+LSIZE+B+PD	464.964	10	485.488	3.583
A+A^2+CP+PCP+LSIZE+B+PD+A×LSIZE	463.219	11	485.849	3.944
A+A^2+CP+PCP+LSIZE+B+PD+A×B	463.409	11	486.039	4.134
A+A^2+CP+PCP+B+PD+A×B	468.927	10	489.451	7.546
A+A^2+CP+B+A×B	473.738	8	490.079	8.174
A+A^2+LSIZE+B+A×LSIZE+A×B	474.966	9	493.394	11.489
CP+LSIZE+B+A×LSIZE+A×B	478.348	8	494.689	12.784
A+CP+PCP+LSIZE+B+PD+A×LSIZE+A×B	474.007	11	496.637	14.732
A+CP+LSIZE+B+A×LSIZE+A×B	478.348	9	496.776	14.871
A+A^2+PCP+LSIZE+B+PD+A×LSIZE+A×B	474.930	11	497.560	15.655
CP+PCP+LSIZE+B+PD	484.190	8	500.531	18.626
Intercept (null model)	510.469	3	516.525	34.620

Table 7.2 Decline in survival when litter size at weaning increased from 0 to 4 according to age and bequeathal behaviour for females in a North American red squirrel population, Kluane, Yukon, Canada. Values are estimated from the model selected in table 1.

Age of females (years)	Decline in survival	
	No bequeathal	Bequeathal
6	19%	20%
7	18%	36%
8	7%	28%

Table 7.3 Number of juveniles successfully weaned by females at time t+1 according to their breeding outcome at time t (i.e. litter size at weaning at time t or LSIZE) in a North American red squirrel population, Kluane, Yukon,Canada. Current cone production (CCP) corresponds to food available for females after reproduction at time t, and previous cone production (PCP) to food available during reproduction at time t. The bequeathal variable (B) had two modalities: females gave part of or all their territory to their juveniles at weaning or females kept their territory at weaning. Date of parturition (PD) corresponds to the difference (in days) between the date of parturition for a particular female and the average date of parturition of the current year. Age of females is indicated as A in models. 239 observations have been made on 133 females.

Model	Deviance	np	AICc	ΔAICc
A+A^{2}+CP+PCP+LSIZE+B+PD+A×LSIZE+A^{2}×LSIZE+A×B+A^{2}×B	752.306	14	781.316	10.185
A+A^{2}+CP+PCP+LSIZE+B+PD+A×LSIZE+A^{2}×LSIZE+A×B	753.595	13	780.468	9.337
A+A^{2}+CP+PCP+LSIZE+B+PD+A×LSIZE+A×B+A^{2}×B	752.329	13	779.202	8.071
A+A^{2}+CP+PCP+LSIZE+B+PD+A×LSIZE+A×B	754.507	12	779.253	8.122
A+A^{2}+CP+PCP+LSIZE+B+PD+A×LSIZE	756.751	11	779.381	8.250
A+A^{2}+CP+PCP+LSIZE+B+PD+A×B	755.437	11	778.067	6.936
A+A^{2}+CP+PCP+LSIZE+B+PD	756.820	10	777.785	6.654
A+CP+PCP+LSIZE+B+PD	757.038	9	775.824	4.693
CP+PCP+LSIZE+B+PD	763.889	8	780.515	9.384
A+A^{2}+PCP+LSIZE+B+PD	758.623	9	777.409	6.278
A+A^{2}+CP+LSIZE+B+PD	764.016	9	782.802	11.671
A+A^{2}+CP+PCP+B+PD	756.821	9	775.607	4.476
A+A^{2}+CP+PCP+LSIZE+PD	756.863	9	775.649	4.518
A+A^{2}+CP+PCP+LSIZE+B	759.916	9	778.702	7.571
A+PCP+PD	**758.769**	**6**	**771.131**	**0.000**
PCP+PD	766.675	5	776.933	5.802
A+PD	769.602	5	779.860	8.729
A+PCP	762.368	5	772.626	1.495
Intercept (null model)	775.310	3	781.412	10.281

7.5 Discussion

Costs of reproduction, and more generally trade-offs between life-history traits, “are contingent on conditions” (Roff, 2002, p. 115). Growing individuals or individuals in a poor physiological state are likely to bear high costs of reproduction because reproduction occurs under more stressful conditions (Reznick, 1985; Roff, 2002).

Expensive breeding for senescent females

In our population of North American red squirrels, we found that an increase in litter size at weaning led to a decrease in subsequent survival for old females (≥5 years old), and this decrease in survival with increasing litter size accelerated from five of age onwards. It was thus costly to raise a large number of offspring after five years of age, and these costs increase with increasing age.

On the opposite, an increase in the number of juveniles successfully weaned was positively correlated to an increase in survival for females <5 years of age. This does not mean that reproduction is not costly for prime-age females, but that differences in individual quality within the prime-age class were more influent on the apparent variation in survival and reproduction than costs of reproduction (van Noordwijk *et al.*, 1986; McNamara *et al.*, 1996). This could be explained by a higher homogeneity among prime-age females than among senescent ones, or by higher costs of reproduction for senescent females. As it seems unlikely that females ≥5 years old were a more homogeneous group than females 1-4 years old (CV of their litter size at weaning, respectively: 0.95 vs. 0.80), our results suggest that survival costs of reproduction were higher for old females than for prime-age ones. Senescence in this red squirrel population appears after four years of age, and is more pronounced after six years old (Descamps, Boutin, Berteaux, Gaillard, unpubl. data, chapter 3). Consequently, it seems very likely that costs of reproduction increased after five years of age in this red squirrel population as a result of senescence, and thus physiological decline.

In addition, the decrease in survival with increasing litter size at weaning tended to be more pronounced for females bequeathing their territory at weaning than for females keeping it. Territory bequeathal combined to a large number of offspring successfully weaned thus tended to decrease subsequent survival after five years of age. Females who bequeathed their territory needed to establish a new territory, which probably requires considerable energy (Larsen *et al.*, 1994), and it is not surprising that senescent females (i.e. females in low physiological state) did not meet such energetic demands without suffering high somatic costs.

We did not find any effect of current reproduction on subsequent reproduction. To wean a large number of offspring at time t did not affect breeding outcome at time t+1, whatever the age of females. This suggests that costs of reproduction in our population essentially affected survival abilities of individuals, but those who managed to survive had no "memory" of their previous history of reproduction. With a theoretical approach, Caswell (1982) showed that survival costs of reproduction should increase with age, whereas fertility costs should be nearly age-invariant. His predictions were supported by data on humans, but to our knowledge, no other study has given support to them since that time. Our results on female red squirrels suggest that costs of current reproduction on survival increased with age, and that costs of current reproduction on future reproduction did not show any age-specific variation, which clearly supports Caswell's predictions (1982).

Our study indicates that food availability during reproduction had a negative effect on subsequent reproduction. As food availability during reproduction is highly correlated to density in our population (Stan Boutin, unpubl. data), this suggests that costs of reproduction increase with increasing density as previously found in ungulates (Festa-Bianchet *et al.*, 1998). This also supports the hypothesis that costs of reproduction increase under conditions of stress.

Territory bequeathal is costly for young females

One and two year old females tended to have a lower survival when they bequeathed their territory to their juveniles at weaning than when they kept it. It has been shown that dominance is associated to mass in our population (Stuart-Smith *et al.*, 1994), and as female red squirrels grow until three years of age, young females are likely to be sub-dominant. Access to territory may thus be more difficult for young females than for prime-age ones as observed in Eurasian red squirrels (Wauters *et al.*, 1989, 1992). Consequently, females one or two years old that bequeathed their territory may be unable to establish and defend new boundaries without suffering very high energetic costs, which could explain their lower survival hereafter. Territory bequeathal was thus costly for young females. As bequeathal had no apparent fitness cost in prime-age class, it seems very likely that bequeathal was more costly for young growing females, which supports our prediction.

Cost of reproduction and individual heterogeneity

Our results support the hypothesis that costs of reproduction are more important under conditions of stress. These stressful conditions may correspond to harsh environmental conditions (e.g. Festa-Bianchet & King, 1991; Festa-Bianchet *et al.*, 1998), but also to some particular age classes (i.e. very young or very old individuals). As costs of reproduction are supposed to increase under such stressful conditions, they are more easily detectable from the study of phenotypic correlations. According to Festa-Bianchet et al. (1998), "it is […] likely that for many mammals the costs of reproduction in females are evident only for individuals that are in poor condition, either because they are small or because they are in high-density populations". Our study also indicates that such a "poor condition", or more exactly a condition not suitable for reproduction, may be related to the age of females.

It has been previously suggested that costs of reproduction are difficult to study in the wild with phenotypic correlations (Reznick, 1985) because of individual heterogeneity (van Noordwijk *et al.*, 1986; McNamara *et al.*, 1996). Our study shows that even in a heterogeneous population in terms of individual quality, costs of reproduction may be apparent. Our results indicate clear survival costs of reproduction for young growing and old senescent females, whereas no cost was apparent for prime-age ones. As costs of reproduction were likely to be higher for young and old females, the variation in individual quality was likely too small to mask the important costs of reproduction for these two groups of individuals. On the opposite, costs of reproduction were likely too small compared to variation in individual quality among the prime-age class, and no cost was apparent. Therefore, the detection of costs of reproduction based on phenotypic correlations seems to be mainly a matter of balance between individual heterogeneity and intensity of the costs.

Our study shows that despite the technical difficulty of studying costs of reproduction in the wild, the use of long-term data on phenotypic correlations that incorporates age of individuals could give much insight in our understanding of trade-offs and reproductive tactics.

Chapitre 8 Conclusion

8.1 Principales avancées scientifiques

8.1.1 Effets cohortes et stratégies de reproduction

Effets cohorte : une source d'hétérogénéité

L'hétérogénéité de la qualité (sensu McNamara *et al.*, 1996) des individus au sein d'une population peut fortement influencer notre perception de certains phénomènes, notamment dans l'étude des compromis évolutifs ou des effets de l'âge (van Noordwijk *et al.*, 1986; Cam *et al.*, 2002). Si les conditions environnementales l'année de naissance sont variables, et que ces variations déterminent, au moins en partie, la qualité des individus, une population composée d'individus provenant de différentes cohortes sera fortement hétérogène.

La population d'écureuils roux de Kluane est soumise à d'importantes variations environnementales d'une année à l'autre. En effet, la principale ressource alimentaire peut passer d'une disponibilité quasi nulle à une disponibilité quasi illimitée (McAdam and Boutin 2003). Ainsi, la ressource disponible pour les femelles pendant la période d'élevage est extrêmement variable, ainsi que la ressource disponible pour les jeunes après le sevrage. Ces effets cohortes (sensu Albon *et al.*, 1987; Gaillard *et al.*, 2003c) ont d'importantes répercussions sur les histoires de vie des écureuils (chapitres 2, 3 et Humphries *et al.*, 2000; McAdam *et al.*, 2003; Réale *et al.*, 2003b). En particulier, une forte production de cônes l'année de naissance a un effet sur la survie des jeunes après le sevrage, et donc sur le recrutement dans la population. Elle influence également le succès reproducteur à vie des femelles. En effet, une femelle née une année de forte abondance de cônes vivra plus longtemps et élèvera plus de jeunes avec succès (jusqu'au sevrage) qu'une femelle née une année de faible abondance de cônes, et ses jeunes seront de meilleure qualité. Comme le suggèrent la plupart des chapitres de cette thèse, cette population d'écureuils roux d'Amérique du Nord est composée d'individus de qualité variable, et cette hétérogénéité est due, entre autres, à la variation des conditions environnementales l'année de naissance.

Les effets cohortes sur la qualité des individus sont communs chez les grands herbivores (Gaillard *et al.*, 2003c), et ont été aussi mis en évidence chez des oiseaux (e.g. Cam *et al.*, 2003) et reptiles (e.g. Madsen *et al.*, 2000). Ce travail sur les effets cohortes à long terme dans une population d'écureuils roux montre que les petits mammifères sont aussi sujets à de tels effets. Ce travail concernait seulement les effets cohortes liés à la disponibilité alimentaire l'année de naissance. D'autres variables environnementales sont susceptibles d'influencer la performance des individus à long terme. En particulier, il a été montré que la température au printemps influence la date de mise-bas des femelles (Réale *et al.*, 2003b). La date de naissance a été proposée comme un déterminant de la qualité du territoire obtenu après le sevrage (Price *et al.*, 1990) et est corrélée à la fitness des individus (Réale *et al.*, 2003a). Ainsi, il semble raisonnable d'imaginer que les conditions climatiques l'année de la naissance ont également un effet à long-terme sur la performance des individus.

Effets cohorte, stratégies de reproduction et fitness

La variation des conditions environnementales l'année de naissance influence la performance future des individus, mais également les stratégies de reproduction dans notre population d'écureuils. Le chapitre 3 montre que les femelles nées et élevées dans des conditions favorables, en terme de disponibilité alimentaire, vont produire des portées plus grandes au début de leur vie, mais vont en payer le prix en fin de vie, avec des portées diminuant plus rapidement à mesure qu'elles vieillissent. Ces résultats témoignent de l'importance des effets cohortes dans les stratégies de reproduction des femelles, et les patrons de la sénescence. Un individu né une année favorable sera de meilleure qualité, se reproduira plus intensément en début de vie, mais aura une sénescence plus marquée qu'un individu né une année moins favorable. La mise en évidence de ce type de compromis est rare dans les populations étudiées à l'état naturel, et il s'agit probablement des premiers résultats de ce genre dans une population sauvage de petits mammifères.

8.1.2 Importance de l'âge dans l'étude des stratégies de reproduction

Sénescence et hypothèse du soma « jetable » (disposable soma theory)

La sénescence correspond dans sa définition la plus stricte à une détérioration du fonctionnement de l'organisme, qui conduit à une diminution des performances démographiques.

Plusieurs hypothèses tentent d'expliquer dans un contexte évolutif pourquoi la sénescence existe, malgré ses effets apparents négatifs sur la *fitness* des individus. Trois hypothèses se retrouvent généralement dans la littérature, deux se basant sur la génétique des populations (mutation accumulation hypothesis, Medawar, 1952; antagonistic-pleiotropy hypothesis, Williams, 1957), la troisième se basant plutôt sur des notions de physiologie (disposable soma theory, Kirkwood, 1977; Kirkwood *et al.*, 1991). Ces hypothèses ne sont pas exclusives et se basent sur l'idée que la sélection est plus forte pour les traits exprimés tôt dans la vie de l'individu que pour ceux exprimés tard (Medawar, 1952; Williams, 1957; Charlesworth, 1994). Peu d'études empiriques permettent de supporter l'une ou l'autre des ces hypothèses. Quelques rares études faites sur des vertébrés en conditions naturelles vont dans le sens de l'hypothèse du soma jetable ou « *disposable soma theory* » (Westendorp & Kirkwood, 1998 sur l'humain; Poizat, Rosecchi & Crivelli, 1999 sur l'épinoche; Orell *et al.*, 2002 sur la mésange boréale; Reid *et al.*, 2003a sur le crave à bec rouge; Carranza *et al.*, 2004 sur le cerf élaphe; Wiersma *et al.*, 2004 sur le diamant mandarin). Nos travaux sur une espèce de petit mammifère en conditions naturelles ont également permis de supporter l'hypothèse du « soma jetable», en montrant clairement l'existence d'un compromis entre reproduction en début de vie et performance en fin de vie. Ces résultats sont donc une contribution majeure dans la compréhension de l'évolution de la sénescence, mais également dans la compréhension des coûts de la reproduction et des stratégies d'histoire de vie.

Sénescence et effets à long-terme

Une diminution nette de la masse et de la performance démographique a été mise en évidence dans notre population d'écureuils roux (chapitre 3). Ces résultats montrent tout d'abord que la structure en âge peut-être très nette dans une population de petits mammifères. D'autres travaux concernant les sciuridés montrent aussi d'importants effets de l'âge sur les traits d'histoire de vie (Sherman *et al.*, 1984; Broussard *et al.*, 2003; Broussard *et al.*, 2005). Ainsi, les modèles démographiques appliqués à des populations de *sciuridés* ne devraient pas uniquement considérer une structure à deux classes, juvéniles et adultes (Dobson *et al.*, 2001; Oli *et al.*, 2001), et devraient notamment considérer distinctement un stade « sénescent ».

D'autre part, nos travaux ont montré un effet à long terme de l'âge de la mère sur la performance des juvéniles. Il ne s'agit pas de la première étude suggérant une baisse de la qualité des individus nés de mères âgées, mais de tels travaux restent extrêmement rares chez les vertébrés en conditions naturelles (voir références citées dans chapitre 3), et les conséquences de ces effets à long terme sur l'évolution de la sénescence et la dynamique des populations restent à déterminer.

Sénescence, âge et effort reproducteur

D'après la théorie d'histoire de vie (Fisher, 1930; Williams, 1966b; Charlesworth *et al.*, 1976; Stearns, 1976), une diminution de la valeur reproductive résiduelle d'un individu doit être associée à une augmentation de l'effort reproducteur. C'est à dire, moins un individu a de chances de survivre et/ou de se reproduire dans le futur, plus il a intérêt à investir dans sa reproduction actuelle. Dans les populations où la sénescence a été mise en évidence, on s'attend donc à voir l'effort reproducteur augmenter avec l'âge. Peu d'études ont clairement montré une augmentation de l'effort reproducteur avec l'âge chez les mammifères, et il est difficile de vérifier la pertinence de cette hypothèse chez les mammifères en se basant sur les résultats empiriques existant actuellement. Notre travail (chapitre 4), en plus de discuter la façon dont de telles études ont été menées, suggère fortement une augmentation de l'effort reproducteur pour les femelles écureuils roux au cours de leur vie, et supporte donc très clairement la théorie.

La majorité des études sur la relation entre âge et effort reproducteur chez les mammifères se basent sur le changement de masse au cours de la saison de reproduction et sur la masse totale de jeunes produits. Ces deux variables, souvent considérées comme des mesures directes de l'effort reproducteur, peuvent ne pas représenter l'énergie investie dans la reproduction et donc ne pas être pertinentes pour étudier la variation de l'effort reproducteur. Imaginons une population où les femelles âgées, moins performantes, sont reléguées à des territoires de faible qualité. Pour produire une portée de même masse que des femelles possédant un meilleur territoire, elles devront fournir une plus grande énergie (via une activité de recherche alimentaire plus intense par exemple). Ainsi, produire une portée de même masse pour des jeunes et des vieilles femelles ne correspondra pas à un même effort reproducteur.

D'autre part, l'effort reproducteur peut augmenter avec l'âge mais seulement à une période du cycle reproducteur (Clutton-Brock, 1984). Dans notre population d'écureuils, jeunes et vieilles femelles ont des changements de masse équivalent au cours de la reproduction, produisent des jeunes de même masse mais les vieilles femelles lèguent plus souvent leur territoire à leurs jeunes au moment du sevrage que les jeunes femelles. Il est donc vraisemblable d'imaginer une population de mammifères où l'augmentation de l'effort n'aurait lieu qu'à la fin de la période de reproduction, quand les jeunes produits ont la plus grande espérance de vie. Ainsi, les études portant sur la variation de l'effort reproducteur en fonction de l'âge devrait idéalement prendre en compte plusieurs composantes liées à l'effort reproducteur, décrivant l'énergie investie tout au long de la période de reproduction.

Coûts de la reproduction, âge et investissement reproducteur

Le chapitre 4 de ce doctorat met en évidence certains problèmes méthodologiques dans l'étude des liens entre âge et l'effort reproducteur. Le chapitre 7 ajoute certains éléments qui peuvent également être importants à prendre en compte pour étudier les liens entre effort et investissement reproducteurs, et donc pour comprendre les stratégies de reproduction des êtres vivants.

Les notions d'effort et d'investissement reproducteurs sont souvent utilisés de manière synonyme, mais correspondent à des notions différentes. L'effort reproducteur correspond à l'énergie investie par un individu dans sa reproduction, sans tenir compte des coûts (sur sa fitness) qui y sont associés, alors que l'investissement prend en compte ces coûts (sensu Evans, 1990). Ainsi, il serait plus exact de dire que la théorie d'histoire de vie prédit une augmentation de l'investissement reproducteur lorsque la valeur reproductive résiduelle diminue, plutôt qu'une augmentation de l'effort (Partridge *et al.*, 1988; Pärt, Gustafsson & Moreno, 1992). Si on suppose que les coûts associés à un même effort sont constants, ou tout du moins ne diminuent pas, au cours de la vie de l'individu, une augmentation de l'effort reproducteur implique effectivement une augmentation de l'investissement. Cependant, lorsque les coûts de la reproduction (pour un même effort reproducteur) changent avec l'âge, les liens entre investissement et effort peuvent être plus complexes.

Le chapitre 7 de cette thèse montre que les coûts en terme de survie associés à un même effort reproducteur des femelles peuvent varier avec l'âge, et notamment augmenter en fin de vie (après 5 ans). Par exemple, produire une portée de quatre individus est moins coûteux (en terme de survie) pour une femelle de trois ans que pour une femelle de six ans. Plus généralement, dans notre population d'écureuils roux, à un même effort reproducteur sont associés différents coûts, fonction de l'âge de l'individu. Observer un effort reproducteur constant au cours de la vie dans une population où la sénescence existe peut donc, paradoxalement, supporter l'hypothèse selon laquelle l'investissement reproducteur augmente avec l'âge. Très peu d'études ont permis de supporter cette hypothèse, de par la difficulté d'étudier les coûts de la reproduction (Pärt *et al.*, 1992) et également la difficulté de quantifier l'effort reproducteur (voir chapitre 4).

Dans notre population d'écureuils roux, la probabilité qu'une femelle se reproduise et qu'elle donne son territoire à ses jeunes augmente avec l'âge. D'autre part la perte de masse de la mère au cours de la reproduction et la masse totale des jeunes produits ne varient pas avec l'âge. Ainsi, l'effort reproducteur augmentant avec l'âge, et les coûts liés à la reproduction étant plus grand pour les vieilles femelles, notre travail est l'une des rares études empiriques montrant que l'investissement reproducteur augmente avec l'âge.

8.1.3 Étude des coûts de la reproduction

L'étude des coûts de la reproduction est centrale en écologie évolutive, mais se révèle souvent complexe. De nombreux facteurs viennent biaiser l'interprétation des coûts de la reproduction, notamment lorsqu'ils sont étudiés à partir de corrélations phénotypiques. L'hétérogénéité de la qualité des individus au sein de la population a souvent été mise en avant pour expliquer pourquoi les coûts peuvent ne pas être apparents (Reznick, 1985; van Noordwijk *et al.*, 1986; Reznick, 1992). Cependant, ce travail de doctorat montre que, malgré une forte hétérogénéité au sein de la population d'écureuils roux, des coûts de la reproduction peuvent être mis en évidence. Ces coûts sont très probablement sous-estimés, mais restent néanmoins apparents dans certains groupes de femelles (voir chapitres 5 et 7).

L'étude des coûts de la reproduction devrait idéalement prendre en compte l'hétérogénéité des individus (Cooch *et al.*, 2002). Dans notre population, comme dans toutes les populations structurées en âge (i.e. les populations où la performance démographique varie en fonction de l'âge), l'âge est un facteur d'hétérogénéité. Le chapitre 7 montre que la prise en compte de l'âge peut effectivement permettre de détecter certains coûts liés à la reproduction, en se basant sur l'hypothèse que les coûts sont plus visibles en condition de stress (Reznick, 1992; Roff, 2002). Inclure l'âge dans l'étude des coûts de la reproduction peut donc permettre d'aller plus loin dans notre compréhension des compromis évolutifs et stratégies d'histoire de vie, mais n'a que rarement été fait.

Un autre aspect concernant l'étude des coûts de la reproduction mis en évidence dans ce travail est l'existence de coûts retardés dans le temps. En effet, dans notre population d'écureuils, une reproduction intense en début de vie a des conséquences importantes en fin de vie (i.e.

sénescence plus prononcée, chapitre 3). Ainsi, étudier les coûts de la reproduction en se basant simplement sur la survie ou le succès reproducteur l'année suivante peut être insuffisant, si les coûts sont cumulatifs et/ou exprimés plus tard, avec un certain délai. La majeure partie des études portant sur les coûts de la reproduction à partir de corrélations phénotypiques teste l'existence de coûts à court terme (l'année suivante). Étudier les coûts à plus long terme pourrait là encore permettre d'explorer plus en détail les compromis évolutifs au sein des populations animales.

8.1.4 Qualité individuelle et stratégie de reproduction

L'hétérogénéité individuelle a souvent été mise en avant pour expliquer l'absence d'effets apparents de l'âge par exemple, ou l'absence de coûts apparents de la reproduction au sein des population étudiées à partir de corrélations phénotypiques. Cependant, ce doctorat montre que malgré une importante hétérogénéité au sein de la population d'écureuils de Kluane, l'étude de telles corrélations peut permettre d'aller assez loin dans la compréhension des stratégies de reproduction.

Sénescence et hétérogénéité

Dans notre population d'écureuils roux, cohabitent des individus plus ou moins performants, ayant des taux de survie plus ou moins élevés, ce qui est supposé masquer les effets de l'âge sur les paramètres démographiques (Vaupel *et al.*, 1985; Cam *et al.*, 2002). En effet, les individus de plus faible qualité vont mourir plus jeunes que les individus de forte qualité et la qualité moyenne des individus dans chaque classe d'âge augmente avec l'âge (Service, 2000). Ainsi, les performances démographiques apparentes augmentent également avec l'âge, masquant le processus de sénescence. Dans une population fortement hétérogène, le processus de sénescence ne devrait donc pas pouvoir être mis en évidence. Or, dans notre système d'étude, la diminution de la performance démographique est très nette pour les deux sexes. Une explication serait que, même au sein d'une population hétérogène, si la sélection contre les individus de faible qualité est faible (faible taux de mortalité due à des facteurs extrinsèques) alors la qualité moyenne observée à chaque âge n'augmente pas suffisamment avec l'âge pour masquer le processus de sénescence. Dans ce cas, la diminution des performances démographiques observée au niveau de la population serait tout de même sous-estimée comparativement au réel processus de sénescence appliqué au niveau individuel.

Les faibles taux de prédation (Krebs et al., 2001) observés dans cette population vont dans le sens de cette hypothèse. D'autre part, le climat, ou tout du moins la température, semble n'avoir que peu d'impact sur la survie des écureuils (Humphries *et al.*, 2005). Finalement, nos résultats montrent que les individus (femelles) de faible qualité évitent de se reproduire (chapitres 5 et 6). Ainsi, si les individus de faible qualité ne sont pas éliminés de la population par la prédation, ni par le climat ou suite à une reproduction coûteuse, l'hypothèse d'une faible sélection contre les individus de faible qualité semble plausible dans notre population, malgré son hétérogénéité, rendant alors possible la mise en évidence d'une diminution avec l'âge de la performance des individus.

Hétérogénéité, performance et coûts de la reproduction

La variation des conditions environnementales l'année de naissance influence la performance démographique des individus, mais d'autres facteurs déterminent également cette performance et influencent les stratégies de reproduction.

La date de naissance des femelles semble liée à la qualité individuelle et à l'âge de première reproduction, indépendamment des variations environnementales. Ainsi, les écureuils nés les plus tôt en saison sont de haute qualité, se reproduisent dès un an, mais paient un coût important en terme de survie suite à cette reproduction précoce. Ceux nés plus tard sont de moindre qualité, ne peuvent se reproduire tôt, mais bénéficient ainsi d'une plus grande longévité.

La performance des individus au sein d'une population, et par conséquent les coûts de la reproduction, sont également fonction de l'âge. En particulier, dans notre population d'écureuils, les jeunes femelles encore en croissance et les vieilles femelles sénescentes ont une reproduction coûteuse en terme de survie. Ces coûts importants sont sans doute liés à une condition individuelle moins propice à assumer les coûts énergétiques de la reproduction.

Les femelles adultes mais non-sénescentes ne paient pas de coûts apparents de la reproduction, et une association positive existe dans notre population entre l'intensité de la reproduction et la survie, ou la reproduction future, pour ces femelles. Il semble donc que la variation de la qualité individuelle au sein des femelles non-sénescentes soit trop importante (et les coûts de la reproduction trop faibles) pour détecter des variations de survie ou succès reproducteur liés à la reproduction (van Noordwijk *et al.*, 1986; McNamara *et al.*, 1996).

8.2 Perspectives de recherche

8.2.1 Qualité de l'habitat et qualité individuelle

La notion d'hétérogénéité au sein de la population d'écureuils roux de Kluane est sous-jacente à la majeure partie des chapitres de ce doctorat, et doit être prise en compte pour correctement interpréter l'association entre de nombreux traits. Ainsi, pour aller encore plus loin dans la compréhension des stratégies démographiques au sein de cette population, il semble nécessaire de déterminer les facteurs à l'origine de cette hétérogénéité (Cooch *et al.*, 2002).

L'habitat est généralement considéré comme l'un des facteurs principaux influençant les traits des individus, et donc leur qualité (Southwood, 1977). La qualité de l'habitat est souvent corrélée au succès reproducteur et/ou à la survie (e.g. Haughland & Larsen, 2004), donc à la performance démographique des individus. Ainsi, un habitat hétérogène peut conduire à une hétérogénéité de la qualité des individus au sein d'une population, notamment pour une espèce territoriale où tous les individus n'ont pas un accès libre aux meilleurs habitats. Notre population d'écureuils se situe dans une forêt de conifères peuplée principalement d'épinettes blanches. La qualité de l'habitat, en terme de production de cônes d'épinettes, est très variable temporellement, et semble l'être aussi spatialement (travail de doctorat de J. M. Lamontagne, University of Alberta, en cours). Dans la mesure où les graines de cônes d'épinettes représentent la principale ressource alimentaire des écureuils, il semble hautement probable que l'hétérogénéité spatiale de cet habitat induise des différences de performance démographique. Un travail de doctorat est en cours afin de faire le lien entre qualité de l'habitat et dynamique de la population, et devrait permettre de mieux comprendre les liens entre survie, succès reproducteur et variation spatiale de la qualité de l'environnement. Les facteurs, ou attributs phénotypiques, déterminant le fait d'obtenir, et éventuellement de conserver, un habitat de plus ou moins bonne qualité restent encore peu connus. Les effets supposés de la date de naissance d'une part sur la qualité du territoire obtenu (Price *et al.*, 1990), et d'autre part sur la fitness des individus (Réale *et al.*, 2003a, ce doctorat), apportent une réponse partielle à cette question.

8.2.2 Des stratégies d'histoire de vie à la dynamique de la population

Cette thèse de doctorat a permis de confirmer certaines hypothèses issues de la théorie d'histoire de vie, et de mieux comprendre pourquoi d'autres ne sont que rarement supportées par les données empiriques. Elle a permis de mieux comprendre certains aspects des stratégies d'histoire de vie dans cette population d'écureuils roux, et de mettre en évidence des compromis entre différents traits. Cependant, les liens entre le cycle de vie de cette population et la dynamique de la population restent à explorer.

Parmi les mammifères, la dynamique des populations d'ongulés est certainement la mieux connue (Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard *et al.*, 2000). Certaines caractéristiques communes à toutes les populations étudiées d'ongulés ont été mises en évidence : la survie des adultes est relativement constante dans le temps, alors que la survie juvénile varie selon les conditions environnementales. La dynamique des ongulés semble être essentiellement influencée par la survie des juvéniles, malgré la faible élasticité de ce paramètre démographique. Plusieurs travaux concernant la dynamique de sciuridés (Dobson *et al.*, 2001; Oli *et al.*, 2001; Oli *et al.*, 2003) ont montré que parmi les paramètres les plus influents sur le taux de croissance (i.e. les paramètres dont l'élasticité est la plus élevée), on trouve l'âge de première reproduction et la survie juvénile**.** Ce travail de doctorat a montré que la variation de l'âge de première reproduction avait des effets importants sur les paramètres démographiques des individus. Il a également montré que la survie des jeunes variait de façon importante selon la production de cônes d'épinettes. Il serait donc intéressant d'étudier en détail l'importance de ces deux paramètres (âge de première reproduction et survie juvénile) sur la dynamique de cette population d'écureuils, afin de voir si un patron commun semble se dessiner pour les sciuridés, et afin de mieux comprendre l'importance de certaines variables environnementales (notamment la disponibilité alimentaire) sur la dynamique de cette population.

Ce système d'étude est un des rares systèmes chez les mammifères où l'âge des individus et leur succès reproducteur est connu (au moins pour les femelles), et où la principale ressource alimentaire, fluctuante, peut être quantifiée au niveau de la population. Les projets en cours devraient permettre de quantifier la qualité du territoire de chaque individu de cette population et de déterminer le succès reproducteur des mâles. Tous ces éléments font de la population d'écureuils roux de Kluane un système exceptionnel pour comprendre les principaux processus démographiques qui régissent la dynamique de cette population, en relation avec différentes variables environnementales.

Annexe 1 Modèles d'étude en écologie

Modèles des travaux ayant cité Lebreton et al. (1992), article de référence pour les analyses de survie se basant sur des données de capture-marquage-recapture [a]

Modèle	% de l'ensemble des travaux
Oiseaux	47
Grands mammifères	11[b]
Micromammifères	5
Autres petits mammifères	2[c]
Poissons	4
Reptiles et Batraciens	6
Autres (insectes…)	8
Problématiques de statistiques	17

[a] : Source : Web of Science 1992-2002, 634 articles concernés, mais seuls les 500 plus récents (juillet 1996 à septembre 2002) ont été pris en compte.

[b] : 5% des articles concernent les ongulés, 5% les mammifères marins, 1% d'autres grands mammifères comme les ours, wallabies, tigres.

[c] : 0.6% concernaient les chiens de prairie, 0.4% les spermophiles, 0.4% les lapins, 0.2% les marmottes, 0.2% les mustélidés, 0.2% les opossums.

Nombre de travaux concernant les cervidés et sciuridés publiés entre 1900 et 2005

Mot clé	Nombre d'espèces	Nombre de références
Deer(s)	45	1503
Squirrel(s)	280	1136
Red deer(s)	10	501
Red squirrel(s)	6	167

[a] :Source : Web of Knowledge, années 1900-2005; journal sources: SO=(american naturalist or ecology or journal of animal ecology or oecologia or oikos or nature or science or canadian journal of zoology or animal behaviour or behavioral ecology or Proceedings of the royal society of London Series B Biological sciences or Behavioral ecology "AND" sociobiology or ecography or evolution or evolutionary ecology or ethology or journal of zoology or journal of mammalogy)

Annexe 2 Sélection de modèles - chapitre 3

(a) Results of the model selection for capture rates of North American red squirrels, Kluane, Yukon, Canada. Models in bold represent selected models.

	Females				Males			
Models	Deviance	np	AIC	ΔAIC	Deviance	np	AIC	ΔAIC
ϕ(t) p(t)	1287.218	29	1345.218	5.266	851.081	29	909.081	2.688
ϕ(t) p	**1307.952**	**16**	**1339.952**	**0.000**	905.476	16	937.476	31.083
ϕ(t) p(a)	1284.328	30	1344.328	4.376	889.979	27	943.979	37.586
ϕ(t) p(e)	1307.210	17	1341.210	1.258	**872.393**	**17**	**906.393**	**0.000**

t: time; **a**: age (full-age dependant model); **e**: capture effort intensity

(b) Age effect on mass of female (mass after parturition, taking into account the litter size at birth) and male (average mass in May) North American red squirrels, Kluane, Yukon, Canada. The food availability variable corresponds to the cone production one year before. Model in bold represents selected model.

Mass of females (n_{obs}=423, n_{ind}=226)

Model	Deviance	np	AIC	ΔAIC
Mass of females~Age+Age^2+Food availability +Litter size	**3863.286**	**7**	**3877.286**	**0.000**
Mass of females~Age+Food availability+Litter size	3869.019	6	3881.019	3.733
Mass of females~1/Age+Food availability+Litter size	3870.868	6	3882.868	5.582
Mass of females~(Yearling, Prime Age 2-4, Senescent ≥5)+Food availability+Litter size	3882.395	7	3896.395	19.109
Mass of females~(Yearling, Adult)+Food availability+Litter size	3884.865	6	3896.865	19.579
Mass of females~(Yearling, Prime Age 2-6, Senescent ≥7)+Food availability+Litter size	3884.849	7	3898.849	21.563
Mass of females~(Yearling, Prime Age 2-5, Senescent ≥6)+Food availability+Litter size	3885.581	7	3899.581	22.295
Mass of females~(Prime Age 1-4, Senescent ≥5)+Food availability+Litter size	3889.542	6	3901.542	24.256
Mass of females~Food availability+Litter size	3894.269	5	3904.269	26.983
Mass of females~(Prime Age 1-5, Senescent ≥6) +Food availability +Litter size	3894.117	6	3906.117	28.831
Mass of females~(Prime Age 1-6, Senescent ≥7) +Food availability +Litter size	3894.187	6	3906.187	28.901

Mass of males (n_{obs}=480, n_{ind}=205)

Model	Deviance	np	AIC	ΔAIC
Mass of males~Age+Age^2+Food availability	**4017.123**	**6**	**4029.123**	**0.000**
Mass of males~1/Age+Food availability	4035.552	5	4045.552	16.429
Mass of males~Age+Food availability	4039.220	5	4049.220	20.097
Mass of males~(Yearling, Prime Age 2-5, Senescent ≥6) +Food availability	4069.284	6	4081.284	52.161
Mass of males~(Yearling, Prime Age 2-4, Senescent ≥5) +Food availability	4069.825	6	4081.825	52.702
Mass of males~(Yearling, Adult) +Food availability	4074.814	5	4084.814	55.691
Mass of males~(Yearling, Prime Age 2-6, Senescent ≥7)+Food availability	4073.337	6	4085.337	56.214
Mass of males~(Prime Age 1-4, Senescent ≥5) +Food availability	4111.461	5	4121.461	92.338
Mass of males~(Prime Age 1-5, Senescent ≥6) +Food availability	4111.741	5	4121.741	92.618
Mass of males~(Prime Age 1-6, Senescent ≥7) +Food availability	4121.245	5	4131.245	102.122
Mass of males~Food availability	4123.352	4	4131.352	102.229

(c) Results of the model selection for the size of the litters at birth according to mother's age in a North American red squirrel population, Kluane, Yukon, Canada (n_{obs}=580, n_{ind}=259). The food availability variable corresponds to the cone production one year before. Model in bold represents selected model.

Model	Deviance	np	AIC	ΔAIC
Litter size~Age+Age^2	**1429.921**	**5**	**1439.921**	**0.000**
Litter size~1/Age	1433.436	4	1441.436	1.515
Litter size~Age+Age^2+Food availability	1429.731	6	1441.731	1.810
Litter size~1/Age+Food availability	1433.158	5	1443.158	3.237
Litter size~(Yearling, Adult)+Food availability	1436.472	5	1446.472	6.551
Litter size~Age+Food availability	1436.682	5	1446.682	6.761
Litter size~(Yearling, Prime Age 2-6, Senescent ≥7) +Food availability	1434.918	6	1446.918	6.997
Litter size~(Yearling, Prime Age 2-5, Senescent ≥6) +Food availability	1436.100	6	1448.100	8.179
Litter size~(Yearling, Prime Age 2-4, Senescent ≥5) +Food availability	1436.293	6	1448.293	8.372
Litter size~Food availability	1443.359	4	1451.359	11.438
Litter size~(Prime Age 1-6, Senescent ≥7) +Food availability	1442.043	5	1452.043	12.122
Litter size~(Prime Age 1-5, Senescent ≥6) +Food availability	1442.507	5	1452.507	12.586
Litter size~(Prime Age 1-4, Senescent ≥5) +Food availability	1443.353	5	1453.353	13.432

(d) Results of the model selection for the number of weaned juveniles according to mother's age in a North American red squirrel population, Kluane, Yukon, Canada (n_{obs}=580, n_{ind}=259). The food availability variable corresponds to the cone production one year before. Model in bold represents selected model.

Model	Deviance	np	AIC	ΔAIC
Number of weaned juveniles~Age+Age^2+Litter size	**1716.928**	**6**	**1728.928**	**0.000**
Number of weaned juveniles~Age+Age^2+Food availability+Litter size	1716.869	7	1730.869	1.941
Number of weaned juveniles~(Yearling, Prime Age 2-4, Senescent ≥5)+Food availability+Litter size	1717.179	7	1731.179	2.251
Number of weaned juveniles~(Yearling, Prime Age 2-6, Senescent ≥7)+Food availability+Litter size	1717.492	7	1731.492	2.564
Number of weaned juveniles~(Yearling, Prime Age 2-5, Senescent ≥6)+Food availability+Litter size	1717.913	7	1731.913	2.985
Number of weaned juveniles~(Yearling, Adult)+Food availability+Litter size	1720.907	6	1732.907	3.979
Number of weaned juveniles~(Prime Age 1-6, Senescent ≥7)+Food availability+Litter size	1723.066	6	1735.066	6.138
Number of weaned juveniles~1/Age+Food availability+Litter size	1723.690	6	1735.690	6.762
Number of weaned juveniles~Food availability+Litter size	1726.044	5	1736.044	7.116
Number of weaned juveniles~(Prime Age 1-4, Senescent ≥5)+Food availability+Litter size	1724.127	6	1736.127	7.199
Number of weaned juveniles~(Prime Age 1-5, Senescent ≥6)+Food availability+Litter size	1724.174	6	1736.174	7.246
Number of weaned juveniles~Age+Food availability+Litter size	1726.043	6	1738.043	9.115

(e) Results of the model selection for the mass of juveniles at weaning (average per litter) according to mother's age in a North American red squirrel population, Kluane, Yukon, Canada. The food availability variable corresponds to the cone production one year before (i.e. food available during juveniles rearing). Model in bold represents selected model. Discrete models including an age class ≥7 years were not considered because data were missing for 7 and 8 year old squirrels (n_{obs}=258, n_{ind}=159).

Model	Deviance	np	AIC	ΔAIC
Weaning mass~Age+Food availability +Litter size	2303.556	6	2315.556	0.000
Weaning mass~Food availability+Litter size	**2306.226**	**5**	**2316.226**	**0.670**
Weaning mass~1/Age+Food availability +Litter size	2304.431	6	2316.431	0.875
Weaning mass~(Prime Age 1-5, Senescent ≥6) +Food availability +Litter size	2304.958	6	2316.958	1.402
Weaning mass~(Prime Age 1-4, Senescent ≥5) +Food availability +Litter size	2305.498	6	2317.498	1.942
Weaning mass~(Yearling, Adult) +Food availability +Litter size	2305.544	6	2317.544	1.988
Weaning mass~Age+Age^2+Food availability +Litter size	2303.548	7	2317.548	1.992
Weaning mass~(Yearling, Prime Age 2-5, Senescent ≥6) +Food availability +Litter size	2304.439	7	2318.439	2.883
Weaning mass~(Yearling, Prime Age 2-4, Senescent ≥5) +Food availability +Litter size	2305.026	7	2319.026	3.470

(f) Results of the model selection for the number of weaned juveniles surviving to 1 year of age according to mother's age in a North American red squirrel population, Kluane, Yukon, Canada (n_{obs}=286, n_{ind}=212). The food availability variable corresponds to the cone production the current year. Model in bold represents selected model.

Model	Deviance	np	AIC	ΔAIC
Number of recruited juveniles~(Yearling, Prime Age 2-5, Senescent ≥6)+Food availability+Number weaned+Bequeathal	**553.667**	**9**	**571.667**	**0.000**
Number of recruited juveniles~(Yearling, Prime Age 2-4, Senescent ≥5)+Food availability+Number weaned+Bequeathal	556.790	9	574.790	3.123
Number of recruited juveniles~Age+Age^{2}Food availability+Number weaned+Bequeathal	559.038	9	577.038	5.371
Number of recruited juveniles~(Yearling, Adult)+Food availability+Number weaned+Bequeathal	562.596	8	578.596	6.929
Number of recruited juveniles~(Prime Age 1-5, Senescent ≥6)+Food availability+Number weaned+Bequeathal	565.431	8	581.431	9.764
Number of recruited juveniles~Food availability+Number weaned+Bequeathal	572.500	6	584.500	12.833
Number of recruited juveniles~1/Age+Food availability+Number weaned+Bequeathal	569.003	8	585.003	13.336
Number of recruited juveniles~(Prime Age 1-4, Senescent ≥5)+Fod availability+Number weaned+Bequeathal	569.628	8	585.628	13.961
Number of recruited juveniles~Age+Food availability+Number weaned+Bequeathal	572.460	8	588.460	16.793

Annexe 3 Sélection de modèles - chapitre 4

(a) Age effect on the breeding probability, taking into account the food available for reproduction (cone production the year before) in a population of North American red squirrels, studied at Kluane, Yukon, Canada. Model in bold represents the selected model. Logit corresponds to the logit link function used for a binomial distribution.

First breeding attempt of the season (n_{obs}=782, n_{ind}=322). There was not enough data available to test models with an age class corresponding to individuals ≥6 years old.

	Model	Deviance	np	AIC	ΔAIC
1	Logit(Probability_Reproduction)~Age+Previous Cone Production	726.777	5	736.777	0.000
2	**Logit(Probability_Reproduction)~Age**	**729.236**	**4**	**737.236**	**0.459**
3	Logit(Probability_Reproduction)~Age+Age^2+Previous Cone Production	726.454	6	738.454	1.677
4	Logit(Probability_Reproduction)~1/Age+Previous Cone Production	733.315	5	743.315	6.538
5	Logit(Probability_Reproduction)~(Yearling, Prime Age 2-4, Senescent ≥5)+Previous Cone Production	765.257	6	777.257	40.480
6	Logit(Probability_Reproduction)~(Yearling, Adult)+Previous Cone Production	779.385	5	789.385	52.608
7	Logit(Probability_Reproduction)~(Prime Age 1-4, Senescent ≥5)+Previous Cone Production	866.869	5	876.869	140.092
8	Logit(Probability_Reproduction)~ Previous Cone Production	906.621	4	914.621	177.844

Second breeding attempt of the season. We considered only females successful at weaning at least one juvenile at the first breeding attempt. We did not consider discrete models including three age-classes and/or an age class ≥6 years because sample sizes were too small to compute maximum likelihood estimates (n_{obs}=67, n_{ind}=66). Models in bold represent the selected models.

	Model	Deviance	np	AIC	ΔAIC
1	**Logit(2nd attempt)~1/Age**	**57.521**	**2**	**61.521**	**0.000**
2	**Logit(2nd attempt)~Age**	**57.833**	**2**	**61.833**	**0.312**
3	Logit(2nd attempt)~Age+Age^2	57.617	3	63.817	2.296
4	Logit(2nd attempt)~(Yearling, Adult)	62.371	2	66.371	4.850
5	Logit(2nd attempt)~(Prime Age 1-4, Senescent ≥5)	65.651	2	69.651	8.130

(b) Age effect on the proportion of female mass change during reproduction taking into account the litter size and the food available for the reproduction (cone production the year before) in a population of North American red squirrels, studied at Kluane, Yukon, Canada.

Mass change from parturition to emergence ($n_{obs.}$=265; $n_{ind.}$=165).

	Model	Deviance	np	AIC	ΔAIC
1	Mass Change ~ Litter size	-630.202	4	-622.202	0.000
2	Mass Change ~ Previous Cone Production	-630.029	4	-622.029	0.173
3	Mass Change ~1/Age+Previous Cone Production +Litter size	-633.098	6	-621.098	1.104
4	Mass Change~Age+ Previous Cone Production +Litter size	-632.988	6	-620.988	1.214
5	Mass Change ~Age+Age^2+ Previous Cone Production +Litter size	-634.499	7	-620.499	1.703
6	Mass Change ~ Previous Cone Production +Litter size	-630.333	5	-620.333	1.869
7	Mass Change ~(Prime Age 1-6, Senescent ≥7)+ Previous Cone Production +Litter size	-631.293	6	-619.293	2.909
8	Mass Change ~(Yearling, Adult)+ Previous Cone Production +Litter size	-630.976	6	-618.976	3.226
9	Mass Change ~(Prime Age 1-5, Senescent ≥6)+ Previous Cone Production +Litter size	-630.355	6	-618.355	3.847
10	Mass Change ~(Prime Age 1-4, Senescent ≥5)+ Previous Cone Production +Litter size	-630.335	6	-618.335	3.867
11	Mass Change ~(Yearling, Prime Age 2-6, Senescent ≥7)+ Previous Cone Production +Litter size	-631.908	7	-617.908	4.294
12	Mass Change ~(Yearling, Prime Age 2-5, Senescent ≥6)+ Previous Cone Production +Litter size	-631.029	7	-617.029	5.173
13	Mass Change ~(Yearling, Prime Age 2-4, Senescent ≥5)+ Previous Cone Production +Litter size	-630.983	7	-616.983	5.219

Mass change from emergence to weaning ($n_{obs.}$=265, $n_{ind.}$=165).

	Model	Deviance	np	AIC	ΔAIC
1	**Mass Change ~ Previous Cone Production+Litter size**	**-763.551**	**5**	**-753.551**	**0.000**
2	Mass Change ~(Yearling, Adult)+ Previous Cone Production+Litter size	-764.542	6	-752.542	1.009
3	Mass Change ~1/Age+Previous Cone Production+Litter size	-764.250	6	-752.250	1.301
4	Mass Change ~(Prime Age 1-5, Senescent ≥6)+Previous Cone Production+Litter size	-764.151	6	-752.151	1.400
5	Mass Change ~(Prime Age 1-4, Senescent ≥5)+Previous Cone Production+Litter size	-763.587	6	-751.587	1.964
6	Mass Change~Age+Previous Cone Production+Litter size	-763.583	6	-751.583	1.968
7	Mass Change ~(Prime Age 1-6, Senescent ≥7)+Previous Cone Production+Litter size	-763.564	6	-751.564	1.987
8	Mass Change ~(Yearling, Prime Age 2-5, Senescent ≥6)+Previous Cone Production+Litter size	-765.385	7	-751.385	2.166
9	Mass Change ~Age+Age^2+Previous Cone Production+Litter size	-765.195	7	-751.195	2.356
10	Mass Change ~(Yearling, Prime Age 2-4, Senescent ≥5)+Previous Cone Production+Litter size	-764.693	7	-750.693	2.858
11	Mass Change ~(Yearling, Prime Age 2-6, Senescent ≥7)+Previous Cone Production+Litter size	-764.550	7	-750.550	3.001

(c) Age effect on the litter mass at weaning taking into account the mass of the mother and the food available for the reproduction (cone production the year before) in a population of North American red squirrels, studied at Kluane, Yukon, Canada. Models in bold represent the selected models ($n_{obs.}$=180; $n_{ind.}$=133).

	Model	Deviance	np	AIC	ΔAIC
1	Litter mass ~Age+Age^2+Previous Cone Production+Mother mass	2229.285	7	2243.285	0.000
2	**Litter mass ~1/Age+Previous Cone Production+Mother mass**	**2231.378**	**6**	**2243.378**	**0.093**
3	**Litter mass ~(Yearling, Adult)+Previous Cone Production+Mother mass**	**2231.938**	**6**	**2243.938**	**0.653**
4	Litter mass ~(Yearling, Prime Age 2-4, Senescent ≥5)+Previous Cone Production+Mother mass	2230.677	7	2244.677	1.392
5	Litter mass ~(Yearling, Prime Age 2-5, Senescent ≥6)+Previous Cone Production+Mother mass	2231.938	7	2245.938	2.653
6	Litter mass~Age+Previous Cone Production+Mother mass	2235.553	6	2247.553	4.268
7	Litter mass ~ Previous Cone Production+Mother mass	2237.776	5	2247.776	4.491
8	Litter mass ~(Prime Age 1-4, Senescent ≥5)+Previous Cone Production+Mother mass	2236.974	6	2248.974	5.689
9	Litter mass ~(Prime Age 1-5, Senescent ≥6)+Previous Cone Production+Mother mass	2237.662	6	2249.662	6.377

(d) Age effect on the probability to bequeath the territory at weaning (female kept her territory vs. female gave away part of or all her territory), taking into account the food available for reproduction (cone production the year before) and the food available for the next winter (cone production of the current year) in a population of North American red squirrels, studied at Kluane, Yukon, Canada. We did consider discrete models including an age class ≥7 years because of the lack of data for 7 and 8 years old squirrels (n_{obs}=336, n_{ind}=186). Logit corresponds to the Logit link function used for a binomial distribution. Model in bold represents the selected model.

	Model	Deviance	np	AIC	ΔAIC
1	**Logit (Bequeathal)~(Yearling, Prime Age 2-5, Senescent ≥6)+Current Cone Production+Previous Cone Production**	**380.880**	**7**	**394.880**	**0.000**
2	Logit (Bequeathal)~1/Age+Current Cone Production+Previous Cone Production	384.657	6	396.657	1.777
3	Logit (Bequeathal)~(Yearling, Prime Age 2-4, Senescent ≥5)+Current Cone Production+Previous Cone Production	382.788	7	396.788	1.908
4	Logit (Bequeathal)~(Yearling, Adult)+Current Cone Production+Previous Cone Production	385.309	6	397.309	2.429
5	Logit(Bequeathal)~Age+Current Cone Production+Previous Cone Production	385.496	6	397.496	2.616
6	Logit (Bequeathal)~Age+Age^2+Current Cone Production+Previous Cone Production	385.496	7	399.496	4.616
7	Logit (Bequeathal)~(Prime Age 1-5, Senescent ≥6)+Current Cone Production+Previous Cone Production	387.989	6	399.989	5.109
8	Logit (Bequeathal)~(Prime Age 1-4, Senescent ≥5)+Current Cone Production+Previous Cone Production	389.520	6	401.520	6.640
9	Logit (Bequeathal)~Current Cone Production+Previous Cone Production	393.912	5	403.912	9.032

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