De l'individu à la population : dynamique éco-évolutive et effets cohorte chez le mouflon d'Amérique

par

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À tous ceux qui m’ont soutenu

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Une bonne compréhension des facteurs influençant la dynamique de population est cruciale aussi bien en gestion des espèces invasives qu'en conservation des espèces en déclin. Les modèles classiques de dynamique de population sont basés sur la notion de densité dépendance et font souvent la supposition que la population est homogène. Cette supposition est rarement vraie. Les modèles structurés par âge sont une amélioration et considèrent les différences en âge entre individus ; pourtant la différence en âge n'est pas la seule différence individuelle qui est importante. Très peu de modèles considèrent d'autres sources de différences. L'objectif principal de cette thèse est donc d'explorer les causes et conséquences de trois sources de différences entre individus : les différences en génotype, les différences en phénotype et les différences entre cohortes. Pour ce faire, la population de mouflon d'Amérique (*Ovis canadensis*) de Ram Mountain, Alberta, Canada, est utilisée comme modèle d'étude. Cette population est suivie individuellement depuis plus de 40 ans et des informations aussi bien phénotypiques que génotypiques sont disponibles pour la grande majorité des individus.

La chasse au trophée peut imposer de fortes pressions sélectives sur certains traits et peut conduire à des changements évolutifs si ces traits sont héritables. Les effets anthropiques sur l'évolution dans la nature sont d'un grand intérêt pour la biologie de l'évolution et de la conservation parce que les pressions sélectives exercées par l'homme peuvent être plus fortes que celles imposées par les prédateurs naturels. Bien qu'il existe de nombreux exemples de changements phénotypiques induits par l'homme dans les populations de poissons exploités, très peu d'études ont les données nécessaires pour tester les changements génétiques liés aux récoltes chez les mammifères. J'ai utilisé de nouvelles méthodes statistiques combinant une généalogie profonde, des mesures morphologiques répétées et un changement des règlements de chasse pour montrer que l'évolution d'un trait morphologique ciblé par la chasse au trophée est possible (Chapitre 2).

Contrairement à ce qui a longtemps été supposé, les changements évolutifs peuvent survenir relativement rapidement. Ces changements rapides en phénotype ont le potentiel d'avoir un impact sur des processus écologiques. Ces impacts de l'évolution sur l'écologie ont récemment captivé l'attention des scientifiques et mené à l'émergence de l'étude de la dynamique éco-évolutive. Une synthèse des connaissances actuelles de ce domaine d'étude est faite (Chapitre 3) et le manque d'études empiriques en nature est souligné. La majorité des études de dynamique éco-évolutive ont été faites en laboratoire. Parmi celles faites en nature, peu font la distinction entre changements évolutifs et plastiques. Pourtant, cette distinction est cruciale pour bien comprendre l'importance des changements en traits sur les processus écologiques. J'ai donc quantifié l'effet des changements évolutifs et non évolutifs en masse corporelle sur la survie, le recrutement et le taux de croissance de population et comparé leurs importances aux effets des changements en structure d'âge, de densité et de climat (Chapitre 4). J'ai ainsi pu montrer que l'impact sur la dynamique de la population des changements en masse peut être aussi important que celui des changements en densité et en structure d'âge. Les changements évolutifs contribuent beaucoup moins aux changements en taux de croissance que les changements plastiques, mais leur importance augmente avec la durée de la période d'observation.

Les effets cohorte sont une autre source importante de variabilité interindividuelle. Les différences dans l'environnement de naissance peuvent avoir des conséquences à long terme sur la performance individuelle et donc sur la dynamique de la population. J'ai quantifié les effets à long terme de l'année de naissance sur la survie et la probabilité de se reproduire, et j'en ai exploré les causes environnementales (Chapitre 5). Mon étude a révélé que les conditions à la naissance expliquent jusqu'à 34% de la variabilité de la capacité à sevrer un agneau et que les différences entre les cohortes étaient principalement dues à la densité à la naissance. J'ai ensuite exploré les mécanismes par lesquels l'environnement à la naissance conduit à des effets à long terme sur la valeur adaptative (Chapitre 6). L'analyse de piste révèle à la fois un effet à long terme sur la masse adulte et un effet direct de la densité à la naissance sur le succès reproducteur à vie.

En somme, les résultats de ma thèse suggèrent que les différences interindividuelles peuvent avoir des impacts majeurs sur la dynamique des populations et que leurs causes sont complexes et multiples. Mes recherches contribuent ainsi à mieux comprendre l'impact des pressions anthropiques sur les traits et l'importance de ce genre de changement évolutif en trait sur le taux de croissance de population. De plus, mes recherches apportent une meilleure compréhension mécanistique des effets cohorte et de la manière dont ils pourraient induire un délai dans la réponse d'une population aux changements environnementaux.

Mots clés : dynamique de population, évolution contemporaine, effets cohorte, dynamique éco-évolutive, écologie, densité dépendance

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ANODEV : Analyse de déviance (*analysis of deviance*)

Éco-à-Éco : Une influence d’un processus écologique sur un processus écologique

Évo-à-Éco : Une influence d’un processus évolutif sur un processus écologique

NAO : Oscillation nord-atlantique (*North Atlantic Oscillation*)

PAR : Plasticité développementale adaptative-prédictive (*predictive adaptive response*)

PDO : Oscillation décennale du Pacifique (*Pacific Decadal Oscillation*)

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INTRODUCTION GÉNÉRALE

Plusieurs écologistes considèrent que nous sommes maintenant entrés dans l'ère de l'anthropocène, ou la sixième grande extinction (Corlett, 2015). L'Homme pouvant être la cause d'une des plus grandes périodes d'extinction de la planète, il est éthique de tenter de limiter le déclin des espèces en danger. L'Homme est aussi un grand consommateur des ressources naturelles (Darimont et al., 2015). Une gestion durable des populations exploitées, visant un maintien à long terme de la population, est nécessaire pour éviter un effondrement (Hutchings, 2000 ; Neubauer et al., 2013) qui pourrait avoir des impacts sur l'écosystème en entier (Jennings et Kaiser, 1998). Pour agir de façon efficace, il faut comprendre les facteurs qui influencent les fluctuations en taille de population. Déterminer les facteurs régulant les fluctuations en taille de population est le domaine de l'étude de la dynamique de population. Toutefois, ceci repose sur une bonne compréhension des processus sous-jacents. Ces processus peuvent être densité indépendants tels que des épisodes de prédation, des épidémies ou des variations climatiques. Ils peuvent aussi être densité dépendants. Les analyses de densité dépendance s'intéressent généralement aux fluctuations au niveau de la population ; comment la densité influence le taux de croissance. Quand la densité devient élevée, le taux de croissance de la population chute, ce qui entraîne une diminution de la densité (Turchin, 1995). Quand la densité devient faible, la compétition pour les ressources limitées diminue et le taux de croissance augmente.

Cette affirmation simple est rapidement complexifiée si l'on considère que tous les individus ne sont pas équivalents ; trente gros individus en pleine santé dans la fleur de l'âge n'équivalent pas à trente petits individus sénescents en mauvaise condition. Les causes des différences entre individus et les conséquences de ces différences sont d'une grande importance pour une bonne compréhension de la dynamique de population et pour une prédiction fiable des fluctuations en tailles de population. Les individus composant une population peuvent différer de plusieurs façons : en génotype, en phénotype ou en valeurs adaptatives. Ces différences peuvent avoir plusieurs causes telles que les conditions environnementales présentes, les conditions environnementales passées, ou bien des changements évolutifs. Les différences entre individus ne sont pas sans conséquence. Le phénotype d'un individu détermine sa capacité à survivre et se reproduire ; la composition d'une population déterminera donc sa dynamique. Tout comme l'intégration de la densité dépendance (Malthus, 1798) puis de la démographie (Leslie, 1945), l'intégration des différences interindividuelles à la dynamique de population améliorera grandement notre compréhension des fluctuations en densité en nature.

1.1 La dynamique de population

Déterminer les facteurs régulant les fluctuations en taille de population est à la base de la dynamique de population. Il est bien entendu nécessaire de quantifier ces fluctuations pour les étudier. Le taux de croissance décrit la croissance *per capita* d'une population, soit le facteur par lequel la taille de la population augmente chaque année (Stevens, 2009). Il est de façon générale défini comme $\lambda = N_{t+1}/N_t$, où N_t est la taille de population à un temps t (Sibly et Hone, 2002). Dans les analyses matricielles de dynamique de population, λ est aussi utilisé pour faire référence au taux de croissance asymptotique qui est la valeur propre dominante des éléments d'une matrice de Leslie (Caswell, 2001). Cette utilisation double du λ peut se comprendre si l'on considère que dans une population structurée, $\lambda = N_{t+1}/N_t$ quand la structure d'âge a atteint son état stable. Les valeurs de λ varient autour de 1 pouvant aller de 0 à λ_{max}. Quand $\lambda = 1$, la population est stable. Quand $\lambda < 1$, la taille de la population diminue alors que quand $\lambda > 1$, elle augmente.

Le plus simple modèle mathématique de dynamique de population est le modèle de croissance exponentielle. Selon ce modèle bien simple, $N_{t+1} = \lambda N_t$. On peut constater qu'il s'agit en fait d'un simple remodelage de la définition de λ. Ainsi, ce modèle considère un taux de croissance constant, indépendant de la densité. Étant donné le taux de croissance constant, le changement en taille de population (δN) augmente de façon linéaire. Ceci mène à un changement exponentiel de la taille de population au cours du temps (Figure 1.1) qui mènerait éventuellement à une population infinie. Euler (1748) lui-même avait noté cette faiblesse.

Suite aux observations faites par Malthus au sujet du modèle de croissance exponentielle, Verhulst, un mathématicien belge, développa le modèle logistique qui est encore largement utilisé. Selon ce modèle, la croissance de la population est limitée par l'environnement. Au fur et à mesure que la population augmente, sa croissance diminue et la population se stabilise à un certain

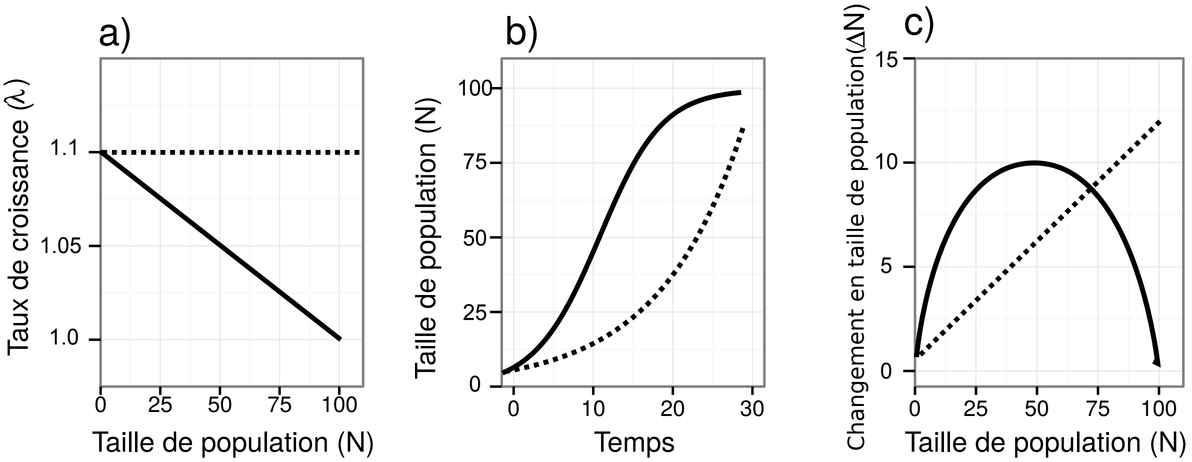

Figure 1.1 Différentes simulations du modèle exponentiel et logistique : a) les taux de croissance utilisés, b) la taille de population en fonction du temps, c) le changement en taille de la population en fonction de la densité. Les courbes représentent le modèle exponentiel (ligne pointillée) et logistique (ligne pleine). La taille de population initiale est de 5 individus et la capacité de support (K) de 100.

niveau. Selon ce modèle : $N_{t+1} = N_t + (\lambda_{max} - 1)N_t \left(1 - \frac{N_t}{K}\right)$. Cette équation apporte une amélioration importante, celle de la capacité de support du milieu (K), qui est un paramètre extrêmement utilisé en dynamique de population. Elle est malheureusement difficile à estimer et variable en nature. Ce modèle mène à la classique courbe de croissance en S (Figure 1.1b). Une caractéristique du modèle logistique qui est immédiatement apparente est la relation linéaire négative entre le taux de croissance et la densité (Figure 1.1a). Cette relation de densité dépendance est un concept clé de la dynamique de population. De multiples interactions sociales ou trophiques dépendent du nombre ou de la densité d'individus et influencent les taux de reproduction et de survie, menant à des changements du taux de croissance de la population. Il y a, par exemple, la compétition pour les ressources. Les ressources étant limitées, quand la densité augmente, les ressources s'en trouvent divisées parmi un plus grand nombre d'individus. La compétition pour ces ressources augmente, les taux de survie et de reproduction diminuent ; il s'ensuit une diminution du taux de croissance de la population. Bien que le modèle logistique suppose un déclin linéaire du taux de croissance avec la densité, des modèles plus complexes existent et utilisent des relations non linéaires. Par exemple, certains modèles considèrent que le taux de croissance peut être positivement associé à la densité quand celle-ci est faible. On parle alors d'effet Allee (Courchamp et al., 1999 ; Stephens et al., 1999 ; Courchamp et al., 2008).

1.2 L’hétérogénéité interindividuelle

Les modèles de dynamique de population discutés jusqu’à présent considèrent que tous les individus sont identiques. Il s’agit bien sûr d’une simplification extrême. Une réalisation récente de l’importance de cette hétérogénéité individuelle met en doute l’utilisation simpliste de variables moyennes populationnelles (Bjørnstad et al., 1994 ; De Roos et Persson, 2005 ; Benton et al., 2006). Les populations peuvent être structurées de plusieurs façons. La structure la plus étudiée est celle de l’âge. Effectivement, les individus de différentes classes d’âge et de sexe auront des contributions différentes au maintien de la population (Caswell, 2001). Il est cependant évident que d’autres sources de différences entre individus existent ; nous sommes tous uniques aussi bien dans nos comportements que dans nos traits.

Les individus composant une population peuvent également différer en phénotype. Une importante source de différences phénotypiques découle des différences génétiques (Postma, 2014). Le génotype n’est cependant pas la seule source de différences phénotypiques ; la plasticité joue également un rôle important. La plasticité permet à un génotype de produire plusieurs phénotypes en réponse aux variations environnementales (Forsman, 2015). La variation plastique en trait est ainsi probablement toute aussi importante pour la dynamique de population que la variation génétique (Hendry, 2016b).

Dans certains cas, les changements induits par l’environnement peuvent rester présents pour de longues périodes. Les conditions environnementales peuvent donc induire des changements phénotypiques à long terme (Smith-Gill, 1983 ; Stearns, 1989 ; Forsman, 2015). Ceci peut mener à une autre source de variation interindividuelle ayant un fort impact sur la dynamique de population : les effets cohorte (Albon et al., 1987). Les individus en bas âge sont particulièrement sensibles aux variations environnementales puisqu’ils sont en plein développement (Madsen et Shine, 2000 ; Metcalfe et Monaghan, 2001 ; Bateson, 2001 ; Lindström, 1999). L’environnement une année donnée pourrait donc avoir un fort impact à long terme sur le phénotype de toute une cohorte d’individus, menant à des délais dans la réponse de la population aux variations environnementales (Beckerman et al., 2002).

1.2.1 La démographie

La démographie est l'étude des taux de survie et des taux de fécondité âge- spécifiques et leur relation avec le taux de croissance de la population. On étudie alors comment des changements dans les différents taux démographiques vont influencer le taux de croissance et la structure d'âge quand la population aura atteint un état stable. Prendre en compte cette structure est important, car des taux de survie et de mortalité âge-spécifiques sont communs. Par exemple, chez le mouflon d'Amérique, la reproduction dépend en partie de l'âge (Martin et Festa-Bianchet, 2011) et la survie dépend aussi bien du sexe que de l'âge (Jorgenson et Festa-Bianchet, 1997). Un outil très puissant souvent utilisé dans les études démographiques est l'analyse matricielle (Caswell, 2001). Ces analyses permettent de déterminer le taux de croissance asymptotique, c'est-à-dire quand la structure d'âge sera stable. Les modèles matriciels permettent aussi de quantifier l'élasticité et la sensitivité des différents paramètres démographiques, ce qui permet de savoir quels paramètres sont les plus importants dans la détermination du taux de croissance de la population. Une des faiblesses de cette approche est qu'elle est en général utilisée de façon densité indépendante. Or, chez les moutons de Soay (*Ovis aries*), la dynamique de la population est déterminée par l'interaction entre des phénomènes de densité dépendance, la structure de la population et le climat (Coulson et al., 2001). Ceci démontre clairement que la dynamique de population est complexe en nature et que de simples modèles de séries temporelles ne suffisent pas pour une prédiction fiable des futures tailles de population. Des estimations d'élasticité pour des modèles densité dépendants n'ont été développées que récemment et sont mathématiquement très complexes (Caswell, 2009). Une autre faiblesse des modèles matriciels est qu'ils supposent que tous les individus à l'intérieur d'une classe d'âge sont identiques et suivront la même trajectoire d'histoire de vie (Vindenes et Langangen, 2015). Or, les individus composant une population peuvent se distinguer les uns des autres par plus qu'une simple différence d'âge.

1.2.2 Les différences phénotypiques

La variation phénotypique entre individus a été au cœur de l'écologie évolutive depuis ses tout débuts. C'est cette variation qui permet l'évolution par sélection naturelle. Certains individus ont un phénotype qui leur confère un avantage par rapport aux autres en termes de valeur adaptative (une meilleure survie ou une meilleure reproduction par exemple). Cette variation est à la base de l'écologie évolutive (Endler, 1986). L'importance des variations entre individus pour la dynamique de population n'a cependant été pleinement réalisée que récemment (van Noordwijk et de Jong, 1986 ; Wilson et Nussey, 2010). La survie et la reproduction sont d'importantes composantes de la valeur adaptative, mais ce sont également d'importants taux démographiques (Caswell, 2001 ; Coulson et al., 2005). De la variation en phénotype des individus présents dans une population résultera donc vraisemblablement en une variation de la survie et reproduction moyenne de la population et donc en un changement en taux de croissance. Par exemple, la variation en masse des moutons de Soay explique entre 3,9% et 9,2% de la variation en taux de croissance selon la qualité de l'environnement (Pelletier et al., 2007a). Chez la morue de l'Atlantique (*Gadus morhua*), la diminution de la taille asymptotique modifie significativement le taux net de reproduction et le taux de croissance *per capita* (Eikeset et al., 2016). Bien que les différences en traits morphologiques soient les plus visibles et les plus facilement mesurables, les différences phénotypiques sont aussi présentes au niveau physiologique (Becks et al., 2012), au niveau comportemental (Duckworth et Aguillon, 2015) ou au niveau des traits d'histoire de vie (Brodersen et al., 2015 ; Turcotte et al., 2011). Ces différences en trait influencent aussi la survie et la reproduction et pourraient donc aussi avoir d'importants impacts sur le taux de croissance. Par exemple, des individus pourraient différer par rapport à leur propension à se disperser, ce qui pourrait influencer non seulement la dynamique de la population, mais aussi sa distribution spatiale (Lomnicki, 1978 ; Fronhofer et Altermatt, 2015).

1.2.3 Les différences génotypiques

Comme mentionné précédemment, les différences en trait peuvent avoir une base génétique. Ces différences en génotypes peuvent être le résultat de mutations, le résultat de processus aléatoires comme la dérive génétique ou le résultat de la sélection naturelle. La réponse à la sélection est particulièrement bien illustrée mathématiquement par trois équations : l'équation des éleveurs (Lush, 1937 ; Morrissey et al., 2010), l'équation de Price (Price, 1970) et le second théorème de Robertson-Price (Price, 1970 ; Stinchcombe et al., 2014). Ces équations décrivent comment la moyenne d'un trait (z) peut changer dans une population d'une génération à une autre. L'équation des éleveurs s'écrit : $\Delta\bar{z} = h^2 \times S$, où h^2 est l'héritabilité et S est le différentiel de sélection. Un des défauts de cette équation, même sous sa forme multivariée, est qu'elle suppose que tous les traits corrélés au trait sous sélection ont été mesurés et incorporés dans l'analyse. Pour ce qui est de l'équation de Price, l'équation peut s'écrire comme suit :

$\Delta\bar{z} = \mathrm{cov}(w, z) + \mathrm{E}(w\overline{\Delta z})$, où w est la valeur adaptative relative. Cette équation apporte un avantage important : elle sépare le changement de trait en 2 composantes. Le premier terme représente la sélection ou la covariance entre le trait et le succès relatif. Le deuxième terme représente la transmission de ce trait, soit comment les descendants diffèrent du parent. Si le trait était héritable à 100%, ce terme serait zéro (Gardner, 2008). Ce second terme inclut tout facteur autre que la sélection qui contribue à un changement du phénotype moyen entre les parents et les descendants (Frank, 2012). Il peut donc s'agir d'effets environnementaux, d'interaction génotype-environnement, d'épistasie, d'effets de la croissance ou de changement de la structure démographique de la population.

Une approche alternative pour prédire la réponse évolutive est d'utiliser le second théorème de la sélection de Robertson-Price. Selon celui-ci, le changement en trait peut être prédit à partir de la covariance additive génétique entre le trait et la valeur adaptative : $\Delta\bar{z} = \mathrm{cov}_a(w, z)$. Cette équation a certains avantages, car elle n'est pas limitée aux cas où tous les traits sous sélection sont connus comme pour l'équation des éleveurs. Cependant, le second théorème ne permet pas de distinguer les effets de la sélection directe et indirecte, ce qui est fort important si l'on est intéressé par les causes du changement évolutif en trait.

Les changements génotypiques n'entraînent pas toujours des changements phénotypiques. C'est le cas de la variation à contre-gradient, par exemple, où la variation environnementale produit un changement plastique s'opposant à la variation génétique (Conover et Schultz, 1995). Similairement, un changement évolutif pourrait permettre de maintenir un phénotype optimal stable malgré la détérioration de l'environnement (Kinnison et al., 2015). Par example, un changement évolutif permet aux rotifères (*Brachionus calyciflorus*) de maintenir une stratégie d'histoire de vie stable malgré une diminution de la qualité de l'alimentation (Declerck et al., 2015). Dans le contexte actuel où la détérioration de l'habitat par des perturbations anthropiques est un problème grandissant, ce genre de changement évolutif pourrait permettre le maintien de populations sauvages (Carlson et al., 2014). Ainsi, certaines populations de vers *Limnodrilus* ont développées une résistance à des concentrations de Cadmium élevées dues à l'exploitation minière, leurs permettant de maintenir une population viable, ce qui est impossible sans changements évolutifs (Klerks et Levintgon, 1989). Certains chercheurs suggèrent ainsi que les conséquences des changements évolutifs pourraient être les plus importantes quand elles sont le moins apparentes (Kinnison et al., 2015).

1.3 Dynamiques éco-évolutives

1.3.1 Évolution contemporaine

Il est de plus en plus accepté que des changements génétiques peuvent se produire sur une relativement courte période de temps (Reznick et Ghalambor, 2001). Des exemples d'évolution rapide ont été rapportés dans une large gamme d'organismes. Chez les plantes, le millepertuis perforé (*Hypericum perforatum*) semble avoir une évolution rapide aux conditions environnementales des milieux qu'il envahit (Maron et al., 2004). Chez les poissons, le saumon rouge (*Oncorhynchus nerka*) a montré une évolution de barrière reproductive après moins de 13 générations (Hendry et al., 2000). Chez les oiseaux, la morphologie des becs des pinsons de Darwin (*Geospiza fortis*) répond rapidement aux fluctuations de ressources liées aux variations climatiques (Grant et Grant, 2002). Des cas d'évolution contemporaine ont même été observés chez les humains, où l'âge à la première reproduction a diminué (Milot et al., 2011). Plusieurs études ont également montré une diminution de la taille et de l'âge de maturation chez plusieurs espèces de poissons (Heino et al., 2015). De tels exemples d'évolution rapide sont particulièrement intéressants dans le contexte des changements et des pressions anthropiques. En effet, les pressions anthropiques sont une source importante de changement évolutif. Une méta-analyse incluant plus de 1600 changements phénotypiques à travers le globe a montré que les taux de changement phénotypique sont plus élevés dans les systèmes montrant des signes d'urbanisation que dans les systèmes naturels ou sans signe d'urbanisation (Alberti et al., 2017).

Les causes anthropiques de changements évolutifs ne sont pas limitées à l'urbanisation (Figure 1.2). Les changements climatiques liés au réchauffement ont aussi attiré, avec raison, l'attention de plusieurs écologistes. Par exemple, une étude expérimentale a montré que les daphnies (*Daphnia magna*) pouvaient montrer une réponse évolutive à un réchauffement de l'eau en trois mois (Van Doorslaer et al., 2009). La chasse est également une source de pression de sélection anthropique pouvant mener à un changement évolutif. La chasse au trophée a été impliquée comme cause d'une diminution évolutive de la taille des cornes chez le mouflon (Coltman et al., 2003 ; Douhard et al., 2016b ; Festa-Bianchet et al., 2014). Les évidences de réponses évolutives chez le mouflon d'Amérique face à la chasse au trophée reste cependant contestées dû à des critiques statistiques de l'article de Coltman et al. (2003) (Postma, 2006 ; Hadfield et al., 2010). Tous ces exemples montrent que l'évolution peut se produire sur une échelle temporelle courte. Ainsi, une interaction entre des changements évolutifs et des processus écologiques est possible (Thompson, 1998 ; Pelletier et al., 2009 ; Schoener, 2011).

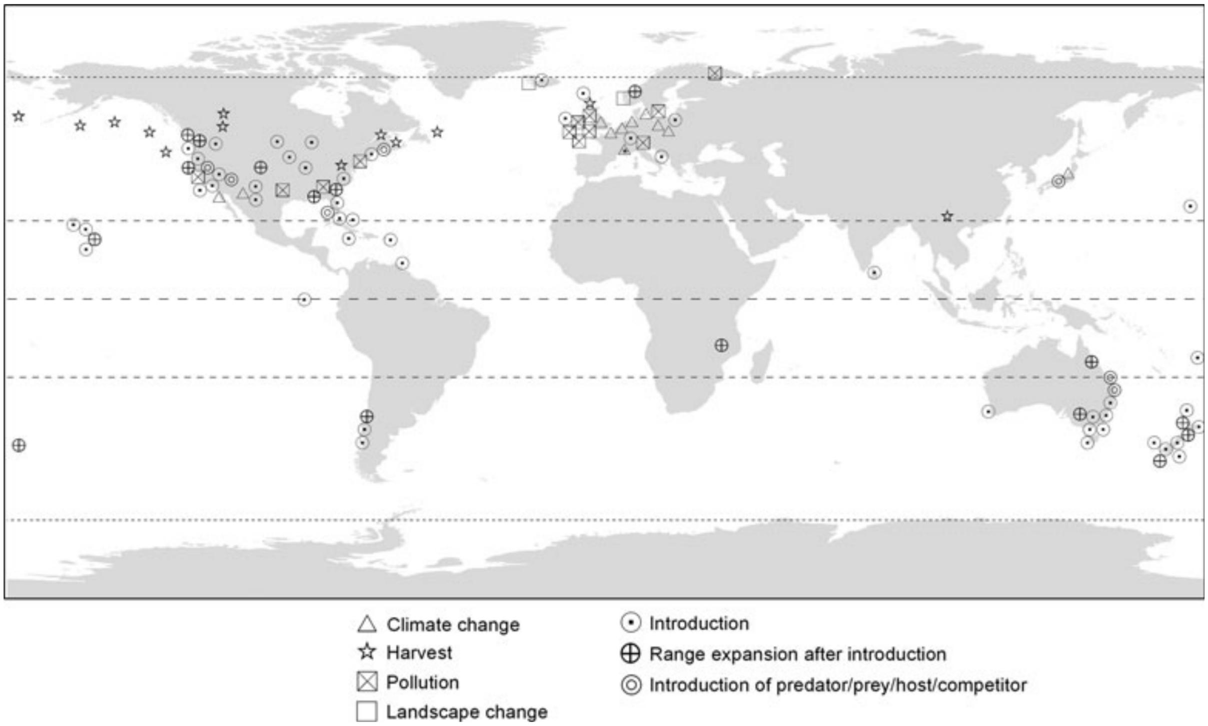

Figure 1.2 Carte du monde illustrant l'emplacement d'études supportant la présence de changements phénotypiques rapides causés par des pressions anthropiques. Le type de pression anthropique est illustré par le type de point (figure tirée de Palkovacs et al. (2012)).

1.3.2 Conséquences des changements évolutifs

Une conséquence de la courte échelle temporelle des changements évolutifs contemporains est qu'il devient possible que les changements phénotypiques en résultant affectent des processus écologiques, menant à des dynamiques éco-évolutives. De plus, si les processus affectés à leur tour influencent les pressions de sélection, il peut en émerger des boucles de rétroaction éco-évolutive. Un cas exemplaire est celui des lézards à flancs maculés (*Uta stansburiana* ; Sinervo et al., 2000). À la source de cette dynamique éco-évolutive se trouve une pression de sélection densité dépendante. En effet, il existe deux stratégies d'histoire de vie chez cette espèce, une de type r qui produit beaucoup de petits œufs et une de type k qui produit peu de gros œufs. À faible densité, les types r sont avantagés, menant à une augmentation de la densité ; les gros œufs des individus de type k sont alors avantagés, mais étant donné leur faible fertilité, la densité diminue, ramenant l'avantage aux types r. Ainsi, les oscillations du système sont dues à des boucles de rétroaction éco-évolutive (Sinervo et al., 2000). Strauss (2013) catégorise les boucles de rétroaction éco-évolutive en trois catégories : 1) les changements rapides de phénotypes peuvent changer les pressions sélectives locales, menant à des états stables alternatifs de communautés écologiques ; 2) des cycles éco-évolutifs peuvent émerger comme illustrés dans l'exemple précédent ; 3) des dynamiques éco-évolutives cryptiques peuvent contribuer à la stabilité d'un écosystème. Ainsi, les voies par lesquelles l'évolution peut affecter des processus écologiques tels que la dynamique de population sont multiples.

Une meilleure compréhension des dynamiques éco-évolutives mènera donc à une meilleure compréhension de la dynamique de population. Un exemple de l'importance de l'effet de l'évolution sur la dynamique de population est l'étude par Turcotte et al. (2011). Dans cette étude, il a été montré qu'une population d'aphidés (*Myzus persicae*) évoluant peut croître plus rapidement et atteindre des densités plus élevées que des populations n'évoluant pas. Yoshida et al. (2003) ont clairement illustré l'impact de l'évolution dans un système à deux espèces constitué d'algues vertes (*Chlorella vulgaris*), la proie, et de rotifères, le prédateur. Dans des cultures d'algues multiclonales où l'évolution était possible, la dynamique des populations était cyclique avec de longs cycles déphasés. Cependant, dans les cultures monoclonales où l'évolution des proies est impossible dû à l'absence de variation génétique, les cycles étaient courts avec un plus petit délai entre les cycles des proies et des prédateurs. Les pressions de sélection anthropiques peuvent aussi causer des changements dans la dynamique de population. Une étude de modélisation a observé que sous pression de chasse sélective, tous les critères phénotypiques de sélection pouvaient produire des changements évolutifs et des changements dans la dynamique de la population (Ratner et Lande, 2001). Ceci est important, car il en découle que les effets de la chasse au trophée peuvent être doubles ; agissant de façon directe par le retrait des individus chassés, mais aussi indirectement via des impacts éco-évolutifs.

Une question clé découlant de cette observation de l'impact de l'évolution sur des processus écologiques est donc la suivante : Quelle est l'importance relative des changements évolutifs, comparée à celle des changements écologiques, sur la dynamique de population (Schoener, 2011) ? Hairston et al. (2005) ont proposé un cadre conceptuel pour répondre à cette question. En utilisant cette méthode, il a été montré que chez les ongulés, un changement phénotypique, comme la masse à la naissance, pouvait avoir autant d'effet sur le taux de croissance de la population qu'un changement climatique (Ezard et al., 2009). Un inconvénient majeur de cette méthode est que tout changement en trait observé était considéré comme un changement évolutif. Cette supposition n'est probablement pas réaliste. En effet, une étude suggère que la plasticité en masse est importante chez le mouflon d'Amérique (Pelletier et al., 2007b). Ellner et al. (2011) ont donc développé une méthode plus efficace pour quantifier l'importance de changements évolutifs et écologiques sur la dynamique de population qui permet de partitionner l'effet de changements héritables et non héritables. Cette nouvelle méthode permettra donc d'avancer notre compréhension de la dynamique éco-évolutive, ce qui pourrait permettre de mieux comprendre les fluctuations en taille des populations susceptibles d'être soumises à des pressions sélectives (donc toutes populations en nature). La chasse aux trophées du mouflon d'Amérique cause une forte pression de sélection sur la taille des cornes qui pourrait engendrer une réponse évolutive indirecte de la masse des femelles due à la forte corrélation génétique entre les deux traits (corrélation de 0,43 , Poissant et al. 2012). Un changement évolutif en masse aurait d'importantes conséquences pour la dynamique de population du mouflon étant donné l'importance de ce trait. Des simulations à bases individuelles suggèrent que de tels effets indésirables de l'évolution due à l'exploitation pourraient être présents chez les morues où la pêche a potentiellement causé une diminution de la taille et de l'âge de la maturation et aurait des impacts majeurs sur la dynamique de population (Kuparinen et al., 2014 ; Dunlop et al., 2015 ; Eikeset et al., 2016).

1.4 Les effets cohorte

Il y a présence d'effets cohorte quand des conditions communes subies par un groupe d'individus à un temps *t* génèrent des différences dans leur future performance qui les distinguent des autres groupes (Beckerman et al., 2002). Ces différences individuelles peuvent jouer un rôle important dans la dynamique d'une population (Benton et al., 2006). Les effets cohorte peuvent induire un délai dans la réponse de la population à la densité et déstabiliser sa dynamique en augmentant la variabilité en taux de croissance (Lindström et Kokko, 2002). Un modèle à base individuelle basé sur un système d'acariens (*Sancassania berlesei*) a suggéré que la variation individuelle et sa provenance pouvaient influencer la dynamique à long et à court terme avec une ampleur similaire à celle d'une réduction de moitié des ressources alimentaires (Benton, 2012). Les effets cohorte ont été documentés dans plusieurs taxons incluant les reptiles (Marquis et al., 2008 ; Baron et al., 2010 ; Le Galliard et al., 2010), les oiseaux (Lindström, 1999 ;

Reid et al., 2003), les rongeurs (Descamps et al., 2008), les ongulés (Hamel et al., 2009a) et les humains (Rickard et al., 2010).

L'impact des effets cohorte sur la dynamique de population est considérable. Leslie (1959) a montré par modélisation que si on assume que la fertilité de chaque groupe d'âge dépend non seulement de l'état actuel de la population, mais aussi de l'état de la population durant lequel les individus qui forment les groupes d'âge sont nés (des effets cohorte), une population vivant dans des conditions constantes optimales devrait osciller plus longtemps pour éventuellement atteindre un point d'équilibre. Dans une autre étude de modélisation, Lindström et Kokko (2002) ont montré que les effets cohorte avaient tendance à modifier la forme de la densité dépendance, la rendant moins abrupte. De plus, les effets cohorte peuvent déstabiliser la dynamique d'une population. Dans le cas où la dynamique de la population était stable, ajouter des effets cohorte avait tendance à la déstabiliser alors que l'effet opposé arrivait quand la dynamique était instable (Lindström et Kokko, 2002). Suite à cette étude, Coulson et al. (2004) ont montré empiriquement chez le cerf rouge (*Cervus alphus*) l'importance des effets cohorte sur la dynamique de la population. En utilisant des matrices de transitions démographiques annuelles, ils ont montré que l'élasticité et la sensitivité totales des différentes cohortes variaient énormément, pouvant jusqu'à doubler.

Les effets cohorte sont le plus communément causés par des facteurs qui affectent la population entière au début de leur vie. Ainsi, les conditions environnementales peuvent résulter en effets cohorte. Chez les grands mammifères, entre le tiers et la moitié de la variation en qualité individuelle peut être expliquée par la variation des conditions environnementales en début de vie (Hamel et al., 2009a). Chez le mouton de Soay, l'indice d'oscillation nord- atlantique (NAO) durant l'hiver peut causer des variations significatives entre cohortes par rapport à certains traits d'histoire de vie comme la masse à la naissance, la date de mise bas, la probabilité de produire des jumeaux ainsi que l'âge de maturation (Forchhammer et al., 2001). Chez le cerf rouge, les précipitations à la naissance interagissent avec la présence de fourrage supplémentaire, les précipitations abondantes menant à une masse plus élevée pour les individus ayant accès à du fourrage supplémentaire (Rodriguez-Hidalgo et al., 2010). Bien que tous les exemples mentionnés précédemment considèrent les conditions en début de vie, les effets cohorte peuvent aussi être causés par les conditions prénatales. Par exemple, les moutons de Soay qui subissent des valeurs de NAO élevées *in utero* , indiquant un environnement difficile, ont un retard de leur première reproduction (Forchhammer et al., 2001).

Un autre facteur environnemental qui est commun à tous les individus et donc qui a le potentiel de créer des effets cohorte est la densité. Par exemple, une forte densité à la naissance retarde l'âge à la première reproduction chez le mouton de Soay (Forchhammer et al., 2001) et réduit la masse corporelle adulte chez le cerf rouge (Mysterud et al., 2002) et le chevreuil (*Capreolus capreolus* ; Pettorelli et al., 2002). L'impact de la densité agit probablement à travers un accès réduit aux ressources durant le développement, qui est une période critique. Dans une étude sur les cerfs rouges de la péninsule ibérique, des effets cohorte sur la masse adulte et la probabilité de gestation étaient causés par la densité à la naissance, mais ces effets n'étaient présents que dans la population qui ne recevait pas de supplément alimentaire et qui était donc plus limitée par les ressources (Rodriguez-Hidalgo et al., 2010).

Deux types d'effets cohorte peuvent être distingués : l'effet numérique et l'effet de qualité (Gaillard et al., 2003). Ces deux types d'effets cohorte considèrent des échelles temporelles différentes. Les effets cohorte numériques sont immédiats, ou à court terme, et résultent en variation du recrutement. Ainsi, les conditions environnementales et maternelles durant les stades juvéniles peuvent influencer la proportion des jeunes qui survivront à l'hiver. Par exemple, chez le mouflon d'Amérique, la combinaison de température au printemps précédent, de précipitations au printemps précédent et de la densité explique 84% de la variation en survie hivernale des agneaux (Portier et al., 1998). Les effets cohorte de qualité sont très intéressants, car ils peuvent avoir des répercussions à long terme. Des études suggèrent que les conditions à la naissance peuvent avoir des conséquences retardées sur des composantes de valeurs adaptatives (Lindström, 1999).

1.4.1 L'effet cuillère d'argent

Un effet négatif des conditions environnementales à la naissance sur les traits d'histoire de vie est appelé effet cuillère d'argent (Grafen, 1988). Les effets cuillère d'argent permettent à certaines cohortes d'atteindre une performance supérieure et ainsi à avoir un succès reproducteur et une survie constamment meilleure que celle des autres cohortes (Figure 1.3b). Des études ont montré que les conditions à la naissance pouvaient apporter des avantages permanents aux individus. Par exemple, les conditions durant l'ontogénie des diamants mandarins (*Taeniopygia guttata*) et des mésanges charbonnières (*Parus major*) affectent de façon permanente la taille de couvée (Haywood et Perrins, 1992). Chez l'écureuil roux (*Sciurus vulgaris*), une haute densité à la naissance diminue significativement le taux de survie des adultes (Descamps et al., 2008). De bonnes conditions à la naissance augmentent significativement le succès reproducteur à vie des craves à bec rouge (*Pyrrhocorax pyrrhocorax ;* Reid et al., 2003). Les conditions à la naissance n'influencent pas seulement la survie et la reproduction des individus d'une cohorte, mais peuvent aussi influencer leurs phénotypes. Par exemple, un effet des conditions à la naissance, soit la densité et la température en mai, sur la croissance précoce et tardive a été observé chez les chevreuils femelles (Douhard et al., 2013). Bien que les différences en masse dues aux effets cohorte semblent s'estomper avec le temps chez le mouflon d'Amérique (Hamel et al., 2016), la croissance compensatoire nécessaire peut engendrer des coûts à long terme comme, par example, une diminution du succès reproducteur (Marcil-Ferland et al., 2013). Ainsi, les conditions à la naissance pourraient avoir un effet sur la performance adulte malgré une absence de différence en condition physique (Metcalfe et Monaghan, 2001).

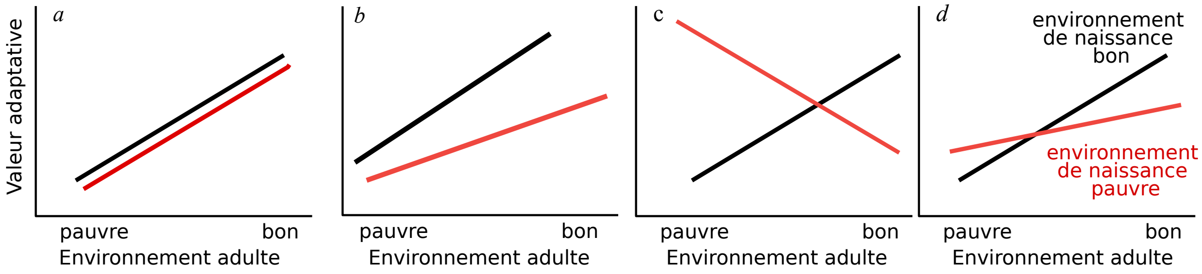

Figure 1.3 Figure théorique des interactions possibles entre les conditions à la naissance, les conditions à l'âge adulte et la valeur adaptative. a) Aucun effet de la cohorte ; la valeur adaptative dépend des conditions à l'âge adulte uniquement. b) Effet cuillère d'argent ; les individus nés dans un bon environnement sont favorisés tout au long de leur vie. c) Plasticité développementale adaptative-prédictive ; aussi bien pour les individus nés dans de bonnes ou mauvaises conditions, la valeur adaptative est maximale quand l'environnement adulte est de qualité équivalente à l'environnement de naissance. d) Plasticité développementale avec un avantage pour tous les individus d'être dans un bon environnement à l'âge adulte (Monaghan, 2008). Les lignes rouges représentent les individus nés dans un environnement de mauvaise qualité alors que les lignes noires représentent ceux nés dans un environnement de bonne qualité.

La théorie de la cuillère d'argent au sens strict prédit un avantage aux individus nés dans des conditions favorables, peu importe leur environnement adulte (Monaghan, 2008). Cependant, l'environnement adulte pourrait aussi, dans certains cas, modérer ces avantages ou bien les masquer. Les avantages engendrés par un environnement de naissance favorable seraient alors contexte dépendants (Engqvist et Reinhold, 2016). Par exemple, un environnement adulte très favorable pourrait masquer les différences entre cohortes, car tous les individus seraient capables d'atteindre la performance maximale possible (des conditions bénéfiques saturées). À l'inverse, un environnement adulte si difficile que tous les individus meurent masquerait les différences entre cohortes. Un exemple d'effet cohorte contexte dépendant a été observé chez les grenouilles *Crinia georgiana*, où la taille des œufs (un environnement à la naissance indicatif d'un effet cuillère d'argent) est beaucoup plus important pour la survie si les ressources alimentaires sont rares plus tard dans le cycle de vies (Dziminski et Roberts, 2006).

1.4.2 La plasticité développementale adaptative-prédictive

L'effet cuillère d'argent n'est pas le seul type d'effet cohorte de qualité possible. Un type alternatif est la plasticité développementale adaptative- prédictive. Selon ce modèle, la performance d'un individu n'est pas seulement influencée par les conditions à l'âge adulte et tôt durant la vie, mais aussi par l'interaction entre les deux (Nettle et Bateson, 2015). Ces facteurs agissant sur la plasticité durant la période de développement mènent à des changements physiologiques, morphologiques ou en traits d'histoire de vie de façon à ce que l'individu puisse faire face efficacement aux conditions de stress auxquelles il sera soumis (Figure 1.4). Ainsi, un individu né dans des conditions de stress se développera pour faire face de façon plus performante à ces conditions de stress au stade adulte qu'un individu ayant eu des conditions favorables durant son développement (revue dans Monaghan, 2008).

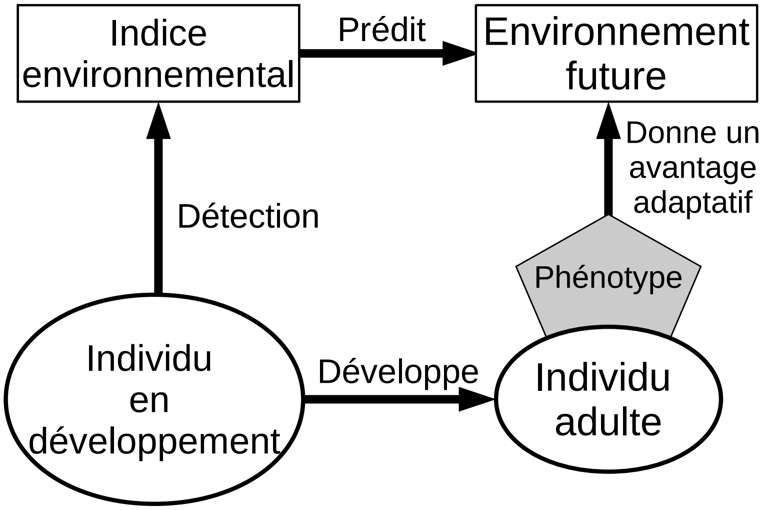

Figure 1.4 Figure théorique représentant les mécanismes menant à de la plasticité développementale adaptative-prédictive (Nettle et Bateson, 2015).

Ce modèle théorique a initialement été développé chez les humains pour expliquer pourquoi l'effet négatif des mauvaises conditions de développement était plus marqué quand l'environnement adulte était très riche en ressources (Gluckman et al., 2005). Elle a attiré un intérêt grandissant en médecine pour expliquer certaines maladies apparaissant principalement dans des conditions favorables. Ainsi, selon cette théorie, les individus ayant eu de mauvaises conditions durant le développement, mais vivant dans des conditions adultes favorables devraient subir un coût, car il y a une discordance entre l'environnement de naissance et l'environnement adulte. Statistiquement, cela résulte en une interaction entre les conditions à la naissance et les conditions à l'âge adulte où la valeur adaptative est supérieure quand les deux sont similaires (Figure 1.3*c*). Cependant, peu d'études ont testé cette hypothèse en nature. Une étude sur le serpent-tigre (*Notechis scutatus*) a montré que les conditions durant le développement jouaient un rôle important dans la détermination de la taille de la mâchoire de telle sorte que celle-ci était adaptée à la taille des proies dans l'environnement (Aubret et al., 2004). Chez le papillon *Bicyclus anynana*, les individus subissant un stress durant le développement avaient une longévité supérieure aux individus ne subissant pas de stress s'ils étaient soumis à un envol forcé de 5 minutes, suggérant un développement favorisant la dispersion (Saastamoinen et al., 2010). La plasticité développementale adaptative-prédictive a cependant plusieurs faiblesses. La principale est le manque de corrélation entre l'environnement adulte et l'environnement de naissance dans la plupart des espèces longévives (Wells, 2007b). Sans cette corrélation, un individu en développement ne peut pas développer un phénotype optimal de façon fiable. Ces faiblesses théoriques pourraient expliquer pourquoi aucun effet de la plasticité développementale adaptative-prédictive n'a été détecté dans une population de cerfs rouges de l'île de Rum en Écosse (Nussey et al., 2007) ou de primates au Kenya (Lea et al., 2015).

Bien que l'existence des effets cohorte et leurs impacts sur la dynamique de population soient connus des écologistes, ils sont étonnamment peu étudiés, probablement dû à un manque de suivis individuels à long terme. Or, pour bien comprendre l'effet des conditions à la naissance, plusieurs cohortes doivent être suivies de la naissance à la mort. Les effets cohorte peuvent affecter différents traits d'histoire de vie (Lindström, 1999). Étant donné que des compromis entre traits d'histoire de vie sont couramment retrouvés en nature, des études considérant plusieurs traits d'histoire de vie sont nécessaires (Beckerman et al., 2003). De plus, un suivi à long terme couvrant l'entièreté de la vie est nécessaire, car les compromis peuvent se faire entre différents stades de vie (ou années de vie) de l'individu (van de Pol et al., 2006). Les études considérant plusieurs traits d'histoire de vie sur l'entièreté de la vie des individus sont pourtant rares (mais voir Hamel et al. (2009a) ; van de Pol et al. (2006)). Une meilleure compréhension des effets cohorte nécessite une analyse intégratrice de plusieurs traits d'histoire de vie sur un grand nombre de cohortes ayant subi une grande étendue de conditions à la naissance et à l'âge adulte.

1.5 Objectifs

L'objectif général de ma thèse est d'explorer les causes des différences entre individus ainsi que leurs conséquences. Je m'attarderai principalement à différents niveaux de différences : les différences génétiques, les différences dans les traits et les différences entre cohortes. Spécifiquement, les objectifs des différents chapitres de ma thèse étaient de :

1. Résumer l'état actuel des connaissances et des pratiques dans le domaine de la dynamique éco-évolutive.
2. Déterminer si la réponse évolutive face à la chasse sélective contribuait au déclin observé en taille de corne chez le mouflon d'Amérique ;
3. Quantifier l'importance relative des changements évolutifs et plastiques en masse sur la survie, la reproduction et le taux de croissance d'une population de mouflons d'Amérique ;
4. Quantifier l'importance des effets cohorte, déterminer leurs causes environnementales et tester pour la présence de réponse adaptative-prédictive ;
5. Explorer l'importance de différents mécanismes reliant la densité à la naissance et le succès reproducteur à vie.

Répondre à ces objectifs demande des données particulièrement rares. Seul un suivi à long terme individuel très détaillé comme celui des mouflons d'Amérique de Ram Mountain m'a permis un tel avancement. Les animaux de cette population sont marqués et suivis de la naissance à la mort depuis 1972. La généalogie de la population a été reconstruite. De plus, des mesures morphologiques sont prises annuellement. Ce trésor d'information a permis la combinaison d'analyses aussi bien génétiques que démographiques nécessaire pour atteindre les objectifs de cette thèse.

1.6 Méthodes

1.6.1 Espèce étudiée

La distribution du mouflon d'Amérique s'étend des prés de hautes altitudes des Rocheuses aux déserts de faible altitude du nord du Mexique. Il s'agit d'un ongulé aisément distinguable de l'autre espèce de mouflon des montagnes retrouvée au Canada (*O. dalli*) par sa couleur brune. *O. canadensis* est caractérisé par un large dimorphisme sexuel, les mâles ayant une plus grande masse et de larges cornes (Shackleton, 1985). Le mouflon d'Amérique a un système d'appariement polygyne où la masse et la taille des cornes sont des déterminants importants du succès reproducteur des mâles (Coltman et al., 2002). Les brebis ont leurs premières reproductions à 3 ans en moyenne, mais l'âge de la primiparité est significativement influencé par la masse à un an, la densité à la naissance ainsi que leurs interactions (Martin et Festa-Bianchet, 2012).Le succès reproducteur à vie des femelles varie entre 0 et 11 (moyenne$\pm$SD = 2,46$\pm$2.85), alors que celui des mâles varie de 0 à 21 (moyenne$\pm$SD = 0.95$\pm$2.45). La sénescence commence dès l'âge de 7 ans chez les deux sexes (Jorgenson et Festa-Bianchet, 1997), quoique certains individus de 14 et 19 ans ont été recensés chez les mâles et les femelles respectivement.

Les mouflons d'Amérique sont considérés comme des « capital breeder » ; c'est-à-dire qu'ils accumulent des réserves énergétiques, généralement sous forme de graisse, avant la reproduction et utilisent ces réserves pour la production de leurs descendants (Festa-Bianchet et al., 1998). Cette stratégie s'oppose à l'autre extrême du gradient, c'est-à-dire les « income breeder » qui utilisent directement l'énergie ingérée pour la production de leurs descendants (Stephens et al., 2009). Chez les « capital breeder », la masse et la condition, qui sont des indices des réserves énergétiques, ont souvent une grande importance pour la reproduction. Par exemple, la condition corporelle des brebis a un effet significatif sur le succès reproducteur, les brebis sevrant un jeune étant 1,5% plus lourdes que celles ne sevrant pas leur agneau (Festa-Bianchet, 1998). De plus, la masse en interaction avec la densité est un prédicteur significatif de la fertilité des brebis (Festa-Bianchet et al., 1998). Les brebis ayant une faible masse à 1 an ont tendance à retarder leurs premières reproductions sauf si la densité est assez élevée pour causer un délai en primiparité chez toutes les brebis (Martin et Festa-Bianchet, 2012).

La masse est également un important déterminant de la survie du mouflon d'Amérique. La masse influence la survie des agneaux, des juvéniles et des brebis, mais pas des béliers (Festa-

Bianchet et al., 1997). Ainsi, la masse influence le succès reproducteur à vie des brebis non pas via la fertilité, mais principalement via une plus grande longévité (Gaillard et al., 2000). La masse est également importante pour les mâles, même si aucun soin paternel aux jeunes n'est présent. En effet, la masse est un important déterminant du rang social et du succès reproducteur chez le bélier (Pelletier et Festa-Bianchet, 2006). Un changement en masse a donc le potentiel d'avoir une grande importance pour une population. L'inclusion de ce trait dans des analyses de dynamique éco-évolutive est donc judicieuse.

La densité est un autre déterminant important de la reproduction et de la survie. La densité, en interaction avec la masse, influence la reproduction (Festa-Bianchet et al., 1998). La densité influence aussi la survie ; la probabilité de survie des agneaux jusqu'à un an dépend de leur masse, mais aussi de la densité (Festa-Bianchet et al., 1997). Jorgenson et Festa-Bianchet (1997) ont montré que la densité semblait également affecter la survie des femelles d'un an. Pour les femelles de 8 ans et plus, la densité peut influencer la survie quand l'on contrôle pour le statut reproducteur de l'année précédente (Festa-Bianchet et al., 1998).

1.6.2 Aire d'étude

La population à l'étude est située à Ram Moutain, Alberta, Canada (52°N, 115°W, 1080 à 2170 m d'élévation). Ram Mountain est un massif situé à environ 30 kilomètres des Rocheuses canadiennes. L'émigration et l'immigration de cette population sont très basses à cause de son isolation des autres populations de mouflons d'Amérique par les forêts de conifères l'entourant et la rivière North Saskatchewan au Nord. L'habitat occupé par les mouflons couvre environ 38 km^2 de végétation alpine et subalpine.

Le suivi à long terme de cette population a débuté en 1971. Depuis, des captures sont effectuées annuellement durant la période estivale à l'aide d'une trappe de type « corral » appâtée avec du sel. La trappe est déclenchée d'une position horizontale à proximité. Tous les individus sont marqués avec un identifiant unique. Un collier de couleur avec un symbole unique est utilisé pour les femelles alors qu'une combinaison d'étiquettes de couleur fixées aux oreilles est utilisée pour les mâles. De 1972 et 2016, 568 femelles et 561 mâles ont été marqués. La probabilité de détection et de recapture est très élevée (mâles $> 95\%$, femelles $> 99\%$) (Bonenfant et al., 2009 ; Loison et al., 1999). La survie des individus est donc connue. Étant donné que les agneaux sont marqués individuellement l'été de leur naissance, l'âge des individus est connu. L'âge des individus n'ayant pas été capturés la première fois en temps qu'agneaux a été estimé par décompte des annuli sur les cornes. Ainsi, la taille et la structure d'âge de la population sont connues avec précision. Le statut reproducteur des brebis est déterminé par examination du pie et par l'observation des interactions brebis-agneaux. Le succès reproducteur des femelles est donc connu depuis 1975 et celui des mâles depuis 1988.

À chaque capture d'individu, des mesures morphologiques (masse et taille des cornes) sont prises. Les mouflons adultes sont recapturés à intervalle de 3 semaines alors que les agneaux sont recapturés à intervalle de 2 semaines. En moyenne, les agneaux, les femelles adultes et les mâles adultes sont capturés respectivement 2, 3,5 et 2,6 fois par année. Ces mesures répétées de masse sont utilisées pour déterminer la masse estimée au 5 juin et au 15 septembre à l'aide de la méthode proposée par Martin et Pelletier (2011).

La généalogie de la population a été reconstruite. Depuis le début de l'étude, les maternités sont assignées à l'aide d'observations comportementales d'interactions entre mère et agneaux. Depuis 1988, des échantillons de tissus sont prélevés sur tous les individus pour faire des assignations génétiques de paternité basée sur 26 loci microsatellite, nous permettant de reconstituer une généalogie où 863 maternités et 571 paternités ont été assignées (Coltman et al., 2005).

1.6.3 La chasse sélective

Le mouflon est très prisé pour ses grandes cornes. En Alberta, plus de 2000 licences sont vendues chaque année, avec un taux de succès d'environ 7%. Pour être chassé légalement, un mouflon doit être un mâle et avoir des cornes faisant plus de 4/5 (Figure A.1). Cette réglementation a changé à Ram Mountain en 1996, augmentant à full-curl et réduisant ainsi la pression de chasse. En plus de résulter en une mortalité accrue, la chasse sélective a aussi le potentiel de causer une pression de sélection artificielle. En effet, une réduction en taille des cornes a été observée en Alberta. De plus, l'âge à la récolte a augmenté depuis 1974, ce qui pourrait être dû à une croissance plus lente (Festa-Bianchet et al., 2014).

CHAPITRE 2

LA DYNAMIQUE ÉCO-ÉVOLUTIVE

2.1 Description de l'article et contribution

La dynamique éco-évolutive est un domaine de l'écologie en plein développement qui vise à comprendre les interactions réciproques entre les processus écologiques et les processus évolutifs. Il a longtemps été cru que ces interactions n'allaient que dans un sens ; l'écologie influençait l'évolution des espèces. Cette croyance était basée sur la supposition que les processus évolutifs étaient trop lents pour pouvoir influencer quelconque processus écologique. Or, il est maintenant de plus en plus évident que l'évolution peut être quantifiable sur de courtes échelles temporelles. Il est donc nécessaire de comprendre comment ces changements rapides en phénotype causés par l'évolution peuvent influencer l'écologie. Ce chapitre de l'*Encyclopedia of Ecology* 2^{nd} *edition* se veut une introduction aux notions de base de dynamique éco-évolutive ainsi qu'un aperçu des connaissances actuelles sur ce sujet.

Étant donné son expertise dans le domaine de la dynamique éco-évolutive, Fanie Pelletier a été invitée à contribuer à la prochaine édition de l'*Encyclopedia of Ecology*. Connaissant mon intérêt et expertise pour ce sujet (voir chapitre 4), elle m'a gracieusement offert d'écrire ce chapitre avec elle. Après avoir établi le plan de notre chapitre, nous nous sommes partagé le travail. Alors que Fanie se concentrait sur la section portant sur le lien entre l'écologie et l'évolution, je me suis concentré sur la section portant sur le lien entre l'évolution et l'écologie et les différentes approches pour aborder ces questions. Le format limitant le nombre de références à un maximum de 10, j'ai également créé une simulation de population où un cycle de rétroaction éco-évolutif influençait la dynamique de la population, ce qui a permis de données un exemple sans nécessiter de citations. Après avoir combiné nos sections respectives, nous avons travaillé de concert pour obtenir le produit final.

Eco-evolutionary dynamics

en révision pour l'*Encyclopedia of Ecology* 2^{nd} *edition*

Gabriel Pigeon and Fanie Pelletier

2.2 Abstract

Eco-evolutionary dynamics can be defined as the study of interactions between ecology and evolution that occur on ecological time scales. Although the links between ecology and evolution have been known for decades or even centuries, most of the emphasis has been placed on the influence of ecology on evolution. Eco-evolutionary dynamics aim to put more emphasis on the influence of evolution on ecology and on the reciprocal dynamics between ecology and evolution. More specifically, this field aims to explore the links between genetically based changes in phenotypic traits generated by selection on ecological processes such as population dynamics, communities and ecosystems processes on short time scale. Studies trying to measure the magnitude of these interactions have mostly emerged in the last two decades. This article first introduces the topic of eco-evolutionary dynamics and the rationale behind it, and then focuses on recent studies that made advances in this field and ends with an overview of the commonly used approaches to the study of eco-evolutionary dynamics. Only a few examples and approaches can be mentioned, and as such the reader is strongly encouraged to engage in additional reading of this multifaceted branch of ecological and evolutionary research.

Keyword : contemporary evolution, ecology, population dynamics, community, ecosystems, co-evolution, ecogenetics, feedback loops

2.3 Glossary

Animal model : a mixed effect model (i.e. a form of linear regression in which the explanatory terms are a mixture of both ‘fixed’ and ‘random’ effects) where one of the random effects of interest is the additive genetic value of individual animals. It is used to partition traits into their genetic and plastic components.

Co-evolution : Evolution of two or more species with a close ecological relationship, where each species adapt to the evolutionary changes occurring in the other species, thereby affecting each other’s evolution.

Contemporary evolution : Evolutionary changes observable over less than a few hundred years. The concept is also sometimes referred to as microevolution or rapid evolution or evolution on short time scale.

Eco-evolutionary feedbacks : the reciprocal interactions between evolution and the ecology of populations, communities and ecosystems

Evolution : Change in allele frequencies in a population over time.

Evolvability : The ability to respond to selection. For truncation selection, evolvability is the response to selection standardized by the intensity of the selection and phenotypic mean.

Extended phenotype : All the effects a gene has on the outside world that may influence its chances of being replicated. These can include effects on the organism in which the gene resides, the environment, or other organisms.

Functional traits : Any morpho-physio-phenological traits which impacts fitness indirectly via its effects on performance traits.

Phenotypic plasticity : Change in the average phenotype expressed by a genotype in different environments.

Standing genetic variation : Allelic variation that is currently segregating within a population ; as opposed to alleles that appear by new mutation events.

2.4 Eco-evolutionary dynamics

A classic view in evolutionary ecology is that natural selection determines which phenotypes persist or go extinct, over a long time scale while population growth, community and ecosystem processes are mostly driven by ecological factors such as density- dependent competition, stochastic factors on a shorter time scale. Thus, micro-evolutionary changes are assumed to occur on an evolutionary time scale and scientists have typically ignored the potential feedback of evolution on ecological processes. However, the realization that selection can be strong and that evolutionary changes can occur over ecological time scale (also termed contemporary time scale) has led researchers to ask a very important question : Can evolutionary changes feedback on ecological dynamics ? Several studies have shown that evolutionary processes can have quantifiable effects on ecological dynamics. Under some circumstances, evolution can occur within a few generations, and it is therefore necessary to consider the possibility that evolutionary changes may feedbacks on ecological processes and vice versa. Eco-evolutionary dynamics studies explore both the unidirectional effects of ecological changes on evolutionary processes (often referred to as the ECO to EVO links) and evolutionary changes on ecological processes (often referred to as the EVO to ECO link), and, even more importantly, they document the bidirectional eco-evolutionary feedbacks on contemporary time scale. Considering that the ECO to EVO links have been recognized for decades and deeply investigated in evolutionary ecology, the main contribution of eco- evolutionary dynamics is to bring insights on the less explored EVO to ECO links and to document feedbacks between these processes over a contemporary time scale.

2.5 Natural selection

All ecological and evolutionary changes ultimately occur as a result of alterations to the birth and death patterns of individuals. As the changes in birth and death are often associated with specific phenotypes (selection) and because those phenotypes generally have a genetic basis, evolutionary responses are expected. Assuming no other changes, it is expected that an evolutionary response should improve reproduction and survival of the next generation. Changes in phenotypes, however, are not always synonymous of evolutionary changes. Indeed, phenotypic plasticity may result in trait changes even in the absence of any evolutionary changes. Furthermore, plasticity itself can evolve and most studies to date have not been able to partition the ecological effects of trait changes into their plastic and evolutionary components. While the distinction between genetic variation and phenotypic plasticity is important to understand phenotypic variation and to identify whether the phenomena of interest is an ECO to ECO link or an EVO to ECO one, the effect of the changes in traits on the ecological processes of interest will be due to changes in the mean phenotype. Because it is the phenotype of individuals that will influence interactions between individuals or the effect of trait changes on the environment, eco-evolutionary dynamics studies often take a phenotypic perspective and assume that part of the trait changes has a heritable component.

The main drivers of natural selection are environmental. Those drivers are very diverse and include changes in predation pressure, density, sex ratio and weather. One of the classical examples that have documented natural selection in the wild is the study on the effects of drought on the beak size of Darwin's finches (*Geospiza fortis*). Another classical example comes from the peppered moth (*Biston betularia*), where the incidence of the dark form increased due to industrialization during the 19th century. Lichen cover had decreased due to industrialization, making the dark form more cryptic and less predated on than the normal form. This selective advantage led to a change in frequency of the dark form ; a change that was later shown to be genetic. This change in frequency of the dark form compared to the light one is thus one of the clearest and most intuitive examples of evolution under natural selection. A dynamic vision of the impact of ecology on evolution is therefore necessary, and all studies investigating the ecological drivers of natural selection on short time scale document the ECO to EVO links of eco-evolutionary dynamics.

2.6 Contemporary evolution

As previously mentioned, evolution was traditionally considered to be very slow, occurring over millions of years. For example, Darwin believed that evolution by natural selection could not allow for rapid changes, since it operated only by taking advantage from slight small successive variations. Experiments from animal breeding, however, have taught us that if selection is strong, evolutionary responses can occur over only a few generations. For instance, evolutionary changes in the resistance of certain breeds of beef (Belmont Adaptaur ; *Bos taurus*) to ectoparasite resistance (tick and worm) have been produced in as little as 15 years of selection by breeders.

Another important step in documenting the ECO to EVO links of eco-evolutionary dynamics is to evaluate whether evolutionary responses to natural selection occur and to identify the circumstances under which these responses are likely to occur on a contemporary time scale. Several empirical studies have indeed revealed that even in a natural context, traits can also evolve over a relatively short time period in response to changing environments. Cases of contemporary evolution were also observed in humans. A study of a pre- industrial human population reported evolutionary changes in the age at first reproduction in less than two centuries. These evolutionary changes in phenotype occurred on similar time scale as ecological processes. Thus, interactions between evolutionary changes and ecological processes are possible. Beyond that realization, however, a critical question is not whether such reciprocal interactions are possible but whether they are strong enough to matter in our understanding of ecological processes. For example, are these changes large enough to change the fate of a population, alter the composition of a community, or to a larger extent, even slow down the nutrient cycles ?

2.7 From evolution to ecology (the EVO to ECO link)

As just exemplified in previous sections, the clear and rapid effect of ecological change on evolution of different phenotypes is well established. The consequence of these phenotypes changes on various levels of biological organizations, however, is still under investigation. The phenotype of an individual can shape its interactions with its biotic and abiotic environment : its competitiveness, its ability to acquire resources, its ability to survive, grow and reproduce. By extension, the phenotypes present in a population will determine the possible interactions this population can have with its environment : its growth or decline, its coexistence with competing species or with predators, its geographical range. These changes in the community can further cascade and cause changes in the properties of the ecosystem. In response to ecological changes, evolutionary changes in traits can hence have a profound impact on the ecological landscape. The ecological processes affected can be on several levels of organization, ranging from the population to the ecosystem level (Figure 2.1). The expectation is that effects should decrease with higher hierarchical levels as the effects of the evolutionary changes are buffered at each level. However, direct links and interactions between levels may also magnify the effects. Research on the impact of evolutionary changes on each of these organizational levels is starting to emerge, with studies at the population and community levels being most abundants.

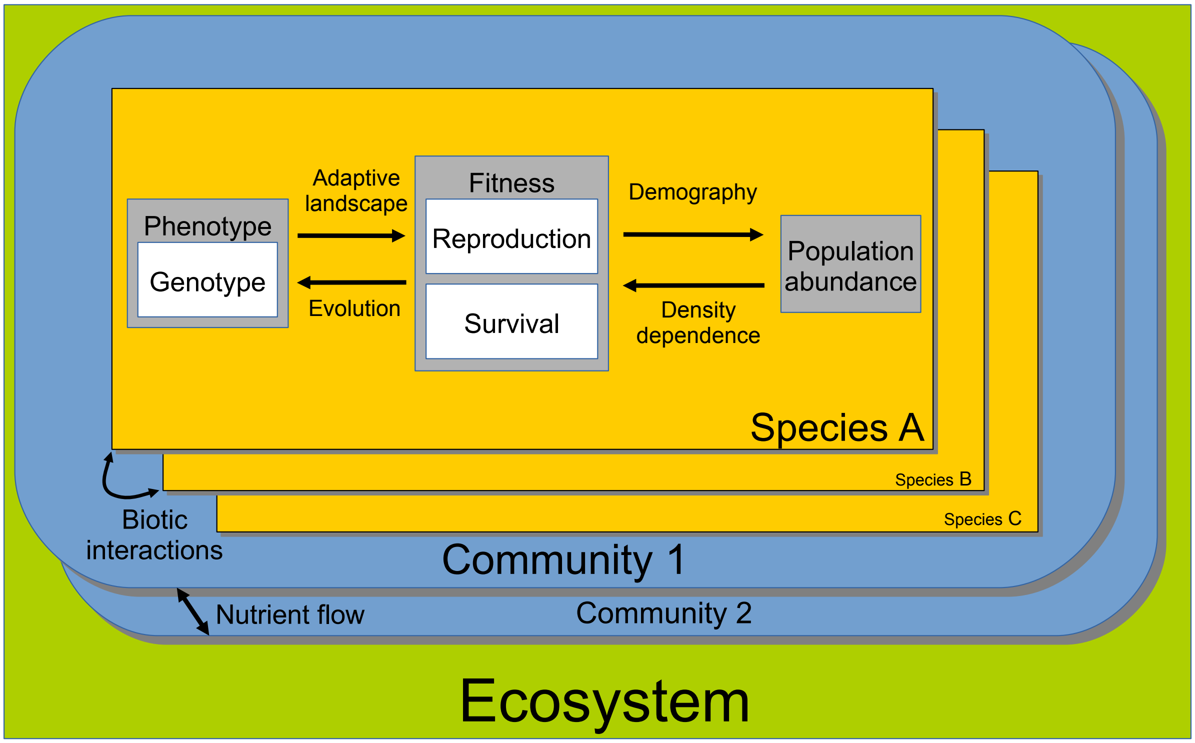

Figure 2.1 Conceptual model of eco-evolutionary dynamics, demonstrating the potential effects of changes in genotype on higher levels of ecological process going from population, community to ecosystem levels of organization. Yellow boxes represent species level process, where phenotype is based on genotype, which affects fitness through the fitness landscape. Fitness is determined by reproduction and survival which influence population abundance. Population abundance can feed back to genotype via density-abundance, which changes the selective pressure, and leads to evolution. Different species interact within a community (Blue box). These interactions can also be based on the genotype of species (not shown on the figure). Communities are linked within the ecosystem (green box) via subsidies and nutrient flow.

2.7.1 Population level eco-evolutionary dynamics

This aspect of evolutionary dynamics aims to document the links between changes in the distribution of phenotypic traits generated by selection and population dynamics (Figure 2.1 ; yellow box). As previously mentioned, natural selection and population dynamics are linked by birth and death. It is therefore necessary to consider the possibility of an eco- evolutionary feedback for traits linked to demography. When the trait change also causes changes in the fitness landscape, feedback loops can occur. The best example would be in the case of a trait under density-dependent selection. Density-dependent selection may favor the evolution of traits more closely linked to competitive ability at high densities than at low densities. These competitive traits, however, are often costly, yielding increased mortality, or reduced growth and fecundity. Consider a hypothetical example where the level of aggressiveness was selected differently according to density. When density is high, competition for resources increases and so does the optimal level of aggressiveness. In this case, the fitness landscape may resemble figure 2.2a, with optimal fitness being high aggressiveness at high density, but low aggressiveness being favored at low densities. When density is high, directional selection, combined with phenotypic variability and heritability may lead to evolutionary changes toward more and more aggressive individuals. If aggressiveness is negatively correlated with population growth rate (e.g. because more aggressive individuals have a lower life expectancy or ability to raise offspring), changes in this trait could lead to a decrease in population growth important enough to lower density. This population level change will, in turn, generate a change in the selective pressures (Figure 2.2d) and will favor a return to less aggressive phenotypes with lower mortality. If the demographic effects of trait changes are faster than the genotypic changes, which is likely, the evolutionary lag can induce cycles in the population dynamics with the density and mean phenotype alternating between states of high density and aggressiveness and low density and aggressiveness (Figure 2.2 b and c). Evidence of such dynamics has been found in the side-blotched lizards (*Uta stansbutiana*), where reproductive strategies have fitness consequences that are density dependent and induced by cycles alternating between morphs with few competitive offspring and morphs with numerous but less competitive offspring (Sinervo et al., 2000).

Additional evidence that traits tightly linked to fitness may lead to EVO to ECO effects come from evolutionary changes in life-history traits. For example, size selective harvesting, targeting large and older individuals, has led to a reduction in the age at maturity of some heavily fished species. Such evolutionary responses favor r-like life-history strategies which, in turn, can result in increased population growth rate as a larger proportion of the population produces recruits. Similarly, selection favoring higher reproductive output can increase the production of recruits, leading to increased population growth rate. However, evolution of earlier maturity is not a guarantee of an increased population growth rate given that trade-offs bet-

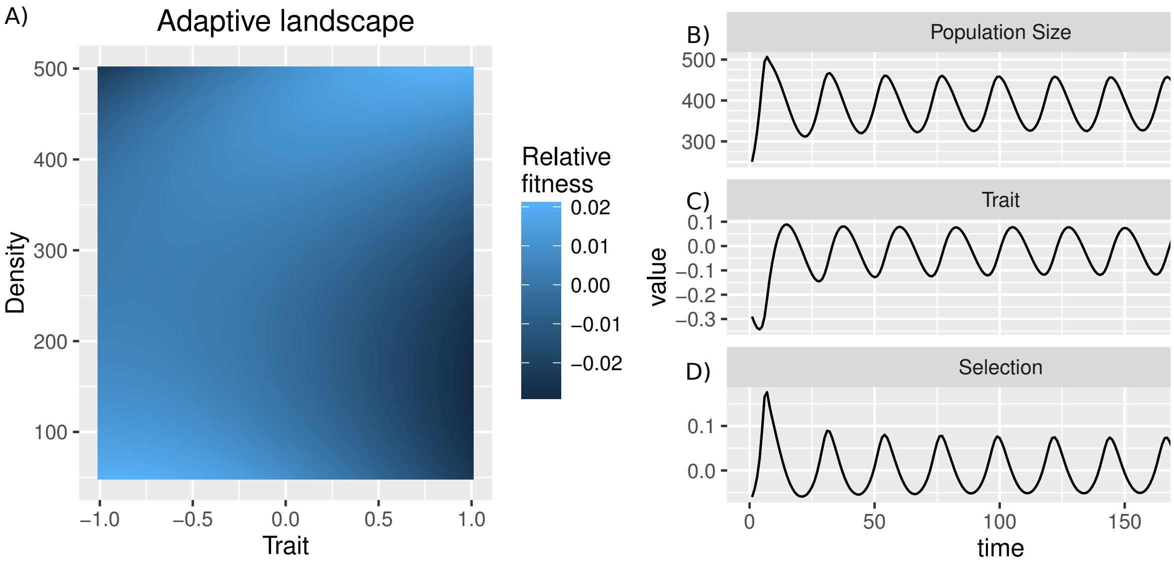

Figure 2.2 Simulated example of eco-evolutionary feedback loops at the population level. A) Fitness landscape where relative fitness of the trait of interest depends on density. The right panel shows the resulting cyclic fluctuations in B) abundance, C) mean trait of the population, and D) selection differential.

ween different life-history traits are common. The increase in population growth rate caused by earlier maturation could be counteracted by a reduction in survival. Similarly, larger recruitment could reduce the quality and survival prospects of the offspring produced. All of these considerations need to be taken into account when trying to predict the ecological response to evolutionary changes in life-history traits. Given this complexity, empirical studies are often necessary to obtain realistic and thorough understanding of the complete ecological response to these changes. As populations become adapted, population growth rates may increase until the population approaches carrying capacity, where density-dependence becomes a constraint. Carrying capacity, however, is also partly determined by the ability of individuals to acquire resources, which is also a phenotypic trait under selection . As such, evolutionary changes in traits may also cause changes in the carrying capacity and in density-dependence in natural populations. Apart from a few exceptions, however, eco-evolutionary theory has seldom been challenged with empirical data outside the lab.

It is worth mentioning that evolution may not always lead to an increase in population growth rate. Frequency-dependent selection may result in the evolution of a phenotype conferring a lower mean fitness. Additionally, it is important to remember that natural selection acts primarily on traits at the individual level. Thus, evolutionary changes in those traits do not necessarily improve the performance of the population as a whole. For example, sexually selected infanticide in carnivores will favor fitness of the perpetrator but will reduce offspring survival potentially reducing population growth. Further, the effects of evolutionary changes on population growth rate may be relatively weak if the population is regulated by other intrinsic or extrinsic factors which are independents of the evolving trait. The real challenge in eco-evolutionary dynamics is therefore not only to show the existence of interactions between trait changes and population parameters, but also to quantify their biological importance at the population level and evaluate whether those effects can cascade at higher level of biological organization such as community.

2.7.2 Community level eco-evolutionary dynamics

Through changes in population growth, eco-evolutionary dynamics will alter the abundance of the evolving species with potential cascading effects on the community. For example, the abundance of predators will undoubtedly influence the abundance of its prey often exemplify by the Canada lynx (*Lynx canadensis*) and snowshoe hare cycles (*Lepus americanus*) in most ecology textbook. However, community processes are not solely determined by the abundance of its constituent species. Trait changes in a species could also have direct effect on community level dynamics because phenotypic traits will affect how species interacts with their abiotic and biotic environments. As a consequence, evolutionary changes in those traits could impact species niche and hence community assemblages. The increased focus on functional traits to study community ecology is a testament of the ecological importance that traits play in structuring communities. Thus, it has been suggested that the impact of evolutionary changes in traits of a species could be as important as those of changes in functional traits in a community assemblage.

Functional traits, in combination with environment filtering, have been found to be key drivers of community assemblage. Evolutionary changes in traits may therefore shift the ecological niche of a species and therefore its distribution, leading to new community compositions as one species range expands or contracts. For example, a plant may adapt to the local climatic conditions at its range margin allowing it to expand its niche toward colder and formerly unsuitable climates. Evolutionary changes in traits can also impact interspecific competition, trophic interactions, mutualism and parasitism. These new biotic interactions can have several ecological consequences. One of the possible community level outcomes of eco-evolutionary dynamics is a switch to an alternative stable state, which is often in response to a strongly altered selective regime. This can lead to changes in community assemblage. A second possible outcome of changes in biotic interactions is co- evolution. Indeed, co-evolution can be considered a special case of eco- evolutionary dynamic. Selection and evolution of one of the co-evolving species induces changes in the selective pressure on the second co-evolving species which, in turn evolves in response to these changes, creating a feedback loop centered on the interaction between the two co-evolving species. Another possible outcome of eco-evolutionary dynamics at the community level is the emergence of cyclic evolutionary dynamics.

A great example of altered cyclic dynamics was shown in an experiment tracking the predator-prey dynamics of rotifer and green algae (Figure 2.3) in the presence or absence of evolution in the prey. The ability of the prey to evolve (or not) in response to a high predation pressure was controlled by setting up the experiment either using clonal populations (i.e. no genetic diversity) or using populations composed of several genotypes. This experiment showed that the population abundance of algae fluctuates with the abundance of rotifers, the main predator, leading short population cycles in absence of evolution by the prey (Figure 2.3A). In prey populations that have the opportunity to evolve, the algae populations develop effective defense mechanisms that allow the populations to increase in size. As those defense mechanisms are costly, they are traded off with competitive abilities and the populations are doomed to crash at high densities. The evolution by the prey increased the duration of cycle and changes the predator-prey dynamics (Figure 2.3B). This experiment provides support for the eco-evolutionary effects on predator-prey interactions.

The impact of evolutionary changes on communities will likely vary depending on which species and traits evolve. For example, the evolution of keystone species, such as an apex predator, is likely to have profound impacts on the community assemblage. For example, a reduction in size for an apex predators will affect is ability to consume large prey. Alternative prey (smaller species) can then be exploited shifting the size distribution of the prey community. However, the ability of a species to influence its community probably also increases with its prevalence, suggesting that community effects are not limited to the evolution of top predators or traits with large ecological effects. Eco-evolutionary dynamics may also play a major role in the dynamics of invasive species. Indeed, invasive species with a high potential for adaptation to new environments will be more likely to be successful invaders. Similarly, the arrival of an

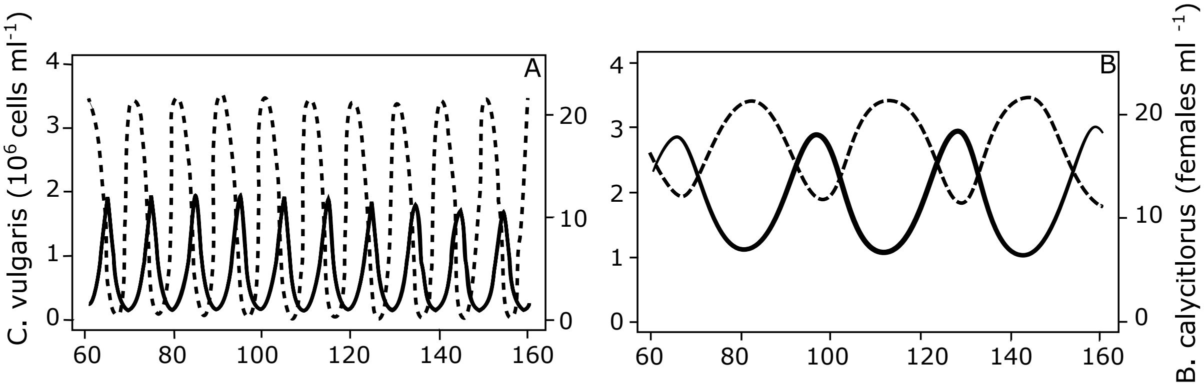

Figure 2.3 Cycles of abundance predicted by the model for the *Brachionus* predator (solid line) and *Chlorella* prey (dashed line) in a single-clone system (A) and a multiple-clone system (B). Adapted from Yoshida et al. (2003).

invasive species will modify the selection pressures on endogenous species, making potential evolutionary changes in the endogenous species with unknown evolutionary consequences. Researchers working on invasive species (e.g. Pimentel) were among the first to underline the potential importance of the EVO to ECO links.

An alternative way to study the EVO to ECO links on community processes that complement the approach used in the studies presented above is the "focal- species composite-response" approach. The community composition, structure and properties can be considered as an extended phenotype. As such, the focal species is able to evolve and as it does, it can have indirect genetic effects on its community. An example of a study using such an approach was conducted on North American cottonwoods (*Populus sp.*) and their arthropod communities. This study revealed that arthropod communities were highly heritable. Their results suggested that cottonwoods possessed an unknown trait that was heritable and which imposed selection upon arthropods. This trait generated indirect genetic effects on the fitness of the arthropod community members and produced distinct arthropod communities with distinguishable phenotypes potentially affecting other processes at the ecosystem level.

2.7.3 Ecosystem level eco-evolutionary dynamics

Eco-evolutionary dynamics at the ecosystem level has proven particularly challenging to study because of the logistic difficulties associated with working at large spatial scales while maintaining the resolution needed to measure evolutionary changes. Quantifying ecosystem level effects of evolutionary changes may be further hindered because many ecosystem processes may require a long time to respond or for the effects to be measurable. Thus, studies focusing on this aspect of eco-evolutionary dynamics have initially relied on contrasting the effect of standing genetic variation on ecosystem processes compared to other ecological variables. One of the best examples of such an approach was conducted on Populus hybrids that differ in their polyphenol production of a genetically based trait. The study revealed that the concentration of condensed tannins was the best predictor of decomposition and nitrogen cycling, suggesting that intraspecific variation in that trait was an important driver of ecosystem functions.

An alternative approach to overcome the logistic difficulties of monitoring ecosystem level eco-evolutionary dynamics has been to use mathematical models. Recently, ecosystem modeling has been used to evaluate the ecological feedback of evolutionary changes in demography and life-history traits in response to size selective fisheries. These models suggest that by selecting against large and more fecund fish, biomass of heavily harvested fish is greatly reduced. Some key studies have now provided strong evidence that those changes are likely to be, at last partially, genetically based. Given the critical importance of fish body size in the dynamics of consumer-resource aquatic networks, allometric trophic network model has revealed that heavily fished ecosystems are more likely to further decrease fish abundance and increase temporal variability in their food resources.

Theory suggests that the consequences of evolutionary changes in dispersal may also play an important role in ecosystem level eco-evolutionary dynamics. For example, the transition of species from an anadromous to freshwater resident life history can be important because anadromous fishes provide important subsidies of marine-derived nutrients to rivers, lakes, and streams. Additionally, studies on experimental metacommunities have suggested that dispersal rates may influence ecosystem properties, with productivity peaking at intermediate dispersal rates. Thus, evolutionary changes in migration propensity could be strong drivers of ecosystem processes.

Studies in mesocosms suggested that evolution could be a strong driver of ecosystem functions. For example, one study compared the relative importance of evolution, coevolution and species invasion, using guppies (*Poecilia reticulata*) and their predator, rivulus (*Rivulus hartii*), as model species, on algal dynamics, invertebrate biomass and decomposition rates. The evolution of guppies in response to alternative predation regimes significantly influenced algal biomass and accrual rates. More importantly, the effects of evolution and coevolution were larger than the effects of species invasion for some ecosystem responses, suggesting that under some circumstances within species changes in color and life-history traits may be as important a driver of ecosystem processes as changes in species composition.

2.8 Eco-evolutionary feedback

Most studies focus on the ECO to EVO link or the EVO to ECO link independently. Eco-evolutionary feedbacks have seldom been studied and can be pictured as the Holy Grail of eco-evolutionary dynamics studies. The occurrence of those two-ways feedbacks over long ecological time scales are evident but are generally ignored over contemporary time scales. It has been proposed that two main requirements need to be met in order to expect eco- evolutionary feedbacks : first, there must be a strong effect of the phenotype on the environment (e.g. organisms may structure or construct their environment) and second, the new environment must cause the subsequent evolution of the phenotype of the organisms inhabiting it. Those requirements have been suggested because for feedbacks to occur on an ecological time scale, the evolving phenotype needs to have enough effects on the environment for new selective pressures to emerge, affecting in return the phenotype of the evolving species. Models of eco-evolutionary dynamics, such as the one presented in section 2.7.3 on ecosystem consequences of size selective fisheries, are looking at those two-way interactions but empirical studies documenting both links are still scarce.

2.9 Cryptic eco-evolutionary dynamics

More recently some researchers have argued that eco-evolutionary dynamics interactions may be most important when they are the least obvious. This phenomenon has been referred to as cryptic eco-evolutionary dynamics. Cryptic dynamics arise in a system when processes interact in a way that effectively conceals the action of one, or more, of those component processes. Thus, eco- evolutionary feedbacks, as described in previous sections, could occur but may not have measurable consequences on ecological processes because several processes can obscure their effects. First, evolution can be cryptic for example, when several genotypes may be favored in a varying environment because they produce the same outward phenotype. Such countergradient variation may be common and result in cryptic eco-evolutionary dynamics. Similarly, evolution of tolerance or resistance may result in no obvious change in the phenotype unless one is careful and controls for the relevant challenging environmental conditions. These types of cryptic eco-evolutionary dynamics may be of great ecological importance because they contribute to ecological stability. Another process leading to ecological stability with the potential for cryptic dynamics is environmental tracking, which would reduce the fluctuation in population size even as the evolving trait changes to accommodate some environmental changes. While the ecological consequences of cryptic eco-evolutionary dynamics are null or quasi-null, their importance become apparent only when compared, in practice or in theory, to an equivalent case in the absence of evolution. Eco-evolutionary biologists should therefore keep in mind that the most parsimonious explanation (no effect of evolution) may not always be the best answer if we are more interested in explanatory theory than mere predictions.

2.10 Approaches to studying eco-evolutionary dynamics

To date, a lot of our knowledge on eco-evolutionary dynamics comes from laboratory systems where the importance of interactions between ecology and evolution might have been amplified due to their quantification in controlled environments. Thus, to evaluate the importance EVO to ECO links over a short- time scale in natural environments, researchers have used various approaches to assess under which conditions feedbacks between ecology and evolution are expected and to quantify their importance in the wild.

2.10.1 Modeling

Modeling is probably the approach to the study of eco-evolutionary dynamics where most progresses have been made thanks to the theoretical study of processes such as co-evolution and host parasite interactions. These theoretical models come in a variety of forms and reviewing them all is outside the scope of this review. Models of adaptive dynamics have also been very informative to understand eco-evolutionary dynamics. In this mathematical framework, an environment generated by genotypes is modeled and mutants are introduced to this fictive initial environment. Mutants with higher fitness are able to invade the environment while mutants with lower fitness are not. The presence of these successful mutants in turn changes the subsequent environment. The ensuing dynamics can be simulated until a steady-state is reached. The elaboration of such models has led to a better understanding of how previously stable coexistence dynamics can be perturbed when evolutionary changes occur much more quickly than ecological changes. Individual based models, where every individual is modeled specifically from its genotype and phenotype to its reproduction and survival, have also been insightful. Such models have been used, for example, to predict evolutionary consequences of commercial fishing on population dynamics as well as the indirect consequences on aquatic communities.

A drawback of a theoretical modeling approach is that while it provides convincing evidence that eco-evolutionary dynamics can happen and could have significant impacts on ecological processes, it does not provide evidence of their presence in nature or information on their strength and prevalence. Mathematical models do provide insight into the condition under which eco- evolutionary dynamics are more likely to be present. Those models also provide hypotheses and predictions which can then be verified in nature. Combining modeling to experimental or observational studies is a powerful approach, having the generalizability and precision of modeling while gaining the realism of the real world. The mechanisms that are supposed to be behind the observed effect can be modeled to verify the interpretation of the observed results. Alternatively, an eco-evolutionary process can be modeled and the result of the modeled compared to the results of a similar experimental setup.

2.10.2 Observational studies

Most observational studies are based on some sort of comparative approaches contrasting situations with and without evolution. This comparison can be made using two different populations (one that went through an evolutionary response and another that did not), or by monitoring one single population that showed an evolutionary response in time. The researchers can then measure the effects that those evolutionary changes had on population dynamics as well as community and ecosystem processes. The changes in ecological processes due to evolution can be measured directly by correlating them to variation in genotypes. For example, such approach was used in our previous example on cottonwood tree and arthropods revealing that the genotype of trees explained around 60% of the variation in arthropod communities (see section 2.7.2). In this way, the community effect of individuals could be considered as an extended phenotype and standard quantitative method could be used.

Mathematical methods, such as the Geber method, strengthen the conclusion that can be made from observational studies by decomposing changes in ecological processes due to evolution from other processes. The Geber method compares the relative importance of different factors in generating the change in some ecological variables. Using the Geber method, one first measures the temporal changes in various factors, including genotypes, phenotypes and environmental variables, as well as their effects on an ecological variable of interest. These resulting effects are then used to estimate the relative contribution of the change in each factor to the observed change in the ecological variable of interest allowing the quantification of the influence of trait changes on population growth. This method was used to partition the effects of traits and environmental conditions on population growth in five populations of wild ungulates and revealed that variation in birth mass in those species explained just as much of the variance in population growth rate as variation in weather conditions.

As previously mentioned, a key distinction to make when studying eco- evolutionary dynamics is that between evolutionary changes and phenotypic plasticity. A useful tool to achieve this in nature is the animal model, provided that pedigree information is available. First developed in the animal breeding and statistical genetic fields, the animal model is a form of mixed effects model which uses relatedness information from a pedigree to decompose phenotypic variance into its different genetic and environmental components. Using this information, the animal model allows estimating key parameters such as the heritability of a trait or the genetic correlations between traits. The animal model is now widely used in the field of quantitative genetics. The major advantage of the animal model over more traditional methods for estimating heritability, such as parent-offspring regressions or half-sib designs, is that it makes use of all the information from all types of relationship within the pedigrees. Further, other factors having potential effects on the phenotype can also be easily incorporated into the animal model.

Another framework in the study of eco-evolutionary dynamics, which has received increasing attention, is the integral projection matrix, or IPM. IPMs are an extension of matrix models where the distribution of continuous trait is tracked over time. IPMs are based on four basic functions : survival, development, recruitment and inheritance. The survival function determines the survival of individuals according to their trait ; the development function determines the change in traits such as size among survivors (growth) ; the recruitment function determines the recruitment from individuals according to their trait ; and the inheritance function describes the relationship between the offspring and parent traits. Extensions of the IPMs which track changes in genotypes through time in addition to the trait are being developed. Given that the model tracks the distribution of the trait over time, its resulting survival, recruitment and population growth, this tool could be well suited to the study of eco-evolutionary dynamic, although careful consideration of the genetic interpretation must be made. For instance, the inheritance function used to parametrize IPMs determine the trait distribution of the offspring at the next model iteration but it is not the heritability of the trait as defined in quantitative genetic.

2.10.3 Experimental manipulation

Experimental manipulation provides the most convincing demonstration of the effects of eco-evolutionary dynamics. Experimental manipulation allows careful decomposition of the plastic, genetic and other environmental effects on population and community dynamics. Chemostat (i.e. aquatic microcosm system used for the culture of microorganisms in which the chemical composition is kept at a controlled level) experiments have provided very convincing evidence of the importance of eco-evolutionary dynamics. This type of experiment was used to study predator-prey cycles of communities (algea-rotifer) with or without genetic diversity as previously explain in this article (section 2.7.2 and Figure 2.3). In a later experiment using a similar experimental setup, it was showed that rapid evolution of rotifers (lower investment in sexual reproduction) caused an important shift in the nutrient balance of the ecosystem.

The major advantage of experimental manipulations such as chemostats, and the reason why they have been so successful in demonstrating effects of evolution on ecology is that environmental conditions can be carefully altered to cause rapid and important evolutionary changes. Changes in genotype, phenotype and their "ecological" consequences can be precisely measured. However, this strength is also their most criticized weakness because such study may amplify the effect size due the controlled environment in which they are conducted. Moreover, whether results obtained in a 'bottle' can be extrapolated to natural populations or not is often questioned. The recent realization that natural conditions can also influence genetic variation, and hence evolvability, also cast doubts on the generalizability of laboratory experiments. Steps have been taken to remedy this issue by using mesocosms, which consist of large experimental set-up which aims at being closer to natural systems while still permitting replication and experimentation.

2.11 Conclusion

The fact that ecology and evolution interact has been known since Darwin. Evolutionary biologists have studied the ECO to EVO links for decades and have shown how natural and artificial changes in ecological conditions can drive evolution. The main novelty of eco-evolutionary dynamics is to emphasise on the EVO to ECO links. The potential for evolution to feedback on ecological processes over long time scales has been recognized for decades, but it is only recently that researchers have realized that interactions between these processes might also be important over short time scales. Eco-evolutionary studies try to identify the circumstances where the EVO to ECO links may matter and more importantly quantify the importance of evolutionary changes relative to all other factors known to affect the ecology of wild species.

2.12 Further readings

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CHAPITRE 3

LA CHASSE SÉLECTIVE ET L'ÉVOLUTION

3.1 Description de l'article et contribution

La taille des cornes est un trait morphologique subissant une forte pression sélective artificielle due à la chasse au trophée. De plus, ce trait possède une forte héritabilité. Une réponse évolutive est donc prévisible. En effet, une diminution de la taille des cornes a été observée au cours du temps chez le mouflon d'Amérique. Cependant, démontrer que ce changement phénotypique est dû à un changement évolutif reste un défi. David W. Coltman a relevé ce défi en 2003, utilisant un modèle animal pour montrer qu'il y avait eu un déclin génétique des valeurs de croisement. Les fondements statistiques de son analyse ont cependant été critiqués. Cet article visait à reprendre les analyses de Dr Coltman tout en prenant en compte les critiques qui avaient été faites. De plus, nous avons profité d'un changement des réglementations de chasse pour distinguer deux périodes, une de forte chasse et une de faible chasse. L'arrêt de la réponse évolutive coïncide avec la diminution des pressions sélectives, renforçant le lien de causalité.

Pour cet article, j'ai participé à l'élaboration des idées avec Fanie Pelletier suite à un article paru en 2016 qui suggérait que la chasse n'avait pas de conséquence évolutive à Ram Mountain. J'ai ensuite effectué les analyses statistiques et l'écriture de la première version du manuscrit. David W. Coltman a fourni la généalogie. Alastair Wilson à contribué en suggérant l'utilisation d'un modèle multitraits. Fanie Pelletier et Marco Festa-Bianchet ont par la suite commenté plusieurs versions du manuscrit. Fanie Pelletier, Marco Festa-Bianchet et David W. Coltman ont contribué à l'interprétation des données et à la révision du manuscrit.

Intense selective hunting leads to artificial evolution in horn size

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Gabriel Pigeon, Marco Festa-Bianchet, David W. Coltman and Fanie Pelletier

3.2 Abstract

The potential for selective harvests to induce rapid evolutionary change is an important question for conservation and evolutionary biology, with numerous biological, social and economic implications. We analyze 39 years of phenotypic data on horn size in bighorn sheep (*Ovis canadensis*) subject to intense trophy hunting for 23 years, after which harvests nearly ceased. Our analyses revealed a significant decline in genetic value for horn length of rams, consistent with an evolutionary response to artificial selection on this trait. The probability that the observed change in male horn length was due solely to drift is 9.9%. Female horn length and male horn base, traits genetically correlated to the trait under selection, showed weak declining trends. There was no temporal trend in genetic value for female horn base circumference, a trait not directly targeted by selective hunting and not genetically correlated with male horn length. The decline in genetic value for male horn length stopped, but was not reversed, when hunting pressure was drastically reduced. Our analysis provides support for the contention that selective hunting led to a reduction in horn length through evolutionary change. It also confirms that after artificial selection stops, recovery through natural selection is slow.

Keywords : Contemporary Evolution, Conservation Biology, Quantitative Genetics

3.3 Introduction

Human activities such as habitat modifications, expanding road networks, overexploitation and climate change affect animal populations. While the demographic impacts of humans on wild species are clear, their evolutionary impacts are debated (Loehr et al., 2007 ; Hard et al., 2008). Intense exploitation by humans may outpace (Darimont et al., 2009) or oppose (Carlson et al., 2007) the selective effects of natural predators, potentially leading to evolutionary changes in behaviour, phenotype or life history (Hard et al., 2008 ; Devine et al., 2012). van Wijk et al. (2013) showed that selective harvesting of guppies (*Poecilia reticulata*) led to changes in size and in the frequency of alleles associated with size in just 2 generation. Human-induced evolution may also impair population persistence or prevent recovery (Swain et al., 2007 ; Uusi-Heikkilä et al., 2015). While numerous studies of fishes report evidence of evolution induced by intense harvest (reviewed in Hutchings and Fraser 2008), evidence for evolution through selective harvest in terrestrial species remains scarce and controversial (Coltman et al., 2003 ; Garel et al., 2007 ; Mysterud, 2011 ; Traill et al., 2014), partly because the statistical techniques used to quantify evolutionary changes using pedigrees in earlier studies have been questioned (Postma, 2006 ; Hadfield et al., 2010).

Trophy hunting can be an important component of many conservation programs (Leader-Williams et al., 2001), and its economic revenues are partly driven by expectation of large trophy size (Festa-Bianchet and Lee, 2009 ; Crosmary et al., 2013). In most of Canada, sport harvest of mountain sheep (*Ovis canadensis* and *O. dalli*) rams is based on a phenotypic definition of minimum horn curl that establishes whether or not a ram can be shot, with an unlimited number of permits available to resident hunters (Festa-Bianchet et al., 2014). In wild sheep, horn size is a key determinant of success in male-male competition over breeding opportunities (Coltman et al., 2002). Artificial selection favoring shorter horns through hunting mortality, however, sets in 2-3 years before natural selection favoring longer horns through reproductive success (Coltman et al., 2002). Multiple studies report that males with fast-growing horns, that would enjoy high mating success at 8-10 years of age, are harvested at 4-7 years, conferring a reproductive advantage to small-horned males that, in the absence of size-selective harvests, would normally be outcompeted (Festa-Bianchet et al., 2004 ; Loehr et al., 2007 ; Hengeveld and Festa-Bianchet, 2011 ; Festa-Bianchet et al., 2014 ; Douhard et al., 2016).

One approach to study evolution in nature, often referred to as the animal model, involves mixed models combining a pedigree with data on phenotype and environmental conditions to estimate genetic parameters (Kruuk, 2004). Using this approach, Coltman et al. (2003) used a pedigree up to six generation deep to report a decline in estimated breeding values of horn length and body mass in bighorn rams over 30 years, suggesting an evolutionary response to size-selective harvests. Their analyses, however, were criticised for not adequately accounting for environmental effects on phenotype, for the error in estimation of breeding values and for the effect of drift ; possibly leading to exaggerated estimates of evolutionary change (Postma, 2006 ; Hadfield et al., 2010). Hence, the importance of evolution in the observed change in phenotype following selective harvesting is still debated.

A recent paper used data from the individually monitored population of bighorn sheep of Ram Mountain to parameterise an Integral Projection Model and show a decline in body mass, but argued that the phenotypic response to harvest was only demographic (Traill et al., 2014). The statistical criticisms and alternative analyses listed above cast doubt on the conclusion that selective hunting could led to evolutionary changes. Coltman et al. (2003) drew that conclusion after analysing data for the only sport-hunted population of ungulates for which a pedigree and horn measurements are available (Pelletier et al., 2012). By extension, these criticisms also question phenotype-based studies that reported long-term trends consistent with an evolutionary impact of selective hunting (Garel et al., 2007 ; Hengeveld and Festa-Bianchet, 2011). A clear understanding of the importance of evolutionary change due to selective harvesting is of critical importance to those responsible for managing harvested wild populations (Allendorf and Hard, 2009). A reanalysis of the Ram Mountain data is therefore warranted, particularly because the ten-fold decline in harvests after 1996 provides an opportunity to test the impacts of changes in harvest pressure on trait evolution (Douhard et al., 2016).

Here, we use a Bayesian animal model to analyse an expanded database on bighorn sheep from Ram Mountain, adding nine years of data to those available to Coltman et al. (2003) and taking into account subsequent statistical criticisms (Postma, 2006 ; Hadfield et al., 2010). We also compare a period of intense harvest with a period when harvest was first dramatically reduced, then stopped. This allowed us to compare temporal trends in genetic values under heavy and very light artificial selection. To maximise the use of phenotypic information, we considered data on male and female traits using a multivariate model. Genetic correlations have already been established among some of these traits (Poissant et al., 2012), and proper estimation of breeding values must account for genetic covariance (Wolak et al., 2015). By including phenotypic data on females we could also compare temporal changes in traits that are (male horn base and female horn length) and are not (female horn base) genetically correlated to male horn length (Poissant et al., 2012). We expected to see temporal changes in estimated breeding values in male horn length only under heavy harvest. Male horn base circumference is particularly interesting because it is correlated with horn length and likely affects male- male competition by contributing to horn mass, but is not a direct target of selective hunting. We expected strong selective effects on male horn length, the trait most directly related to the legal definition of harvestable ram (Festa-Bianchet et al., 2014). We expected a response similar to male horn length for male horn base and female horn length given their strong genetic correlations with male horn length, and no response in female horn base, which has a weak genetic correlation with male horn length (genetic correlations of 0.72, 1 and -0.28 respectively ; Poissant et al. 2012). To compare our results with previous studies on this population, we also built animal models using univariate one-sex (with phenotypic data on males only) and two-sex (phenotypic data from both sexes) animal models. Univariate models are also less prone to problems when fitted with limited data given their simpler structure (Wilson et al., 2010) .

3.4 Material and Methods

3.4.1 Study population and phenotypic data

Bighorn sheep at Ram Mountain, Alberta, Canada are intensively monitored. The study area is 30 km east of the Rockies (52°8'N, 115°8'W, elevation 1082 to 2173 m), on a mountainous outcrop dominated by cliffs, rock scree and alpine meadows. Since 1972, sheep have been marked with ear tags and collars. Each year, between May and September, sheep were repeatedly captured in a corral trap baited with salt. Rams were captured on average 2.6 times per year. At each capture, horn length in cm was measured along the outside curvature with a flexible tape. To reduce the potential measurement error caused by horn wear or breakage, we used the longest horn in analyses. Horn base circumference was also measured in cm, and we analysed the mean of the left and right measurements. Nearly all individuals (95%) were first captured as lambs or yearlings, so their exact age was known. For the others, age was determined using horn annuli.

The study population was hunted until 2011 based on a morphological definition of ‘legal’ ram. From late August to October, rams were at a risk of being shot only if they met that definition, which specified a minimum degree of horn curl and was correlated with horn length (Festa-Bianchet et al., 2014). Artificial selection through hunting, however, changed over time. In 1996, the minimum horn curl of a ‘legal’ ram was increased from 4/5 to full curl (Fig. A.1). This change, implemented at a time when horn size had declined (Coltman et al., 2003), drastically decreased the harvest, with only 4 rams shot in the following 15 years. Mean harvest was 2.26 rams/year in 1973-1995 and only 0.27 rams/year in 1996-2010. Hunting was closed in 2011. Therefore, we compared trends in the estimated breeding values of morphological traits for cohorts of 1973-1996 (referred to as the hunted period) and 1996-2011 (non-hunted period ; see below). Based on the average age of fathers at Ram Mountain (7.3 years), we monitored 3.3 generations under strong artificial selection followed by 2.2 generations under natural selection.

We first adjusted all traits to September 15 using a mixed model approach (Martin and Pelletier, 2011). As adult females and adult males display different growth curves, we used sex-specific linear models to account for capture date and fitted one model per year to allow for environmental variability. Trait was fitted as a function of the square root of Julian date, considering May 25th as day 1. With this modelling approach, individual identity can be used to estimate an individual intercept and slope, providing a more accurate standardization than classical least square regression (Martin and Pelletier, 2011). The procedure was used for horn length and horn base. A total of 2295 adjusted phenotypic measurements where obtained from 510 females and 497 males.

3.4.2 Pedigree reconstruction

Since 1972, maternities were assigned from observation of suckling behaviour. Since 1988, DNA samples have allowed the assignation of paternities based on 26 microsatellite loci with a confidence threshold of 95% using CERVUS (Coltman et al., 2005). The pedigree in 2014 contained 864 maternal links involving 254 dams and 528 paternal links involving 79 sampled and 37 unsampled sires, the latter identified using COLONY (Jones and Wang, 2010). Unsampled sires include rams that died before we began sampling for DNA and immigrants that are on Ram Mountain only for the rut.

3.4.3 Quantitative genetic analyses

Analyses of horn base include phenotypic data of individuals aged 2 to 10 years between 1975 and 2013. For horn length, however, we only included data for sheep aged 2 to 4 years. Horns frequently break, and the chance of horn damage increases with age. Many old males have broken horns, missing up to the first two years of growth. Our data suggest that by 4 years of age ewes have reached 97% of the horn length they will have at age 8 (including the effect of breakage), and rams 73%. In addition, after age 4 the sample of rams is biased because those with longer horns are removed by hunters (Coltman et al., 2002). To reduce the importance of maternal effects on phenotypes (Wilson et al., 2004), analyses excluded phenotypic data of lambs and yearling (Réale et al., 1999 ; Wilson et al., 2005).

The multivariate animal model was fitted using 4 traits : male horn length, female horn length, male horn base and female horn base. Phenotypic variance was then partitioned into its components, including additive genetic variance. The model also included sheep identity, year of measurement and year of birth as random effects to assess the amount of variance due to permanent, yearly and cohort environmental effects respectively. Including year of measurement and year of birth as random effects accounts for both short- and long-term environmental effects, including changes in density, weather and forage quality. The year effect is necessary to obtain unbiased estimates of breeding value but it may also partly absorb temporal genetic trends, making this analysis conservative. Maternal identity was not included since the exclusion of lambs and yearlings minimized maternal effects. Age was included as a categorical fixed effect. To compare our results with previously published studies on this population we also examined univariate animal models (see supplementary material). We tested univariate models using male phenotype only (Annexe 1.2) to obtain results comparable to Coltman et al. (2003). We also fitted univariate models including both male and female phenotype to increase power (Annexe 1.3). These models are further described and their results presented in the supplementary material (Annexe 1.2-1.3).

The animal model estimates the breeding value of each individual. To correctly estimate breeding values and their associated error (Hadfield et al., 2010), the model was fitted using a Bayesian method with MCMCglmm version 2.21. We used a multivariate inverse-Wishart prior to obtain the most objective results possible. Models where run using 2 chains for 8500000 iterations, with a thinning of 75000 and a burn-in of 1000000 iterations. A sensitivity analysis evaluated the robustness of the model to different prior specifications (Fig. A.2).

3.4.4 Temporal change in estimated breeding value

We compared temporal trends in estimated breeding values (EBV) to those obtained based on different models of evolutionary change. For each realization of the MCMC chain of the animal model, we calculated mean EBV by cohort and the slope in mean EBV as a function of cohort (ße) for both the hunted and not-hunted periods to obtain a posterior distribution of slopes. We compared this distribution to the posterior distribution of slopes of alternative models, which included no change, drift, stasis and expected evolutionary response. To compare the posterior distributions of slopes, we subtracted each realization of the posterior distribution of the alternative model to that of the distribution ße, obtaining a distribution of differences. From this distribution, we can obtain the mean difference between the expected and observed distributions as well as the confidence interval of the difference.

First, as done previously by Coltman et al. (2003), we compared slopes in EBV to 0. Second, following Hadfield et al. (2010), we compared the slopes in EBV to those obtained from simulated drift. To do so, we simulated random breeding values down the pedigree for each of the 1000 posterior samples of the animal model based on the estimated additive genetic variance. We then fitted a linear regression to the cohort mean of these random breeding values to obtain the slopes due to drift for each posterior sample. Third, we compared observed change in estimated breeding value to stasis (Hunt, 2007), a pattern likely to occur under stabilizing selection. To simulate stasis, mean cohort breeding values were randomly drawn from a normal distribution with a mean of 0 and a variance equal to the observed variance in mean cohort EBV.

We also compared observed change in EBV to the response to selection predicted by the secondary theorem of selection (Morrissey et al., 2012). This theorem states that change should be equal to the additive genetic covariance between the trait of interest and relative fitness. We used longevity as a fitness measure, which we divided by mean cohort longevity to obtain relative fitness. We used longevity rather than reproductive success because molecular assignments of paternities only began in 1988. We then fitted separate bivariate animal models of trait and fitness for each of the studied traits. The predicted response to selection was then extracted from the G matrix and divided by the mean generation time (7.3 years, the average age of fathers in our population) to obtain a predicted change per year (Table A.1). Predicted response to selection could only be estimated for the hunted period due to the limited number of individuals of known longevity born after hunting pressure was reduced. The proportion of iterations for which the slope for the estimated breeding value (ße) is lower than that of the random breeding value (ßr) was also calculated to estimate the probability that the trend was not caused solely by drift.

3.5 Results

3.5.1 Animal model analyses

Table 3.1 Variance components and heritability of horn length and horn base in bighorn sheep at Ram Mountain, Canada, according to multivariate animal models. The posterior mode of the proportion of phenotypic variance explained by each component is followed by the 95% Bayesian posterior interval of highest density in parentheses. h^2 refers to the narrow-sense heritability, ID refers to the proportion of phenotypic variance explained by permanent environment (identity of the sheep), yr refers to the proportion of phenotypic variance explained by year of measurement and BY refers to the proportion of phenotypic variance explained by year of birth.

	Horn length male	Horn length female	Horn base male	Horn base female
h^2	0.397 (0.203-0.534)	0.223 (0.090-0.446)	0.25 (0.119-0.413)	0.265 (0.148-0.335)
ID	0.025 (0.003-0.211)	0.376 (0.203-0.540)	0.098 (0.016-0.268)	0.171 (0.110-0.265)
yr	0.11 (0.039-0.168)	0.022 (0.010-0.052)	0.193 (0.109-0.289)	0.161 (0.112-0.268)
BY	0.363 (0.211-0.528)	0.149 (0.071-0.286)	0.203 (0.097-0.354)	0.212 (0.107-0.291)

Estimates of variance components and heritability for horn length and base (Table 3.1) showed that heritability was greater than 0 for all traits. The trait with the highest posterior mode for heritability was male horn length, followed by male horn base, female horn length and female horn base. Permanent environmental effects explained much of the variance in female but not in male traits. Cohort always explained a significant part of phenotypic variance, while the effects of year and permanent environment varied among traits (Table 3.1). Confirming previous analyses (Poissant et al., 2012), genetic correlations between male horn length, female horn length and male horn base were high while female horn base had low genetic correlation with other traits (Table 3.2).

Table 3.2 Genetic correlations and covariance matrix for horn size in bighorn sheep. Values on the diagonal (grey shading) are posterior modes of genetic additive variance. Values below the diagonal are the posterior modes of genetic covariance between traits : male horn length (HL-M), female horn length (HL-F), male horn base (HB-M) and female horn base (HB-F). Values above the diagonal are the posterior modes of genetic correlations. Values in parentheses represent the 95% Bayesian posterior interval of highest density.

	Hl-M	Hl-F	Hb-M	Hb-F
Hl-M	17.884 (9.82-25.88)	0.921 (0.557-0.981)	0.878 (0.729-0.959)	0.189 (-0.285-0.538)
Hl-F	5.345 (1.928-8.144)	1.622 (0.748-3.963)	0.799 (0.275-0.939)	0.368 (-0.063-0.610)
Hb-M	5.435 (2.797-9.666)	1.274 (0.318-2.881)	2.915 (1.124-4.485))	0.286 (-0.203-0.656)
Hb-F	0.070 (-0.542-1.059)	0.187 (0.071-0.286)	0.182 (-0.164-0.508)	0.183 (0.119-0.270)

3.5.2 Temporal changes in estimated breeding values

Temporal changes in mean phenotypic values over 39 years differed between traits (Fig. 3.1). A temporal change in EBV was also observed (Fig. 3.2). During the hunted period from 1973 to 1996, the EBV of male horn length declined significantly (ß = -0.119 ; CI = -0.248, -0.006). Similarly, genetically correlated traits also appeared to decline. Female horn length breeding value declined with a slope of -0.027 (CI = -0.063, 0.013), while EBV for male horn base had a slope of -0.030 (CI = -0.076, 0.019). Unlike male horn length, the breeding value of female horn base appeared to increase, with a slope of 0.005 (CI = -0.008, 0.016). We then compared observed changes in EBV for male horn length to those expected under various models of evolutionary change (Table A.2 ; Fig. 3.3). The observed temporal change in estimated breeding value differed significantly from 0 (Pr[ße < 0] = 0.974). While observed EBV did not differ significantly from that predicted by other models, the probability of declining more than expected by drift alone (Pr[ße < ßr]) was 0.901. The observed temporal change in EBV was most similar to that predicted by the secondary theorem of selection (expected change per generation of -0.76, Fig. 3.3) with a posterior difference of 0.016, while the posterior differences of other models of evolution ranged from 0.117 to 0.120 (Table A.2). Similarly, for female horn length, observed trends were most similar to those predicted by the secondary theorem of selection (expected change per generation of -0.10) with a posterior difference of 0.013. Other models of evolution all had similar differences of 0.027. The probability of declining more than expected by drift alone (Pr[ße < ßr]) was 0.816. For male horn base, observed trends were also most similar to those predicted by the secondary theorem of selection (expected change per generation of -0.13) with a posterior difference of 0.013. Other models of evolution all had similar

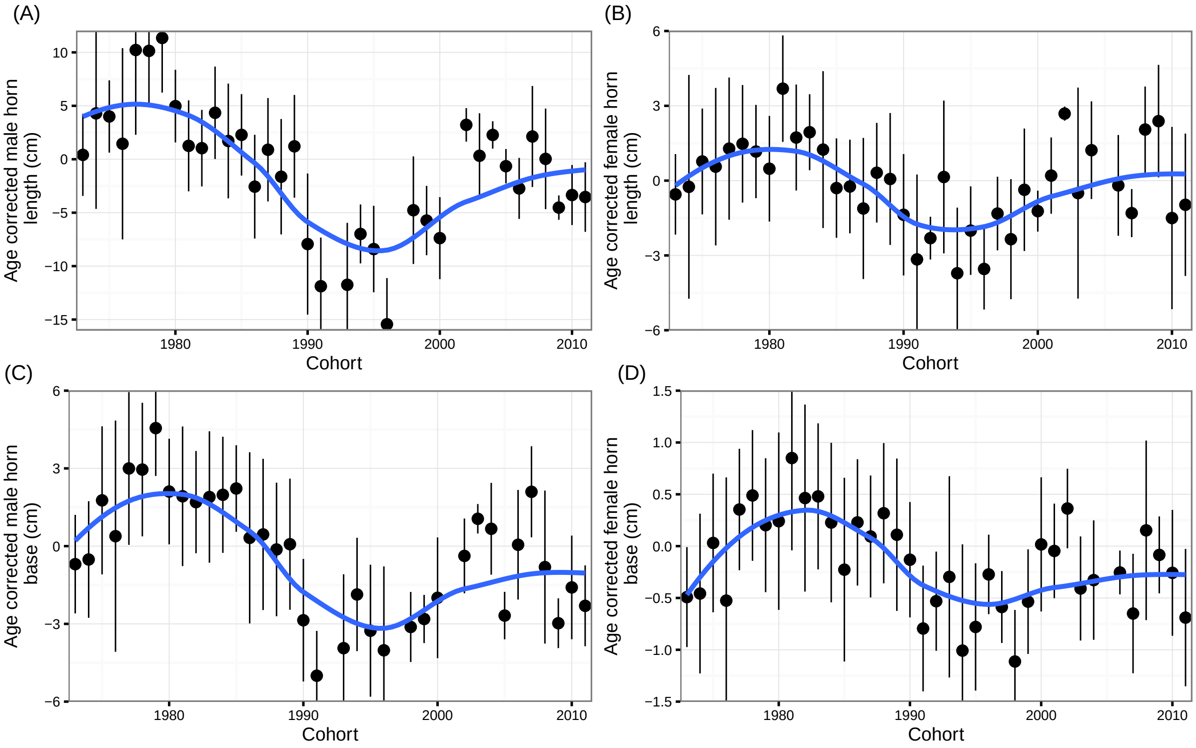

Figure 3.1 Temporal trends in age-corrected phenotypic traits for bighorn sheep cohorts born at Ram Mountain, Canada, between 1973 and 2011. Panels show mean a-b) horn length and c-d) horn base in cm. Black dots and error bars represent the cohort average (±1 sd) phenotype after correcting for age. Smooths (blue line) were fitted using loess.

differences of 0.030. The probability of declining more than expected by drift alone (Pr[ße < ßr]) was 0.796. Finally, for female horn base, all models were similar. The predicted response according to the secondary theorem of selection (expected change per generation of 0.005) had a difference of -0.004. Other models had differences of -0.005.

After the near-cessation of hunting in 1996, average estimated breeding values remained stable or showed a weak tendency to increase, with slopes of 0.053 (CI : -0.174 , 0.282) and 0.021 (CI : -0.054 , 0.104) for horn length of males and females respectively. For horn base, EBVs after the change in regulations had slopes of 0.032 (CI : -0.056 , 0.137) and -0.006 (CI : -0.029 , 0.018) for males and females respectively. The probabilities that the slope in EBV of male and female horn length increased after the change in hunting regulations were 0.894 and 0.847 respectively. Similarly, the probabilities that the slope in EBVs of male and female horn base increased after the change in regulations were 0.866 and 0.226. Unfortunately, we could not compare observed changes in EBVs for male horn length to those expected under

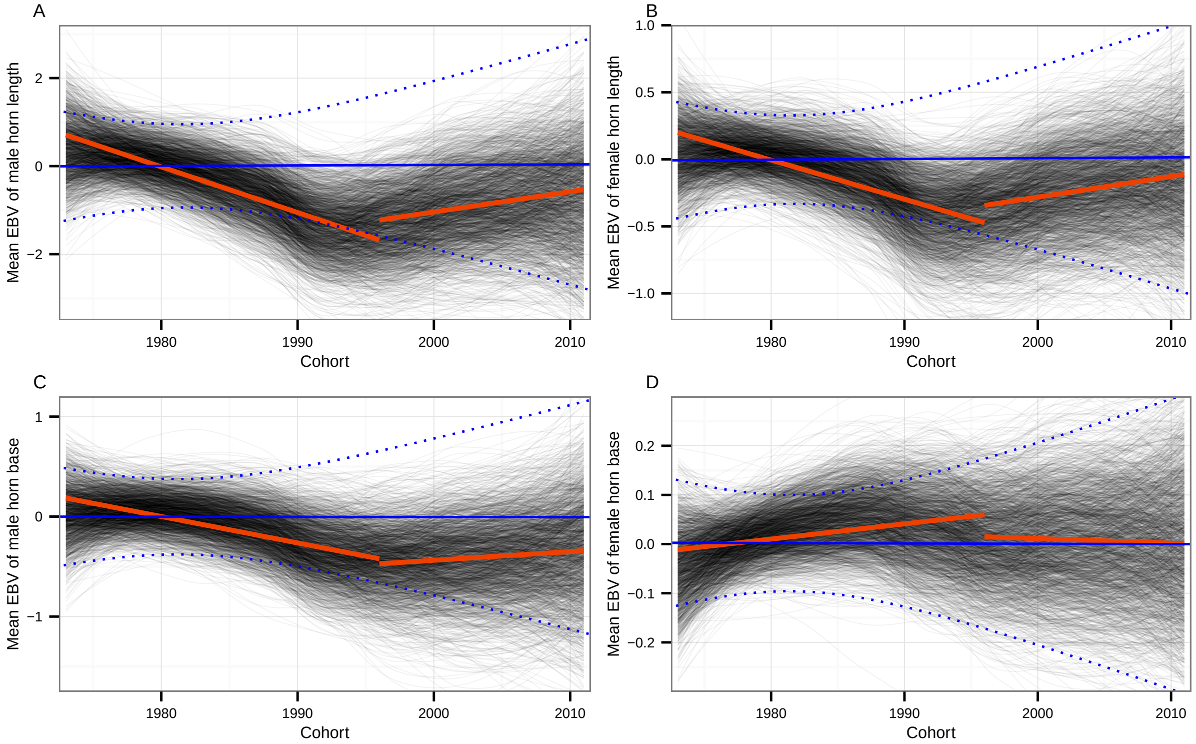

Figure 3.2 Changes in mean estimated breeding values for bighorn sheep cohorts born at Ram Mountain between 1973 and 2011, according to a multivariate model. Panels present the estimated breeding values of a-b) horn length and c-d) horn base in cm. The left column shows results for males and the right column for females. Each grey line represents the average estimated breeding value through time for one iteration of the MCMC chain of the animal model using loess. Red lines represent the posterior mean trend using linear regression for the hunted and non-hunted period. The blue line represents the average response expected by drift alone, with 95% confidence interval in dashed blue lines.

various models of evolutionary change for the not-hunted period. Because of the shorter period and a smaller population size, we did not have adequate statistical power to estimate predicted responses to selection. A comparison of observed temporal trends in EBV to alternative models of evolutions such as drift or stasis suggested that all models where quite similar (Table A.2).

Results for the univariate animal models were qualitatively similar to the multivariate model presented here. For the male-only model, the posterior probabilities of declining more than expected by drift (Pr[ße < ßr]) were 0.874 and 0.629 for horn length and horn base. posterior probabilities of declining more than expected by drift changed to 0.560, and 0.637 respectively after the change in hunting regulations (for complete results, see Table A.1). For the two-sex

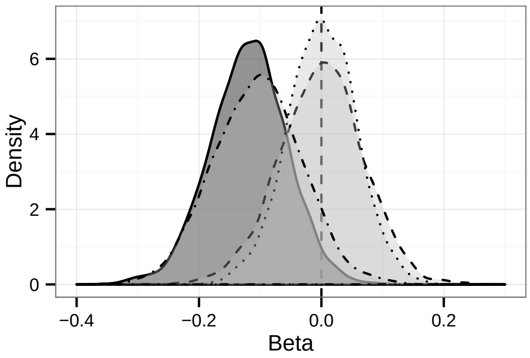

Figure 3.3 Posterior density plots for the slopes in mean estimated breeding values of male horn length and predicted change in estimated breeding value according to different models of evolutionary change for bighorn sheep cohorts born at Ram Mountain from 1973 to 1996. The dark filled distribution with solid line represents the posterior distribution of slopes in mean cohort breeding values (ße) for male horn length. The distribution with dot-dashed line represents predicted annual evolutionary response according to the secondary theorem of selection. The distribution with dotted line represents predicted change according to simulation of stasis. The distribution with dashed line represents predicted changes due to drift according to simulation of random breeding values.

model, the posterior probabilities that breeding values declined more than expected by drift (Pr[ße < ßr]) were 0.985 and 0.503 for horn length of males and females, respectively. These probabilities were 0.745 and 0.582 for horn base of males and females. Changes in breeding value had a low probability of being steeper than expected from drift after 1996 (0.560 and 0.637 for horn length, and horn base of males ; 0.543 and 0.555 for the same traits in females).

3.6 Discussion

We assessed whether temporal genetic trends in wild bighorn sheep were consistent with evolutionary changes expected from selective pressures acting on traits targeted or not targeted by trophy hunting. Using a 39-year dataset, we expand upon previous results (Coltman et al., 2003), using a statistical approach (Hadfield et al., 2010) that is robust to biases likely affecting earlier estimates of breeding values. A model including a term for the random effect of year, as suggested by Postma (2006) confirms a statistically significant negative trend in estimated breeding values for male horn length during a period of intense harvest. Hadfield et al. (2010) suggested an even more conservative test, comparing the observed change in breeding value to simulated changes that may occur through genetic drift. The observed decline in male horn length breeding value had a probability of 90.1% of being greater than expected from drift alone, although this probability varied when using simpler univariate models (87.4% and 98.5% depending on the univariate animal model used ;Table A.1-A.2). The decline in breeding value had a very high probability of being greater than that expected under genetic drift in a univariate model that included information on phenotype and pedigree from both sexes but did not include genetic covariance with other traits (Table A.2).

The decline in male horn length breeding values appeared to stop when hunting pressure was greatly reduced. While horn length declined during the hunting period, female horn base, a trait not subjected to trophy hunting and with low genetic correlation (0.189) to male horn length (Table 3.2), did not decline, supporting the contention that the decline in horn length was partly due to artificial selection. Further, female horn length and male horn base, traits genetically correlated to male horn length but not under selection, showed responses similar to male horn length. Overall, these results provide compelling evidence of a response to artificial selection while refuting the hypothesis that the observed changes were entirely caused by changes in environment. Our study population is small (average of 28.5 adult rams, yearly range 8 – 61) and after the hunting regulations were changed it declined partly through cougar (*Puma concolor*) predation (Festa-Bianchet et al., 2006), averaging 17 rams. Therefore, drift may play a substantial role in changes in allele frequencies and fluctuations in breeding values over time.

Traill et al. (2014) suggested that all phenotypic changes in mass observed at Ram Mountain were due to demographic changes in response to hunting. Our analyses of horn length, however, support the result of Coltman et al. (2003) and suggest that observed changes in horn length were due to an evolutionary response to artificial selection. The difference between these studies can be explained in two ways. First, the simulations presented by Traill et al. (2014) were based on body mass. Although horn length and body mass have a moderate genetic correlation (0.48, (Poissant et al., 2012)), mass is not a direct target of trophy hunting. More importantly, the inheritance function in Traill et al. (2014) links parent and offspring phenotype solely upon the relationship between parental mass at conception and offspring mass at weaning : it does not allow large fathers to produce offspring that grow to become large adults (Hedrick et al., 2014 ; Chevin, 2015) despite strong heritability of adult mass in this population (Poissant et al., 2012). The 'inheritance' function is nearly zero for father-offspring, while the mother-offspring function explains only about 5% of the variance in weaning mass (Festa-Bianchet and Jorgenson, 1998 ; Réale et al., 1999).

Between 1973 and 1996, the horn length of bighorn rams on Ram Mountain declined by nearly 30% (Coltman et al., 2003). It has since recovered by about 13%. When the artificial selection stopped, estimated breeding values did not increase, but there was a phenotypic increase in horn length. The very low population density in the last 15 years may have contributed to the non-genetic increase in mean age-corrected horn length, which remains smaller than 30-40 years ago (Fig. 3.1). Environmental factors such as population density and weather play important roles in horn growth (Jorgenson et al., 1993 ; Festa-Bianchet et al., 2014). For example, a doubling of population size at Ram Mountain contributed to a decline in ram horn length, which, however, remained stable during an earlier period of experimental population control through ewe removals (Jorgenson et al., 1993). Therefore, it is important to adequately partition environmental and genetic phenotypic changes. Including both cohort and year in the animal model should control for both long- and short-term effects of these variables on the phenotype (Wilson et al., 2010).

It seems reasonable to expect that strong artificial selection on heritable traits may lead to evolutionary changes (Garland and Rose, 2009). A study on 74 domestic sheep (*Ovis aries*) breeds found strong genetic signals of selection for the absence of horns and for other traits such as body size, reproduction and pigmentation (Kijas et al., 2012). Evidence for the evolutionary effects of selective hunting in wild terrestrial species, however, remains scarce and controversial (Mysterud, 2011). We suggest that evidence is scarce partly because it requires detailed long-term data on genotypes, phenotypes, vital rates, population fluctuations, harvest pressure and environmental changes in harvested populations. Most longitudinal studies of wild vertebrates that have collected these data have been conducted on unharvested populations. There is abundant support for artificial selection in commercially-exploited fish and recent studies provide evidence of a genetic response to that selection over a few generations (Swain et al., 2007 ; van Wijk et al., 2013). Therefore, it should not be surprising to find an effect of artificial selection over about 3-4 generations of bighorn sheep, given that rams with 4/5-curl horn faced a 40% yearly probability of being shot and that the negative selective pressure through hunting started 2-3 years before large-horned rams could achieve high reproductive success (Coltman et al., 2002). Long-term phenotypic data from harvested rams support this contention by showing temporal declines in horn length in populations subject to high harvest pressure. Age-specific horn size of Rocky Mountain bighorn rams declined in Alberta (Festa-Bianchet et al., 2014) but not in the neighbouring province of British Columbia, where a more conservative definition of 'legal' ram reduces harvest pressure (Hengeveld and Festa-Bianchet, 2011). Similarly, in Stone's rams (*Ovis dalli*), early horn growth declined under intense selective harvest, but not in under lower hunting pressure (Douhard et al., 2016).

Using detailed monitoring of a harvested population, we provide evidence that horn length – a trait directly targeted by trophy hunting – declined in response to intense artificial selection. The lack of evolutionary recovery in mean horn length breeding values after harvest stopped supports the hypothesis that recovery from potentially maladaptive human-induced evolution is slow, likely because natural selective pressures are weaker than artificial ones (Swain et al., 2007 ; Allendorf and Hard, 2009). Given the substantial economic importance of trophy hunting (Foote and Wenzel, 2009) and its potential role in conservation (Leader-Williams et al., 2001), it is critical to assess what levels of selective harvest can drive evolution in game species.

3.7 Acknowledgement

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CHAPITRE 4

IMPORTANCE RELATIVE DES CHANGEMENTS ÉVOLUTIFS

4.1 Description de l'article et contribution

Il est de plus en plus évident que des pressions anthropiques sont à la source de changements évolutifs. En parallèle, plusieurs études en laboratoire ou en microcosme ont montré que les changements évolutifs en traits peuvent avoir des conséquences importantes sur la dynamique de population. Plusieurs ont tenté de quantifier l'impact de ces changements évolutifs sur le taux de croissance en nature, mais peu ont fait la distinction entre l'impact des changements plastiques et l'impact des changements évolutifs. En combinant un modèle animal bayésien, une analyse démographique et une méthode de partitionnement récemment développée, j'ai tenté de combler ce manque dans nos connaissances en dynamique éco-évolutive. De plus, j'ai quantifié l'effet de la période d'observation sur l'importance relative des changements plastiques et évolutifs sur le taux de croissance de la population. Cette étude est une des premières à quantifier l'importance relative de l'évolution et des changements plastiques en traits sur le taux de croissance d'une population sauvage de mammifère.

L'idée de base de cet article avait été élaborée avec Fanie Pelletier au tout début de mon doctorat et consistait à reproduire le papier de Ezard et al. (2009), mais en utilisant la nouvelle méthode de Ellner et al. (2011). J'ai par la suite rendu le tout plus compliqué comme j'en ai l'habitude. J'ai modifié la méthode pour inclure l'importance relative des changements en structure d'âge et en densité. J'ai effectué les analyses statistiques et l'écriture de la première version du manuscrit. Tom Ezard m'a donné plusieurs conseils sur l'incorporation de l'erreur autour de l'estimation de l'effet de la structure d'âge et sur divers aspect à travailler. Dave Coltman a fourni la généalogie. Fanie Pelletier a supervisé le tout et a corrigé plusieurs versions du manuscrit. Tous les co-auteurs ont contribué aux multiples révisions du manuscrit.

Fluctuating effects of genetic and plastic changes in body mass on population dynamics in a large herbivore

In press at Ecology

Gabriel Pigeon, Thomas H. G. Ezard, Marco Festa-Bianchet, David W. Coltman and Fanie Pelletier

4.2 Abstract

Recent studies suggest that evolutionary changes can occur on a contemporary time scale. Hence, evolution can influence ecology and vice-versa. To understand the importance of eco-evolutionary dynamics in population dynamics, we must quantify the relative contribution of ecological and evolutionary changes to population growth and other ecological processes. To date, however most eco-evolutionary dynamics studies have not partitioned the relative contribution of plastic and evolutionary changes in traits on population, community and ecosystem processes. Here, we quantify the effects of heritable and non-heritable changes in body mass distribution on survival, recruitment and population growth in wild bighorn sheep (*Ovis canadensis*) and compare their importance to the effects of changes in age structure, population density and weather. We applied a combination of a pedigree-based quantitative genetics model, statistical analyses on demography and a new statistical decomposition technique, the Geber method, to a long-term dataset of bighorn sheep on Ram Mountain (Canada), monitored individually from 1975 to 2012. We show three main results : (1) The relative importance of heritable change in mass, non-heritable change in mass, age structure, density and climate on population growth rate changed substantially over time. (2) An increase in body mass was accompanied by an increase in population growth through higher survival and recruitment rate. (3) Over the entire study period, changes in the body mass distribution of ewes, mostly through non-heritable changes, affected population growth to a similar extent as changes in age structure or in density. The importance of evolutionary changes, was small compared to that of other drivers of changes in population growth but increased with time as evolutionary changes accumulated. Evolutionary changes became increasingly important for population growth as the length of the study period considered increased. Our results highlight the complex ways in which ecological and evolutionary changes can affect population dynamics and illustrate the large potential effect of trait changes on population processes.

4.3 Introduction

It has recently become apparent that evolutionary changes can occur on an ecological timescale (Thompson, 1998). Rates of phenotypic changes are on average 1/4 (and up to 2/3) the rates of change in population size, suggesting that both processes occur on similar time scales (Delong et al., 2016). Evolution on contemporary timescales has been documented in a wide range of organisms including plants (Maron et al., 2004), fish (Hendry et al., 2000), birds (Grant et Grant, 2006) and humans (Milot et al., 2011). A potential consequence of contemporary evolutionary changes is that they may affect ecological processes including population, community and ecosystem dynamics (Post et Palkovacs, 2009) which could, in turn, produce a new selective landscape. Those reciprocal interactions between evolution and ecology are termed eco-evolutionary dynamics (Pelletier et al., 2009), and their quantification is important for a holistic understanding of factors driving population dynamics. For example, in predator-prey systems of rotifers (*Brachionus calyciflorus*) and green algae (*Chlorella vulgaris*), populations cycles varied according to whether or not prey populations were allowed to evolve (Yoshida et al., 2003). In another rotifer system, phosphorus limitation led to evolution of reduced investment in sex, which impacted population dynamics (Declerck et al., 2015). Most studies of eco-evolutionary dynamics to date, however, have been on short-lived species or in experimental systems (Hendry, 2016a). Given the increasing reports of human-driven trait changes in nature (Darimont et al., 2009 ; Alberti et al., 2017), it is critical to assess the potential consequences of those changes in traits on population processes in wild and exploited species. For example, recent data-based models of the northeast Arctic cod stock suggest that both evolutionary and plastic changes in traits must be considered to accurately explain the observed trends in life-history traits and population dynamics (Eikeset et al., 2016).

Phenotypes can shape an individual's ability to survive, grow and reproduce. Consequently, the distribution of phenotypes in a population can have strong impact on its dynamics (Pelletier et al., 2007a). In five ungulate populations under long-term monitoring, the effect of a change in mean birth weight on population growth was of similar magnitude to that of climatic drivers (Ezard et al., 2009). This suggests that evolutionary changes of traits with a genetic basis can modify population dynamics. Although a change in mean trait value in a population can be due to evolution, it can also be due to other ecological factors including changes in age structure or plastic changes (Coulson et al., 2008). Most published eco-evolutionary analyses to date, however, have not evaluated whether traits changes are due to heritable or plastic changes

(Ezard et al., 2009 ; Hendry, 2016a).

Phenotypic plasticity, the ability of a single genotype to produce a range of phenotypes in response to environmental variation (Forsman, 2015), can have a major effect on population growth and persistence (Reed et al., 2010) because it allows individuals to adjust their traits to variable environments to maximize their survival and reproduction. For example, defense structures, such as the spine in Daphnia pulex, can be induced by high predation risk (Spitze, 1992) and the breeding phenology of red deer (*Cervus elaphus*) can change to match ecological conditions (Moyes et al., 2011). In the context of eco-evolutionary dynamics, it is important to know whether an effect of trait changes on population processes is due to plasticity, genetic evolution, or both to identify whether the feedbacks between traits and population processes are due to an eco-to-eco interaction, caused by a plastic change in trait, or to an evo-to-eco interaction catalysed by genetic change. Eco-to-eco interactions are likely to occur more frequently due to the rapidity of plastic trait change and may be of greater magnitude (Hendry, 2016b), but evo-to-eco effects may be more critical to the persistence of populations facing a changing environment such as in the case of evolutionary rescue (Carlson et al., 2014). Partitioning the relative contribution of plastic and evolutionary changes is also important because phenotypic plasticity may compensate for evolutionary change, leading to cryptic eco-evolutionary dynamics (Kinnison et al., 2015). From an applied perspective, evolutionary changes in traits due to selective harvest are expected to revert to their pre-selection state more slowly than plastic changes when harvesting stops (Swain et al., 2007 ; Allendorf et Hard, 2009 ; Pigeon et al., 2016). Thus, evo-to-eco interactions may have long-term effects on population growth and productivity (Dunlop et al., 2015) and might be critical for conservation and management. Thus, it is important to partition the effects of traits changes into those due to heritable and non-heritable change to obtain realistic effect sizes of the relative importance of evolutionary and ecological processes. Empirical examples of such distinctions remain scarce (Hendry, 2016a).

Several methods have been developed to quantify the importance of trait change on population dynamics (van Benthem et al., 2017). When sufficient data are available, the best approach to evaluate the genetic basis of a trait is to use a pedigree-based quantitative genetics models (e.g., the animal model ; Kruuk 2004), while the best method to partition the effects of plastic and evolutionary trait change on population growth is the Geber approach developed by Ellner et al. (2011). This is an extension of the approach proposed by Hairston et al. (2005), combining it with the Price equation (Price, 1970 ; 1972), to partition trait changes into the effects of heritable change, non-heritable phenotypic change and environment. The Geber approach provides a general framework to partition the contribution of change in breeding values, in trait and in environmental factors on population-level parameter such as population growth rate. It does this by : 1) fitting models to quantify the effects of the trait and ecological factors on population growth rate, 2) distinguishing heritable trait change from non-heritable trait change (i.e. plastic change, also referred to as environmental deviation) by comparing temporal phenotypic changes to changes in breeding values, and 3) partitioning the variance in population growth rate by combining the observed changes in average population breeding values, environmental deviation and ecological factors with their estimated effects obtained from statistical modeling (Ellner et al., 2011).

Here we compare the relative importance of changes in phenotypic traits, climate, density and age structure on population dynamics. We use the Geber approach to decompose the effects of heritable and non-heritable change in mass, age structure, density and a large-scale climate index on survival and reproduction of bighorn sheep (*Ovis canadensis*). Finally, we combine age-specific changes in survival and recruitment with age structure to quantify the effects of a change in environment, focal trait or age structure on population growth (Coulson et al., 2008). We do this for different time periods when the population growth rates increased and decreased. We expect that non-heritable changes in traits should be more important than heritable changes in explaining the association between traits and population growth on a short time scale. Further, we explore the impact of the period length on our quantification of the magnitude of ecological and evolutionary effects. We expected that the importance of heritable trait changes on population processes would increase over longer time periods. We used detailed long-term individual monitoring of female bighorn sheep from a wild population in Canada with a pedigree 8 generations deep (Coltman et al., 2005). By combining pedigree-based quantitative genetics models, demographic statistical analyses and the extended Geber approach (Ellner et al., 2011), we bring novel insights into the relative importance of density, age structure, heritable and non-heritable changes in mass on changes in population size. Our results suggest that while the distribution of body mass can have as much impact on population dynamics as density or age structure, this effect is mostly due to plastic changes. Heritable changes in morphological traits of long-lived species tend to be slow and may become larger than the non-heritable effect of traits changes only over a long temporal scale.

4.4 Methods

4.4.1 Population and study area

We studied bighorn sheep on Ram Mountain, Alberta, Canada (52°N, 115°W, elevation 1080 to 2170 m). The study area covers about 38 km^2 of alpine and subalpine habitat approximately 30 km east of the Rocky Mountains. The population has been closely monitored each summer since 1975 (Jorgenson et al., 1993). Individuals are marked using ear tags or visual collars. Annual resighting probability for ewes is over 99% (Jorgenson et Festa-Bianchet, 1997), so they can be considered dead when not seen for a year. Since all females in the population are marked and an exact census is made yearly (Jorgenson et Festa-Bianchet, 1997), we can precisely determine their annual survival rate. Recruitment rate is estimated by ewe-lamb associations. Sheep were captured each year between late May and late September in a corral trap baited with salt (Jorgenson et Festa-Bianchet, 1997). Ewes were typically recaptured every 4 to 5 weeks (mean=3.10 captures/year, SD=1.41).

4.4.2 Phenotypic and environmental measurements

Individuals were weighed at each capture. We adjusted mass to September 15 using linear mixed models with restricted maximum likelihood where both the intercept and the slope were allowed to vary for each individual (Martin et Pelletier, 2011). Density was the number of adult females alive in June each year, because females are the recruitment-limiting sex. Climate was represented by the Pacific Decadal Oscillation (PDO) index, obtained from the Joint Institute for the Study of the Atmosphere and Ocean website (http ://jisao.washington.edu). We used winter PDO, the average of monthly values from December to April, to evaluate the effect of winter harshness. Winter PDO affects population growth (Ezard et al., 2009) and horn length (Douhard et al., 2017) in mountain sheep.

4.4.3 Quantifying age structure

Several age classes were needed to quantify age structure because survival and recruitment have different age-specific patterns in large mammals. To choose age classes that best represent how survival and recruitment differ through age, we compared the Akaike Information Criterion corrected for small sample size (AICc) of all possible age class groupings and selected the classification that minimized AICc for both survival and recruitment (Appendix A2 : Fig A.1). Animals were thus classified as lamb, yearling, 2-3, 4-5, 6-7, 8-12 and older than 13 years. These classes broadly represent the ontogenetic changes in mass, survival and recruitment identified previously using alternative techniques (Bérubé et al., 1999 ; Loison et al., 1999).

4.4.4 Model fitting

The first step to partition variation of female population growth rate into the effects of five factors of interest (non-heritable and heritable change in mass, density, PDO and age structure) was to build models of individual annual survival and recruitment as a function of these factors. Population growth rate, in a closed population like Ram Mountain, can be approximated by the combination of survival and recruitment. Body mass was centered and scaled within each of the 7 previously determined age class to facilitate model convergence and remove multicollinearity with age class. This procedure also removed any effect of age from the change in mass, making it easier to partition the effect of age structure from the effect of change in mass. Density was also centered and scaled to one standard deviation to facilitate convergence (Bolker et al., 2013). We modeled survival from one year to the next and recruitment (the probability of weaning a lamb the following year) using binomial generalized mixed models, which controlled for non- independence due to repeated measurements by including individual identity and year as random effects. We used model selection based on AICc to identify parsimonious models with good predictive power. Candidate models included age class, mass, density, winter PDO and years of high cougar (*Puma concolor*) predation (Festa-Bianchet et al., 2006) as explanatory variables. Previous work detected positive density-dependence in a bighorn sheep population at very low densities (Bourbeau-Lemieux et al., 2011). We therefore tested quadratic effects of density to account for potential non-linear effects. We also tested the quadratic effects of mass and PDO as well as the interactions between mass, density, PDO and age. Given that multiple candidate models had similar support (difference in AICc < 4 ;(Burnham et Anderson, 2002), we used model averaging (Mazerolle, 2016) to obtain predicted responses and unconditional standard errors weighted according to each model's AICc weight.

4.4.5 Distinguishing heritable from non-heritable changes in mass

To estimate breeding values, we constructed a pedigree of the population. The pedigree included 1066 marked sheep with 836 maternities and 508 paternities. Maternities are established from field observations. From 1988 (except 1994 to 1996), tissue samples were collected for genetic analysis (Poissant et al., 2012). Paternities were assigned using CERVUS (Marshall et al., 1998) at a confidence level of >95% following Coltman et al. (2005).

Estimated breeding values (EBV) of mass, which represent an individuals' genetic value for this trait, were obtained with a bivariate animal model with female and male mass as response variables using a Bayesian framework with the "MCMCglmm" R library V2.21 (Hadfield, 2010 ; Hadfield et al., 2010 ; Wilson et al., 2010). More details on this animal model are reported in Pigeon et al. (2016). In dimorphic species with imperfect genetic correlation between male and female traits, a bivariate model maximizes information while accounting for genetic correlations (Wolak et al., 2015). Estimation of genetic parameters must account for the high genetic correlation between female and male mass (posterior mean= 0.74, CI= 0.39 – 0.99) in order to obtain less biased estimates. We centered and standardized mass in each age/sex (females aged 13 years and older were pooled due to low sample size (N= 91) above that age) to have a mean of 0 and a variance 1 before analysis, because phenotypic variances differed between sexes and increased with age. Centering and standardizing keeps EBV on the same scale for further analysis. The initial model partitioned the phenotypic variance in male and female body mass into its additive genetic (Va), permanent environmental (Vpe), maternal (Vm), cohort (Vce) and yearly environmental (Ve) components and residual variance (Vr) (see Pigeon et al. (2016) for details on model parameterization). To obtain a comprehensive EBV accounting for the above variance partitions, models with different random effects were compared using the deviance information criterion (DIC), which balances model fit and complexity simultaneously (Wilson et al., 2010). The maternal variance component was dropped from the final model since it did not reduce DIC. The model was first fitted with a multivariate inverse-Wishart prior (Wilson et al., 2010) and run for 9000000 iterations with a burn-in period of 1500000 and a thinning of 7500. Sensitivity to the prior was tested by re-running the model with more informative priors, leading to similar results (Pigeon et al., 2016). We extracted the posterior distribution of breeding values from this final model, to reduce bias in error estimation (Hadfield et al., 2010).

Finally, we distinguished the effect of heritable from non-heritable changes in population average body mass. To do so, we fitted two linear regressions for each age-class, one of annual average population mass as a function of time and a second of annual average EBV as a function of time. The difference between the fitted values of these two regressions each year is the environmental deviation for that year. The environmental deviation is, therefore, the change in trait mean expected if genotype frequencies were constant. Any deviation from this constant expectation is a non-heritable change in the trait and considered to be a plastic change in trait. This smoothing using regression has been suggested to reduce noise due to yearly environmental stochasticity (Ellner et al., 2011).

4.4.6 Variance partitioning

During our study, population size varied substantially through periods of increase and decline (Fig. 1b). To ensure parsimony while allowing time for heritable change in mass to occur, we separated the study into periods characterized by changes in population growth rate. To define these periods, we fitted a generalized additive model of mean annual growth rate as a function of year. We then compared this model to broken stick regressions using version 0.5-1.1 of the "segmented" R library (Muggeo, 2003) with an increasing number of breakpoints. The most parsimonious model included three periods : period 1 (1975-1989), period 2 (1989-1997) and period 3 (1997-2012) (Appendix A2 : Fig A.8). We partitioned the variance in survival and recruitment independently for each period using an extension of the Geber method (Ellner et al., 2011). The method partitions the changes in each focal variable between the first and the last years of the period. To test the importance of period length, we also applied the variance partitioning approach (without error estimation, using posterior mode of EBV) on a range of periods from 37 one-year periods to a single 37-year period. We therefore produced an additional 115 periods lasting 1 to 37 years (mean = 6), which started in different years to cover systematically the entire study. We then tested for linear and quadratic effects of period length on the absolute effect size of heritable change in mass, non-heritable change in mass, change in density, age structure and climate on population growth rate using linear regressions.

Partitioning the variance in survival and recruitment was done in several steps to account for age structure. First, assuming a constant reaction norm, we added the mean annual EBV predicted by the linear regression with time to the environmental deviation to obtain a prediction of the expected trait for a given breeding value and environmental deviation. Second, we used the previously parameterized models (see model fitting section) to predict the expected value of survival or recruitment for each age class, given all combinations of annual mean EBV, annual environmental deviation, density and PDO. Cougar predation was fixed as absent, as it only occurred in 5 of 38 years. Age-specific predicted survival and recruitment were obtained using model averaging (Mazerolle, 2016). The age-specific predicted survival and recruitment rates were then combined to produce a weighted population average according to their respective proportions in the population at each given time (Coulson et al., 2008) to account explicitly for changes in age structure (Appendix A2 : Fig A.9). Finally, we estimated the average effect of the observed change in a given variable on population mean survival and recruitment when all other factors were kept constant. For example, the following equation was used to estimate the effect of heritable change on survival and recruitment (Ellner et al., 2011).

$$EVO = \frac{\sum_{e=1}^{2}\sum_{d=1}^{2}\sum_{a=1}^{2}\sum_{w=1}^{2}(X_{2edaw} - X_{1edaw})}{16}$$

Where X_{2edaw} is the predicted survival or recruitment of a population with mean breeding value at the end of the period, the environmental deviation e, density d, age structure a and PDO w. X_{1edaw} is the same but with the mean breeding value at the beginning of the period. Values of 1 or 2 for e, d, a and w refer to their given value at beginning and end of the period respectively. The resulting value of EVO is the expected change in survival or recruitment due to the observed change in breeding value during the period. Equivalent formulas were used for all other factors of interest. The effects of the 5 partitioned factors (ECO, EVO, AGE.STR, DENS and PDO) sum to the change in survival and recruitment predicted by the models for a given period. To better understand the impact of these effects on population dynamics, we also repeated this last step with the predicted population growth rate, obtained by dividing the predicted recruitment by 2 (to account for the production of male lambs assuming an even birth sex-ratio) and adding the predicted survival.

4.4.7 Measuring uncertainty

We measured uncertainty at multiple levels. We used a Bayesian framework to estimate breeding values and properly quantify EBV errors (Hadfield et al., 2010). For each sample of the posterior distribution in breeding value, we re-calculated the temporal trend in breeding value and the yearly environmental deviation. We then used model averaging as previously described to estimate expected survival and recruitment for each age class and unconditional errors (eq. 6.12 of Burnham et Anderson (2002)) around these values. To account for errors in these estimates, we randomly drew values from a normal distribution centered on the expected value with standard deviation equal to the unconditional errors of the expected value. Hence, we obtained distributions of predicted survival and recruitment for each age-class that reflected uncertainty in both the estimation of environmental deviance and in the estimation of the model parameters. We then applied the variance decomposition approach described above on each realization of the Markov chain. The effects were considered significant when the 95% highest posterior density interval did not overlap 0. All analyses were done in R (Version 3.3.3).

4.5 Results

4.5.1 Model fitting

Model selection for survival revealed that age class, density, their interaction and body mass best explained female survival, as these variables were present in all models with difference in AICc < 4 (Appendix A2 : Table A.3 and Fig A.10). Density had a strong negative effect on lamb survival but no effect on survival for prime age classes (Fig A.10). Body mass had a positive effect on survival of all age classes. Predation decreased survival, while PDO had a very small quadratic effect. Predictions of mean survival by year fitted observed values with a correlation of 0.36 ($P < 0.001$). Model selection for recruitment revealed that age class, body mass, their interaction, density and predation best explained female recruitment, as these variables were present in all models within 4 AIC units of the best model(Appendix A2 : Table A.4 and Fig A.11). Density had quadratic effects on recruitment, with maximum recruitment at intermediate densities, suggesting an Allee effect. Mass increased the probability of recruitment for females of all ages, although it was least important in prime-aged females, which had a high probability of reproducing even when very light. PDO (associated with warm and dry winter) had negligible effects on recruitment. Finally, predation decreased recruitment. Predictions of average recruitment by year fitted observed values with a correlation of 0.71 ($P < 0.001$).

4.5.2 Variance partitioning

Female mass varied substantially over time (Fig 4.1a) with periods of increase and decrease (Appendix A2 : Table A.5). A significant portion of this variation in phenotype could be explained by additive genetic variance ; female mass was heritable (h2= 0.22, Appendix A2 : Table A.6). Temporal variation in EBV of female mass, however, was much smaller than the observed variation in mass (Appendix A2 : Table A.7 and Fig A.12).

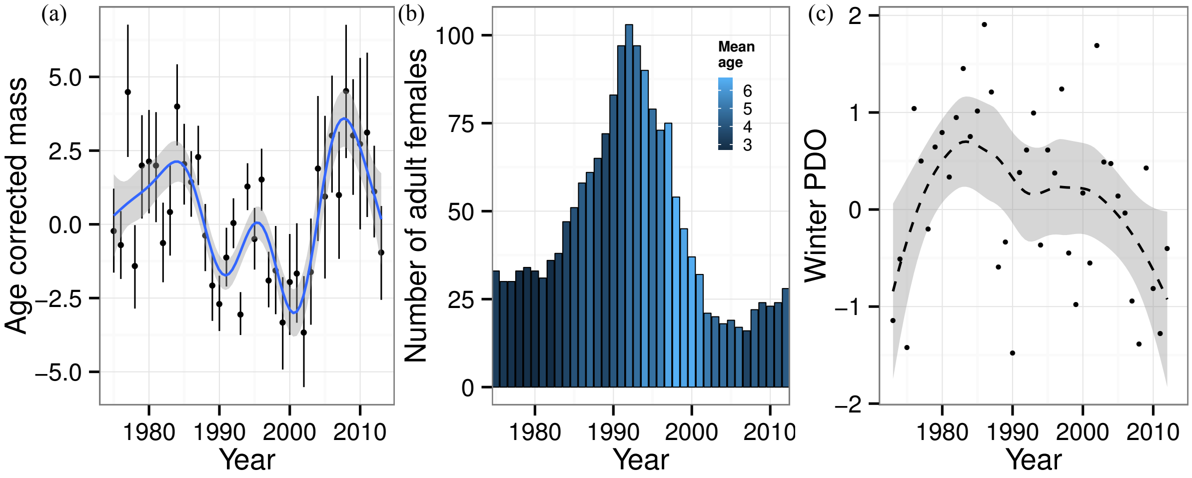

Figure 4.1 Temporal change in a) mean age-adjusted female mass in mid-September (error bars represent SD) ; b) number of adult females and mean age of all females ; c) PDO from 1975 to 2012 for bighorn sheep at Ram Mountain, Alberta, Canada. Splines were fitted using locally weighted scatterplot smoothing (loess).

Partitioning the variance in survival into the effects of heritable change in mass, non-heritable change in mass, change in density, age structure and climate revealed substantial variation in their relative contribution over time (Fig 4.2a), except for PDO whose contribution was negligible over the entire study. During the first period, a change in age structure associated with aging of the population had the strongest effect (posterior mean=0.031, 95% CI = 0.022 – 0.040). Changes in heritable and non-heritable mass made smaller and non-significant contributions (posterior means of 0.002 ; CI=–0.013 – 0.015 and -0.008 ; CI=-0.008 – 0.019, respectively) resulting in an overall increase in survival of 0.044. Changes in both density and PDO made negligible contributions to change in survival during this period. During the second period, the observed non-heritable decline in mass and the observed increase in density contributed most to the decline in survival (posterior means = -0.042 ; CI=-0.054 – -0.031 and -0.020 ; CI=-0.030 – -0.011 respectively), resulting in an overall decrease in survival of 0.071. A non-significant negative effect (posterior mean of -0.002 ; CI=-0.013 – 0.010) of the heritable change in mass was also detected. The third period was characterized by a strong positive effect of non-heritable change in mass (posterior mean of 0.059 ; CI=0.039 – 0.077), which was opposed by the effect of the change in density (posterior mean of -0.031 ; CI=-0.044 – -0.016) to yield a very small increase in survival (0.011). Overall, non-heritable change in mass had the greatest effect on survival, followed by density, age structure and heritable changes in mass (average absolute effect size of 0.036, 0.018, 0.013 and 0.006 respectively). Winter PDO had a negligible effect (average absolute effect size of 0.001) on changes in survival observed over 4 decades.

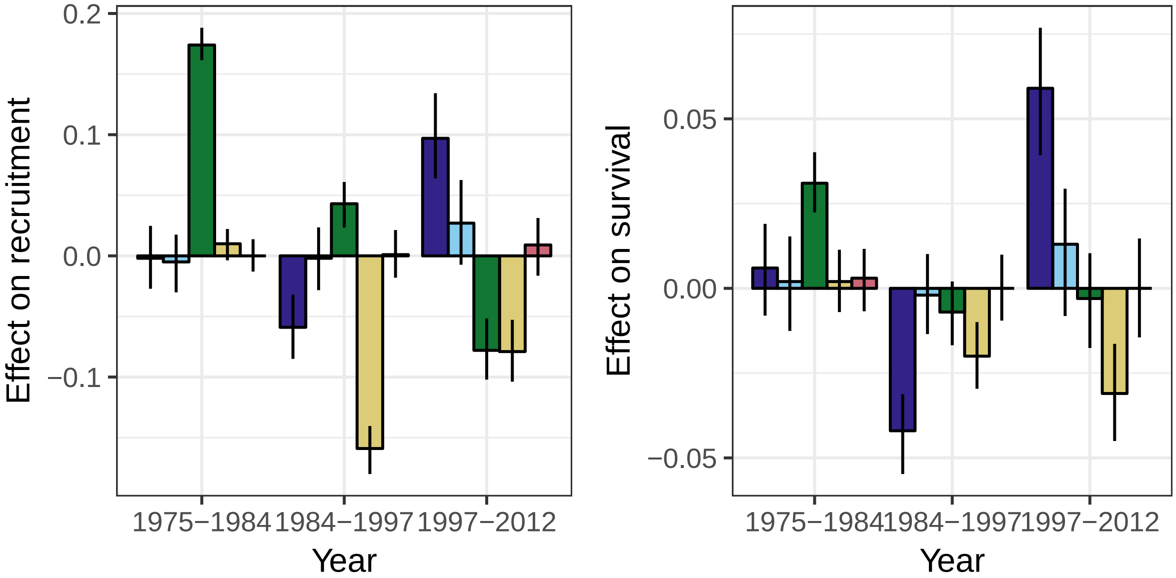

Figure 4.2 Partitioning the change in a) probability to survive and b) to wean a lamb into five components : non-heritable change in mass (dark blue), heritable change in mass (light blue), change in age structure (green), change in population density (beige) and change in PDO (pink). Analyses of a long-term study of bighorn sheep in Canada were conducted separately for 3 periods : 1975-1984, 1984-1997 and 1997-2012. Bars show the effect on survival and recruitment of the observed change in a given variable. The values of the bar and the associated errors represent the mean and 95% CI (see Measuring uncertainty section).

The effects of heritable change in mass, non-heritable change in mass, change in density, age structure and climate on recruitment also varied considerably over the study periods (Fig. 4.2b). The first period was dominated by a positive effect of the change in age structure associated with aging of the population (posterior mean=0.174, 95% CI = 0.161 – 0.188). Ageing reduced the proportion of young females, especially lambs and yearlings, whose survival and recruitment are low (Appendix A2 : Figure A.13). Changes in density, heritable and non-heritable mass made smaller contributions (posterior means of 0.010 [CI=-0.004 – 0.022], -0.005 [CI=-0.030 – 0.017] and -0.002 [CI=0.027 – 0.024] respectively) resulting in an overall increase in recruitment of 0.177. During the second period, the non-heritable decline in mass and the strong change in density explained most of the 0.176 decline in probability to wean a lamb (posterior means of -0.059 [CI=-0.085 – -0.031] and -0.159 [CI=-0.180 – -0.140] respectively). Heritable change in mass had no effect (posterior mean of -0.002 ; CI=-0.0288 –0.024). These effects were counteracted in part by the positive effect on recruitment of the change in age structure, with more females in the more productive age classes (posterior mean of 0.043 ; CI=0.023 – 0.061). The third period was characterized by a strong positive effect of non-heritable change in mass (posterior mean of 0.097 ; CI=0.063 – 0.134). This was opposed by the combined negative effect of the change in density and an increasingly younger age structure (posterior mean of -0.079 [CI=-0.104 – -0.053] and -0.078[CI=-0.102 – -0.051] respectively) resulting in a net decrease in recruitment of 0.024. Overall, change in age structure had the greatest effect on recruitment, followed by density, plastic change in mass and heritable changes in mass (mean absolute effect size of 0.098, 0.083, 0.052 and 0.011 respectively). Winter PDO had a negligible effect (mean absolute effect size of 0.003) on changes in recruitment observed in the 4 decades monitored.

When survival and recruitment where combined into population growth rate, the relative importance of heritable change in mass, non-heritable change in mass, change in density, age structure and climate were similar to those presented above (Fig. 4.3). The first period was dominated by a positive effect (posterior mean=0.118, 95% CI = 0.108 – 0.131) of the change in age structure associated with aging of the population. Changes in density, heritable and non-heritable mass made smaller contributions (posterior means of 0.007 [CI=-0.004 – 0.018], 0.004 [CI=-0.017 – 0.028] and -0.0003 [CI=0.023 – 0.020] respectively). During the second period, the non-heritable decline in mass and the strong change in density explained most of the decline in population growth (posterior means of -0.071 [CI=-0.091 – -0.050] and -0.099 [CI=-0.113 – -0.085] respectively). No effect (posterior mean of -0.004 ; CI=-0.023 – 0.017) of the heritable change in mass was detected. The change in age structure had a slight positive effect on population growth (posterior mean of 0.014 ; CI=0.0004 – 0.026). The third period was characterized by a strong positive effect of non-heritable change in mass (posterior mean of 0.107 ; CI=0.075 – 0.136). This was opposed by the combined negative effects of the change in density and a younger age structure (posterior mean of -0.071 [CI=-0.089 – -0.050] and -0.042 [CI=-0.059 – -0.023] respectively). Heritable change in mass had a small non-significant effect (0.026 [CI=-0.005– 0.056]). In this population, non-heritable change in mass had the greatest effect on population growth, followed by density, age structure and heritable changes in mass (mean absolute effect size of 0.061, 0.059, 0.058 and 0.010 respectively). Winter PDO had a negligible effect (mean absolute effect size of 0.002) on changes in population growth observed in the 4 decades monitored.

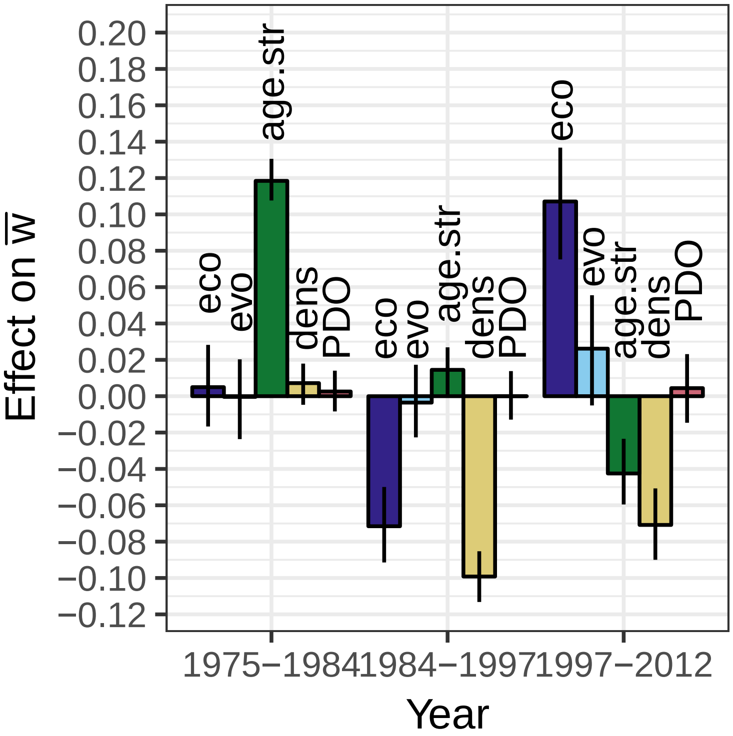

Figure 4.3 Partitioning the change in population growth into five components : non-heritable change in mass (dark blue ; “eco”), heritable change in mass (light blue ; “evo”), change in age structure (green ; “age.str”), change in population density (beige ; “dens”) and change in PDO (pink ; “PDO”). Analyses of a long-term study of bighorn sheep in Canada were conducted separately for 3 periods : 1975-1984, 1984-1997 and 1997-2012. Bars show the effect on population growth of the observed change in a given variable. The values of the bar and the associated errors represent the mean and 95% CI (see Measuring uncertainty section).

By partitioning the relative importance of heritable and non-heritable changes in mass, change in density, age structure and climate on not only population growth rate, but also on survival and recruitment, we obtained a more mechanistic approach to population dynamics. To determine whether the effects on population growth manifested themselves mostly through effects on survival or on recruitment, we compared the absolute effect size of survival to the absolute effect size of half the recruitment, because population growth rate is equal to the mean survival added to half the recruitment (Coulson et al., 2008). Generally, effects through survival and recruitment did not differ significantly, but the relative importance of survival and recruitment upon how the variables we examined affected population growth varied among periods (Appendix A2 : table A.8). Changes in age structure more strongly affected population growth in all 3 periods via their effects on recruitment rather than on survival ($P = 0$, 0.004 and 0.001 respectively). Changes in density had greater effects on population growth rate by affecting recruitment rather than survival, but this difference was only significant ($P < 0.001$) during the second period. In all other period- variable combinations, recruitment and survival did not differ significantly in their contribution to change in population growth rate.

The importance of heritable and non-heritable changes in mass, as well as changes in density, age structure and climate on population growth rate varied according to the temporal scale at which these processes were measured (Fig. 4.4). At smaller temporal scale, effects of change in age-structure and non-heritable changes in mass were most important. However, the direction and magnitude of those effects were highly variable, ranging from -0.164 to 0.111 and -0.061 to 0.070 respectively. The importance of heritable change was minimal over short periods but increased with period length, producing a trend best fitted by a quadratic function ($\beta = 0.6.89e - 4$, $P < 0.001$; $B.quad = 1.5e - 5$, $P = 0.050$). The absolute effects of both density ($\beta = 0.006$, $P < 0.001$; $\beta.quad = -0.0002$, $P < 0.001$) and non-heritable change in mass ($\beta = 0.004$, $P < 0.001$; $\beta.quad = -0.0001$, $P < 0.001$) had strong quadratic trends, being highest for at intermediate lengths. We did not detect any significant trend between period length and the importance of age structure. While a significant quadratic trend was found for PDO, its effect on population growth rate remained very weak regardless of the length of the period considered.

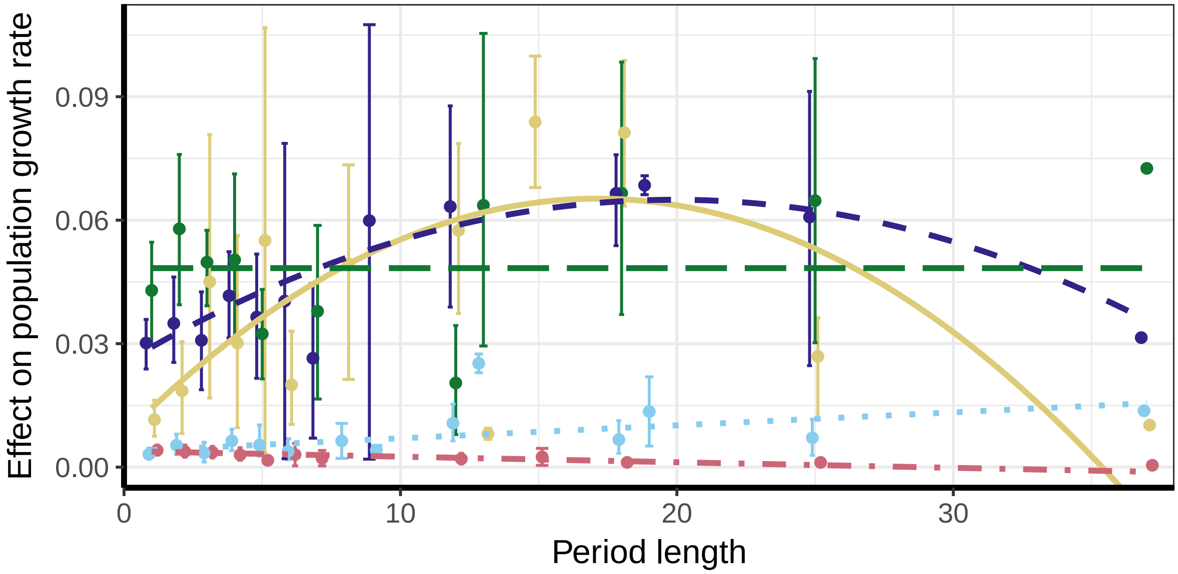

Figure 4.4 Absolute effect of non-heritable change in mass (dark blue ; short dash), heritable change in mass (light blue ; dotted), change in age structure (green ; long dash), change in population density (beige ; solid) and change in PDO (pink ; dot-dash) on population growth rate according to the length of the observation period (in years). Points represent the average absolute effect size (along with 95% confidence limits) for each estimated period length. Lines represent linear or quadratic (depending on which had lowest AICc) relationship between absolute effects size and the length of the period.

4.6 Discussion

By combining a pedigree-based quantitative genetics model, demographic statistical analyses and the recently developed Geber approach (Ellner et al., 2011) to exceptionally detailed data from a wild ungulate population, we found that although ecological variables such as age structure and density are major drivers of population dynamics, ecological and evolutionary changes in trait distribution also have a significant effect that varies between periods of different population trends. When decomposed by period, the most important cause of change in population dynamics was the non- heritable change in mass, closely followed by density and age structure, although the magnitude of these effects varied depending on the period considered. The effect of heritable changes in mass on survival, recruitment and population growth on a yearly basis not significant, but it increased with the length of the period considered. We found only a weak signal of evolutionary change in bighorn ewes mass (Appendix A2 : Table A.7). This result is not surprising given that breeding values for female mass did not show major changes over the study period. Therefore, our retrospective analysis shows that female plastic changes in mass play a dominant role over short time scales. Therefore, our retrospective analysis shows that while eco-evolutionary changes can play a significant role in our system, on short time scale plastic changes in mass play a more dominant role. Altogether, our study serves as an example of how ecological and evolutionary variables can interact in rather complex ways within populations, varying temporally and affecting different fitness components (survival or recruitment) to ultimately drive population growth (Figs. 4.2, 4.3).

It has been suggested that intense selective hunting of males could have undesirable consequences on population dynamics through indirect evolutionary impact on other segments of the population (Conover, 2002 ; Allendorf et Hard, 2009). In bighorn sheep, intense selection for smaller horns is exerted on males by trophy hunting. This anthropogenic selection led to a significant decline in the EBV of male horn length (Pigeon et al., 2016), a trait genetically correlated to female mass (genetic correlation = 0.43, (Poissant et al., 2012)). It was therefore suggested that anthropogenic pressures, such as selective hunting, could lead indirectly to maladaptive changes in female mass and potentially negatively affect population dynamics (Kuparinen et Festa-Bianchet, 2017). Our study shows, however, that heritable change in mass played no significant role in the change in population growth rate of this population, likely because evolutionary changes in mass were minimal despite the evolutionary response of horn length to selective harvest (Pigeon et al., 2016). While female mass has a strong genetic correlation with male horn length, it is also under strong natural selection, which would have opposed any detrimental evolutionary change. In a stable environment, traits with a high impact on fitness are likely to be near evolutionary optimum and are therefore less likely to vary, reducing their influence on population growth. In a changing environment, however, species may find themselves with sub-optimal phenotypes, and evolutionary change could be of crucial importance.

The importance of phenotypic trait distribution for population growth has been recognized (Pelletier et al., 2007a), leading to increased interest in eco- evolutionary dynamics (Pelletier et al., 2009). In line with previous studies, we found important effects of changes in mass, a trait often used as an integrator of condition, for both survival (Côté et Festa-Bianchet, 2001 ; Festa-Bianchet et al., 1997) and recruitment (Jorgenson et al., 1993 ; Martin et Festa-Bianchet, 2011). We also show that this result translates into an important effect of mass on population growth, as previously suggested by a simpler analysis of five ungulate populations (Ezard et al., 2009).

The impact of change in body mass on population dynamics, however, was mostly due to non-heritable changes, suggesting that our system is mostly driven by an eco-to-eco interaction. Mass is a highly plastic trait in bighorn sheep (Pelletier et al., 2007b). Temporal trends in the mean age- adjusted mass (Fig 4.1a) of the population are likely to reflect changes in body condition due to changes in resource availability or environmental conditions. High population density likely played an important role in reducing mass (Festa-Bianchet et al., 1998), through competition for resources. However, on a yearly basis, change in density explained less than 1% of the effects of plastic change in mass on population growth rate (Table A.9). This may be an underestimate, however, since density may have delayed effect on mass through, for example, maternal effects (Monteith et al., 2009). While maternal effects are present in bighorn sheep, they decline with age and mostly disappear by age 2 (Wilson et al., 2004). Hence, on the temporal scale of the 3 observed periods, the effect of density on mass through maternal effect is unlikely to be the main driver of population growth. Further, the effects of density and environmental changes are not always positively correlated : plastic changes in mass and density had opposite effects during the third period of the study, suggesting that drivers of mass change other than density are also present.

Important effects of age structure on population dynamics have been reported for many ungulates including bighorn sheep (Festa-Bianchet et al., 2003), Soay sheep (Coulson et al., 2001) and red deer (Clutton-Brock et al., 1997 ; Clutton-Brock et Coulson, 2002). Survival and recruitment vary substantially according to age (Gaillard et al., 2000). Hence, population age structure can drastically affect population growth. Lambs have much lower survival than adults and do not reproduce, so a small increase in the proportion of lambs can reduce population growth rate. The impact of age structure may be reduced over longer time periods if it was to stabilize, which has yet to happen in this population. While density had a strong negative effect on population growth during the second period, it had no significant effect during the first period. The negative effect of change in density during the third period was unexpected. A decrease in density is usually associated with increased population growth. The opposite effect we detect is due to the quadratic relationship between density and both survival and recruitment, which appeared in all but one of the top recruitment models. Although a quadratic relationship may oversimplify how density affects this population (Sugeno et Munch, 2013), the shape of this curve suggests positive density- dependence at low density (Courchamp et al., 1999). This might reflect Allee effects which have also been observed in another population of bighorn sheep, where probability to wean a lamb increased with density up to a threshold of around 90 sheep (Bourbeau-Lemieux et al., 2011).

Ecological and evolutionary variables may affect population growth by acting through survival and/or recruitment. Our analyses show that while both pathways were significant, the effects through recruitment tended to be larger, especially for age structure and density. This result is novel but not surprising given that adult female survival is high and varies little due to environmental canalization (Gaillard et Yoccoz, 2003). It must be noted, however, that the correlation between fitted and observed values was only 0.36 for the survival model compared to 0.71 for the recruitment model, which may account for the lower importance of survival compared to recruitment. The direction of the effects of change in age structure, density, climate and mass on survival was similar to how these variables affected mean population growth. In large herbivores, density dependence usually first affects juvenile mortality, then age at first reproduction, followed by reproduction of adult females, and finally adult mortality (Bonenfant et al., 2009). There are two likely reasons why density affected population growth less through survival than recruitment. First, density usually affects survival of juveniles to a much greater extent that survival of adults (Eberhardt, 2002). Lambs represent a small proportion of the population (average = 18%, SD= 0.07), therefore changes in juvenile survival cannot have strong immediate impacts on population growth if survival of other age classes remains unchanged (Gaillard et al., 2000). Second, we measured recruitment as weaning success. Hence, changes in pre-weaning lamb survival will drive changes in recruitment while only survival from weaning to 1 year will be included in survival. High variability in recruitment for this species (Gaillard et al., 2000) is consistent with the large effect sizes of the observed variables on population growth rate through recruitment.

Changes in non-heritable and heritable components of mass, density, age structure and PDO varied substantially over 40 years, making the selection of periods used for analysis challenging. With long periods, the choice of start and end-points can influence the results. Choosing the period to maximize change in one of the factors influencing mean population growth will maximize its relative effects on population growth, biasing the analysis. By defining periods based on changes in population growth (the response variable), we sought to minimize these biases while still maximising the change in population growth rate available to partition. However, given the retrospective nature of this analysis, the choice of study period will always have a consequence as shown by the variance in effect sizes (Figure 4.4). Analyses using an annual approach, however, over-emphasize factors with the potential for quick change (Gingerich, 1983 ;

2001). While evolutionary changes can occur over an ecological time scale (Thompson, 1998 ; Delong et al., 2016), significant genetic change requires a turnover of individuals and cannot occur over a single year in a species like bighorn sheep, with a generation time of 6.6 years. At Ram Mountain, the yearly average turnover rate was only 20.1%. Thus, on a very short time-scale, at least for long-lived species, demography and other ecological factors will always prevail, while in this system the relative importance of evolutionary variables increased as longer time periods were considered. For species with higher turnover rate, however, evolutionary variables might drive ecological processes on shorter time scale. This suggests that there may be a partial mismatch between ecological time scales and evolutionary timescales as suggested by Delong et al. (2016). This mismatch may be larger in species with slow life- history such as bighorn. To compare the relative importance of evolution and ecology, one must consider a time span when both processes are possible but also the life history speed of the organism under study. Interspecific comparisons of the relative importance of evolutionary changes should standardize the time span of observations relative to the potential change in genotypes, which will vary with generation time (Haldane, 1949). For example, evolutionary changes over a year are likely to be much more important for species with a short generation time such as *Daphnia* than for bighorn sheep, where accurate knowledge of population age structures is much more important to predict near-term population dynamics. Standardizing time span over generation time would allow for comparison of the relative importance of evolution not only between systems of the same species, but also across taxa.

In conclusion, distinguishing plastic and genetic changes in traits is crucial to quantify the importance of eco-evolutionary dynamics. Ignoring this distinction would have led to a largely inflated importance of evolutionary changes in driving population dynamics in bighorn sheep. Instead, we concluded that changes in female mass, although a very important driver of the population dynamics in our study, were not driven by genetic changes. Therefore, at least for body mass, the effect of trait changes on population dynamics are driven by eco-to-eco feedbacks and less by an evo-to-eco one. Yet, it is important to note that plasticity has been shown to be heritable too (Pelletier et al., 2007b) and therefore our classification of all plasticity as an ecological process is very conservative.We may underestimate the contribution of evolution by using such a narrow definition. Indeed, evolution of plasticity can play an important role in variation in population growth (Stoks et al., 2016). Only three generations exposed to indirect selection through trophy hunting were included in this study, which may be insufficient to detect a strong signal of eco-evolutionary dynamics. More empirical studies, with different traits and species, are necessary to disentangle the effects of plastic and genetic trait changes before broad conclusions can be made about the importance of evolutionary changes in the wild and furthermore about the temporal scale at which these changes substantially affect population dynamics. Our study highlights both the potential of evolutionary changes to modify population growth rate and the dangers of considering all trait changes as signs of evolution. The distinction between plastic and genetic trait change must be an integral part of empirical studies investigating the importance of eco-evolutionary dynamics.

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CHAPITRE 5

LES CAUSES ENVIRONNEMENTALES DES EFFETS COHORTE

5.1 Description de l'article et contribution

Les effets cohorte sont une source de différences interindividuelles importante pour la dynamique de population car ils ont le potentiel d'induire des délais dans la réponse de la population aux fluctuations environnementales. Cet article avait trois objectifs : 1) quantifier l'importance des effets cohorte sur la survie et la reproduction des femelles mouflon d'Amérique, 2) déterminer quelles sont les variables environnementales qui causent ces effets cohorte et 3) tester pour la présence de réponse prédictive adaptative. Bien que je n'ai trouvé aucune réponse prédictive adaptative dans la population de Ram Mountain, d'importants effets cohorte contexte-dépendants sont présents. Ceux-ci sont causés principalement par la densité à la naissance qui interagit avec la densité adulte pour réduire la probabilité de sevrer un agneau.

Pour cet article, j'ai participé à l'élaboration des idées avec Fanie Pelletier et j'ai effectué les analyses statistiques et l'écriture de la première version du manuscrit. Mathieu Douhard a grandement retardé la parution de cet article en me convainquant d'utiliser une méthode statistique plus robuste pour quantifier l'importance des effets cohorte. Il m'a aussi influencé grandement par rapport à l'intérêt de tester pour la présence de réponse adaptative prédictive. Fanie Pelletier a supervisé le tout. Fanie Pelletier et Marco Festa-Bianchet ont par la suite contribué à l'interprétation des résultats et à la révision du manuscrit.

Long-term fitness consequences of early environment in a long-lived ungulate

In press at Proceedings of the Royal Society : B.

Gabriel Pigeon, Marco Festa-Bianchet, and Fanie Pelletier

5.2 Abstract

Cohort effects can be a major source of heterogeneity and play an important role in population dynamics. Silver-spoon effects, when environmental quality at birth improves future performance regardless of the adult environment, can induce strong lagged responses on population growth. Alternatively, the external predictive adaptive response (PAR) hypothesis predicts that organisms will adjust their developmental trajectory and physiology during early life in anticipation of expected adult conditions, but has rarely been assessed in wild species. We used over 40 years of detailed individual monitoring of bighorn ewes (*Ovis canadensis*) to quantify long-term cohort effects on survival and reproduction. We then tested both the silver-spoon and the PAR hypotheses. Cohort effects involved a strong interaction between birth and current environments : reproduction and survival were lowest for ewes that were born and lived at high population densities. This interaction, however, does not support the PAR hypothesis because individuals with matching high-density birth and adult environment had reduced fitness. Instead, individuals born at high density had overall lower life-time fitness suggesting a silver-spoon effect. Early-life conditions can induce long-term changes in fitness components and their effects on cohort fitness vary according to adult environment.

Keyword : cohort effects, predictive adaptive response, silver-spoon, climate, density dependence, ungulate

5.3 Introduction

Individual differences in life-history traits play an important role in population processes [1, 2], where sex and age are important structuring factors. Sex ratio and age structure affect population dynamics because survival typically varies between sexes [3] and reproduction and survival are often strongly dependent on age [4]. Cohort effects are another source of variation, and occur when environmental conditions early in life generate average differences in future performance among individuals born in different years [5]. Cohort effects have been documented in many taxa including reptiles [6, 7, 8], birds [9, 10], mammals [11, 12] and humans [13] and can have strong influence on population dynamics.

Early-life conditions can have delayed consequences on fitness components [9]. For example, conditions during ontogeny by zebra finches (*Taeniopygia guttata*) and great tits (*Parus major*) permanently affect clutch size [14]. In red squirrels (*Tamiasciurus hudsonicus*), high density at birth reduces adult survival [11]. These permanent influences of early-life conditions on life-history traits, independent of the adult environment, have been termed silver-spoon effects [15]. They increase heterogeneity because cohorts born under more favorable environmental conditions have higher lifetime performance. For example, cohorts of red- billed choughs (*Pyrrhocorax pyrrhocorax*) born in favorable years fledge more offspring over their lifetime than cohorts born in unfavorable years [10]. Hence, conditions during early life can have long-term consequences on population dynamics. Models have shown that in populations with overlapping generations, delayed performance effects can increase individual differences in fitness, potentially destabilizing population dynamics [16]. Cohort effects, however, can also be influenced by environmental conditions during adulthood. For example, a favorable adult environment could mask cohort differences induced by poor early conditions. This situation has recently been referred to as 'beneficially saturated conditions' [17] because very favorable adult conditions may enable maximum possible performance for all individual and mask differences between cohorts.

The external predictive adaptive response (PAR) hypothesis [18] suggests, however, that if conditions during early life anticipate those likely met as adults, early environment may adaptively shape development and physiology to anticipate predicted adult conditions. Thus, individuals encountering matching environments when young and adult should have higher fitness. In meadow voles (*Microtus pennsylvanicus*), maternal exposure to different photoperiods influences the development of coat thickness of newborns [19], improving fitness by matching phenotype to birth season. In zebra finches, early-life exposure to heat stress increased survival of individuals who also experienced heat stress as adults [20]. Although support for this hypothesis has been found in humans [21] and in laboratory experiments [18, 19], evidence for PAR in wild animals is weak [22, 23, 24]. In roe deer (*Capreolus capreolus*), fitness consequences of early-life environment fit the silver-spoon better than the PAR hypothesis [25]. Similarly, in red deer (*Cervus elaphus*), the effect of birth density on aging is independent of density as adult [4]. The assumption that early-life environmental conditions reliably predict future environment has been questioned [26]. For long-lived species, short-term environmental and ecological fluctuations may considerably reduce the predictive power of birth environment on future environment.

Interactions between environments during adulthood and early-life can also involve developmental constraints on future plasticity. Beckerman et al. [27] found such cohort variation in the plastic response to adult environment in soil mites (*Sancassania berlesei*). For example, rearing conditions interacted with density as adult so that the response of fecundity to adult density was stronger when rearing conditions had been favorable than when they had been unfavorable. Nussey et al. [28] also found that plasticity in offspring birth weight was constrained for red deer hinds born at high density. Hence, the consequences of early-life conditions on plasticity can be adaptive, as suggested by PAR, or non-adaptive as when individuals born in harsh conditions suffer reduced lifetime performance though silver-spoon effects.

Cohort effects are most commonly caused by factors affecting the entire population during early-life, such as environmental variation. Indeed, up to 30-50% of variation in individual performance can be explained by early-life environment in large mammals [12]. In Soay sheep (*Ovis aries*), the North Atlantic Oscillation index (NAO) during winter is linked to cohort variation in birth mass, birth date, twinning rate and age of primiparity [29]. In red deer, the amount of rainfall near parturition interacts with forage supplementation ; high rainfall leads to higher body mass in the un-supplemented population [30]. In red squirrels, cohort effects on breeding success are linked to food abundance when pups are in the nest and to spring temperature in the year of birth [11]. Another source of cohort effects is density at birth. For example, high birth density delays primiparity in Soay sheep [29] and reduces body mass in red deer [31]. Cohort effects can also be caused by pre-natal conditions. Soay sheep that experience high NAO values in utero delay primiparity [29]. With ongoing climate change, understanding how climate can cause cohort effects is crucial, because directional changes in early-life conditions may allow predictions of long-term population dynamics, which may differ from those observed under previous climate regimes.

Our study has three main objectives. First, we quantify the variance in survival and in weaning success of adult bighorn ewes (*Ovis canadensis*) explained by cohort, and identify the environmental drivers of this variability. Second, we contrast the predictions from the silver-spoon and the PAR hypotheses. PAR predicts an interaction between early and current environmental conditions : individuals experiencing similar early and adult environments have higher fitness than those with dissimilar environment. The silver-spoon hypothesis, on the other hand, predicts long-term additive effects of early environment : individuals experiencing favorable conditions early in life will have superior fitness as adults. Third, we assess whether the variation observed at the cohort level arises from individual differences in fitness or from individual plasticity [32]. We used the long-term individual monitoring program of bighorn sheep on Ram Mountain to identify the main environmental drivers of cohort effects and their life-long consequences on survival and weaning success. Over 40 years, this population has experienced important changes in density (figure 5.1), weather, and climate, and shown substantial variation in reproduction and survival rates. We characterized early-life environment using density, a global climate index and local weather variables. We tested for the presence of PAR by determining whether animals with matching early-life and adult environments had higher fitness.

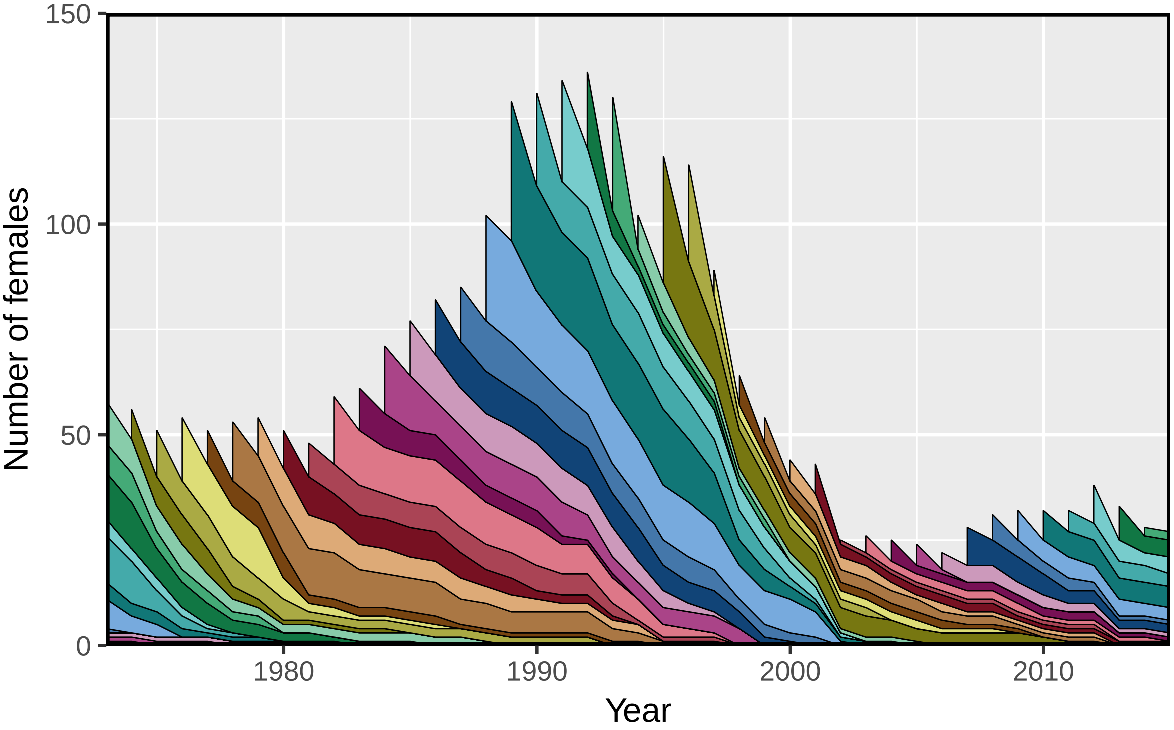

Figure 5.1 Population size and composition of female bighorn sheep at Ram Mountain between 1973 and 2014. Color bands represent cohorts, with band height indicating the number of ewes.

5.4 Methods

5.4.1 Study area & population

The study population is in Alberta, Canada (52°N, 115°W, elevation : 1080 to 2170 m). The study area covers about 38 km2 of alpine and subalpine habitat approximately 30 km east of the Rocky Mountains. The population has been closely monitored each year between late May and late September since 1972 [33]. Ewes are marked using visual collars. Lambs are marked with colored ear tags, mostly within a few weeks of birth. Individuals were assigned to a cohort based on their year of birth (table A.16). Resighting probability is over 99% [34], so ewes are considered dead when not seen for a year. Since all females are marked and an exact census is made each year, we can precisely determine their survival rate. A female was considered to have weaned a lamb when the lamb survived past September 15th. She was considered unsuccessful if she either did not produce a lamb (i.e. was not seen with a lamb and was not lactating) or lost it before weaning. We restricted analyses to cohorts born from 1973 to 2005. Complete lifetime data on weaning success and survival up to 2014 are available for all individuals in these cohorts (N=235), except for 1 female born in 2004 still alive in 2014 and 25 females from cohorts 1973 to 1977 which were experimentally removed [33]. We censored the last year of life of these experimentally removed ewes from analyses. Removing entirely individuals without complete life-history or cohorts containing individuals with incomplete life-history resulted in qualitatively identical results (results not shown), therefore we present the results of analyses including truncated data to maximize sample size. Density was the number of females aged 2 years and older in June.

5.4.2 Climatic & weather data

Data on precipitation (rainfall plus water equivalent of snowfall in mm) and average temperature (°C) were obtained from the Environment Canada meteorological station at Nordegg (52°30' N, 116°03'W, elevation : 1320 m). Local weather variables from when a cohort was in utero until its first winter were aggregated by seasons relevant to early development of bighorn sheep : winter of gestation (December-March before birth), spring (April-May during gestation), summer (June-15 September ; mean birth date until approximate weaning date), autumn (mid-September to November) and first winter (December-March after birth). We calculated average daily temperature and total precipitation over each of these seasons. We used the annual mean of the Pacific Decadal Oscillation (PDO ; [35]) as a global climate index, characterized by shifts between warm and cool phases over decades. PDO values were obtained from http ://research.jisao.washington.edu/pdo/PDO.latest and average by year.

5.4.3 Statistical analyses

Analysis of deviance (ANODEV)

We tested for the effects of 12 early-life environment variables : total precipitation and mean temperature during winter and spring preceding birth (in utero), total precipitation and mean temperature during summer, autumn and winter after birth, annual mean PDO in the year of birth, and density at birth. Variables were standardized (centered to 0 and divided by 1 standard deviation) prior to analyses. We tested the effects of standardized variables on ewe survival and probability of weaning a lamb with analysis of deviance (ANODEV) as advocated by Grosbois et al. [36], because it is more robust than Likelihood ratio tests when the residual temporal variance in the focal model is high [37]. This approach also allows testing for annual variation while taking full advantage of individual-based data. The ANODEV approach is based on three hierarchical models : a constant null model with no early-life environment covariate (M_{cst}), a model including an early-life environment covariate of interest (M_{co}), and a fully time-dependent model where all possible deviance is captured by adding the year of birth as a discrete factor (M_t). We tested the linear effects of early-life environmental variables, their quadratic effects, and their interactions with density by sequentially including them in the M_{co} model. When considering interactions between weather and density at birth, density was included in the null model (M_{cst}) to test for the added effect of the interaction only. To test for PAR, the M_{co} model included the additive effect of the environmental variable of interest both during early-life, and as adult, as well as the interaction between the two. Further, the base model (M_{cst}) included the environmental variable of interest experienced as an adult and at birth without the interaction, to test the interaction between early-life and adult environments rather than just the addition of current environment. The ANODEV approach then compares the deviance of the three previously described models using the following formula :

$$Ftest_{cst/co/t} = \frac{\left(\frac{Dev(M_{cst})-Dev(M_{co})}{n_p(M_{co})-n_p(Mcst)}\right)}{\left(\frac{Dev(M_{co})-Dev(M_t)}{n_p(M_t)-n_p(Mco)}\right)}$$

where Dev and n_p are the deviance and the number of parameters of their respective models. $Ftest_{cst/co/t}$ follows a F-distribution with $(n_p(M_{co})\breve{\ }n_p(M_{cst}))$ and $(n_p(M_t)\breve{\ }n_p(M_{co}))$ degrees of freedom. We also calculated the $R^2.Dev$ as described in Grosbois et al. [36] to measure effect size for early-life environment variables. This ANODEV approach was used to test the significance of environmental covariate on both the probability to wean a lamb and survival.

Probability of weaning a lamb

To test for cohort effects on the probability of weaning a lamb, we built generalized mixed effects models, including three maternal age-classes (prime-aged= 2-7 years ; old= 8-13 ; senescent=14+) as a fixed effect [38]. Current year was added as a random effect to account for annual variability in survival and reproduction due to current environment. Ewe identity was included as a random effect to account for repeated individual responses. All models were fitted using the lme4 package (V1.1-10)[39] in R (V3.2.3)[40].

To evaluate if the interaction between current and early-life density on reproduction arose from variation between cohorts, between individuals or within-individual, we used the within-subject centering procedure of van de Pol and Wright [32]. This approach combines centering of explanatory variables within each subject with mixed effects models to partition “between” from “within” subject effects. We centered density within cohort, then within individual. In each case, we also applied likelihood ratio tests for variation in slope among subjects (random regression model) to determine if the response of weaning success to density varied between cohorts or between individuals. To test for the presence of selective disappearance, another mechanism that could explain variation in response to density, we added longevity as an explanatory variable [41]. A positive effect of longevity would suggest selective disappearance of individuals with low reproductive output.

Survival

To test for cohort effects on annual survival probability, we first used mixed models to determine the amount of variance attributable to year of birth then tested each environmental covariate using ANODEV. Analyses of survival included ewes aged 2 years and older, to quantify only long-term effects and to use the same individuals included in the analysis of the probability of weaning a lamb. Given the limited variability in annual survival, we also looked at effects on longevity using a Cox proportional hazard models. This approach also allowed us to include truncated information on 25 individuals which were experimentally removed [33]. Age was not included in these models because it was already accounted for by the baseline hazard function. When testing for PAR, current environment was included in the model as a time-dependent covariate along with the interaction with early environment. Similarly to the logistic models described previously, the deviance of these proportional hazard models was used according to the ANODEV approach to test for significant cohort effect. All models were fitted using the survival library (V2.39-4) in R [42]. In our approach, the many ways to quantify the environment result in a multitude of tests. Therefore, we corrected p-values for multiple testing using the Benjamini & Hochberg method [43], that controls the false discovery rate without reducing statistical power as drastically as the Bonferroni method. We used an α-level of 0.05.

5.5 Results

We analyzed weaning success and survival of 227 ewes from 32 cohorts. Cohort identity explained 34.2% of variation in weaning success, compared to 64.0% for year and 1.4% for ewe identity. Very few effects were significant after correcting for multiple testing (table A.10), but a very strong effect of birth density on weaning success remained ($p = 0.03$; table 5.11). Birth density explained 32.1% of annual variation in weaning success, which was lower for cohorts born at higher density ($\beta = -0.525$; CI=-0.721,-0.329). Adding the interaction between birth and current density ($p < 0.001$, table 1) increased the proportion of variance explained to 55.6% (table A.10). Contrary to the PAR hypothesis, however, harsh birth conditions did not increase fitness when adult conditions were also harsh (figure 5.2a). The weaning success of ewes born at low density increased slightly with the density they encountered as adults (slope of current density when born at lowest density = 0.682 ; CI=0.372, 0.991). Ewes born at high density, however, were very sensitive to future environment and suffered a drastic reduction in weaning success when faced with high density as adults (slope of current density when born at lowest density = -1.385, CI=-1.076,-1.695). Models containing only birth or adult density reveal that birth density had a stronger effect ($\beta = -0.54, p < 0.001$) than adult density by itself ($\beta = -0.25, p = 0.05$).

Table 5.1 Parameter estimates of the best model of weaning success for bighorn ewes at Ram Mountain, Canada (1975-2014). Prime-aged ewes (2-7) were used as reference.

	Estimate	SE	Z-value	P-value
Intercept	0.522	0.161	3.241	0.001
Age class (older)	-0.14	0.172	-0.083	0.943
Age class (senescent)	-1.155	0.398	-2.902	0.004
Current density	0.009	0.141	0.062	0.950
Birth density	-0.268	0.121	-2.211	0.027
Density interaction	-0.642	0.118	-5.419	<0.001

Cohort identity explained only 5.7% of variation in adult annual survival. Precipitation during the first winter as well as density explained some of the variation in adult survival between cohorts, but no early environment covariate remained significant after correcting for multiple testing (table A.12). The effect of early density on survival was weak and non- significant ($\beta = -0.24$, CI=-0.46, 0.0009 ; figure 5.2b), and it may simply be too small to be detected given our statistical power. Density at birthreduced longevity (hazard = 1.412, CI= 1.196-1.667) suggesting that cumulative small differences in yearly survival lead to shorter lifespan (table

A.14). Density explained 27% of the variation in longevity between cohorts. Overall, the results showed no support for PAR.

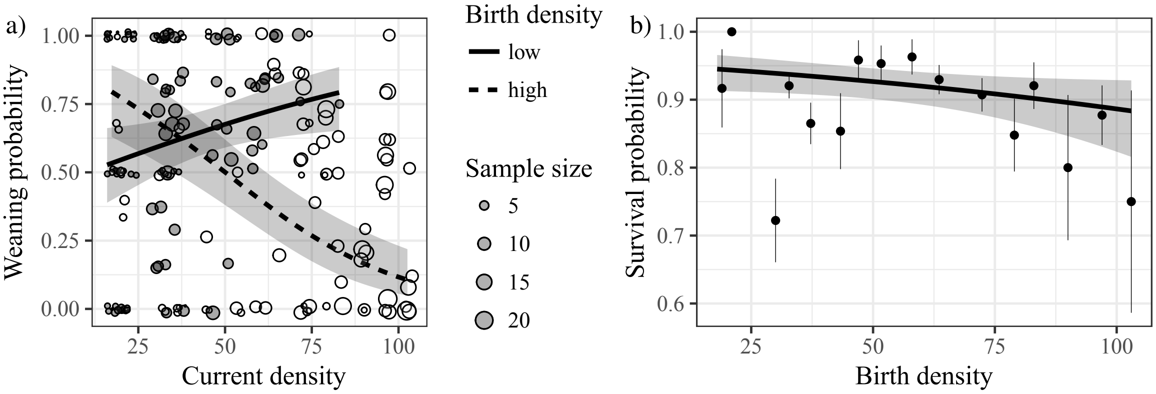

Figure 5.2 a) Weaning success of prime-aged bighorn ewes as a function of current and past density. For illustrative purposes, curves represent the 10th and 90th percentile of birth density. Points represent the observed data, grey for cohorts born above average density and clear for those born below average density. b) Annual survival probability of prime-aged bighorn ewes as a function of birth density. Grey ribbons indicate 95% confidence interval. Points represent mean (and standard error) of observations binned according to birth density (bins of 5 individuals).

A mixed model of weaning success as response variable using within-subject centering revealed both within and between-subject effects of current density. When using within-subject centering by cohort, we found significant negative between-cohort effects of current density (β-between=-0.478, s.e.= 0.214, $p = 0.025$). On average, there was no within-cohort response to current density (β-within= -0.221, s.e.= 0.350, $p = 0.530$). However, we detected significant variation in the response to current density of different cohorts (Var= 1.795 ; $\chi^2 = 33.897$, d.f.=2, $p > 0.001$, figure A.14a). Within-cohort response to current density, however, cannot distinguish between-individual effects from within-individual effects. We therefore also used within-subject centering by individual. Within-subject centeringrevealed significant between-individual effects of current density (β-between=-0.334, s.e.= 0.145, $p = 0.021$). On average, there was no within-individual response to current density (β-within= -0.078, s.e.= 0.151, $p = 0.610$). Unlike at the cohort level, we did not detect any significant variation in response of individuals to current density ($\chi^2 = 0.056$, d.f.=2, $p = 0.97$, figure A.14b). Change within cohort and no change within individual implies a change in cohort composition through selective disappearance. Accordingly, we found a significant effect of longevity ($\beta = 0.07, p < 0.001$) : individuals with low reproduction die at a younger age.

5.6 Discussion

Strong cohort effects are likely to cause important lag responses in population dynamics and increase individual differences in performance. Cohort explained a significant proportion of the variance in weaning success, which was only affected by density. None of the weather variables or the climate variable, PDO, significantly explained differences between cohorts in the probability of weaning a lamb. The effect of birth environment on reproduction included a strong interaction between adult and birth density. This interaction, however, was opposite in direction to the predictions of the PAR hypothesis. The probability of weaning a lamb was lowest for ewes that lived under matching high-density birth and adult environments. The effect of density on annual survival of ewes of different cohorts was weak and could only be detected through its cumulative effect on longevity. Traits with large fitness impact are expected to have lower variability due to canalization [44]. Canalization of adult survival is well documented in ungulates [45]. Additionally, selective early disappearance of unfit individual may reduce the detectability of long-term cohort effects. Overall, our results show that birth environment can strongly influence population dynamics over the lifetime of a cohort, but do not support the PAR hypothesis in this wild ungulate.

We did not find any strong effects of weather on either adult ewe survival or the probability of weaning a lamb. Spring and winter temperature and spring precipitation affect lamb survival [45]. Spring temperature also affects annual horn growth of rams [46]. Effects of weather, however, appear mostly short-term. Spring temperature during the first year of life accounted for less than 1% of the variation in horn length of three-year-old rams [46]. The long-term effects of spring temperature at birth on the probability of weaning a lamb were not significant after correction for multiple testing, suggesting that they are either non- existing or weak. Long-term effects of early-life condition on fitness components may be primarily driven by other extrinsic factors such as density.

Long-term effects of early density on reproduction were highly significant. Delayed density-dependence has been documented in many ungulates [31, 47, 48], and plays an important role in their population dynamics. Populations showing lagged responses tend to be more variable over time [49]. Our results confirm that cohort effects can be an important mechanism by which density can have lagged effects [5, 29]. Indeed, the effects of density at birth on reproduction were stronger than the effects of density as adult. As a consequence, delayed density dependence, driven by cohort effects, likely plays an important role in the regulation of this population. Although most studies test the effect of current density [50], given the importance of density at birth on reproduction and its marginal effect on survival, considering density at birth may be more informative. Our results underline the complexity of density effects on population growth. Indeed, the interaction between adult and birth density was highly significant in the reproduction models. Reproduction was highest for ewes that spent their entire life at low density. In addition, good conditions at birth (low density) seem to partly buffer individuals from adverse conditions later in life. Individuals born in harsh condition (high density) benefited from no such protection and suffered reduced reproduction when faced with high density as adults. While a strict definition of silver–spoon effects implies a fixed advantage of favorable birth environment, several studies have found similar context-dependent silver-spoon effects [17, 51]. Some have termed the protective effects that are more evident when adult conditions are harsh 'beneficially saturated' conditions [52]. Overall, our results support this protective silver-spoon effect rather than PAR [53]. Early nutrition is the main hypothesized cause of silver-spoon effects [54]. These differences impact later life due to the correlation in size from one year to the next or through the cost of increased growth. However, while high density lowers fitness, ewes born at high density appeared able to compensate for the poor start if environmental conditions improved [54]. Adult bighorn ewes show catch-up mass gain [55]. When density remains high, however, no compensation can occur and weaning success is reduced. The interaction between birth and adult environment may mask cohort effects if it is not specifically accounted for [11]. Surprisingly, when ewes were born at low density, density as an adult seemed to have a positive impact on weaning success. This unexpected result may be partly explained by the history of the population. Most of these ewes were monitored during the last 15 years of the study when density increased but remained low (figure 5.1). Their low weaning probability at very low density may indicate a component Allee effect [56], possibly caused in part by heavy cougar (*Puma concolor*) predation [57] in some recent years.

Individual plasticity appears unlikely to explain the negative effects of density on weaning success, because the within-individual effect of current density on reproduction was very small and non-significant. Further, there was no Individual x Environment interaction in response to current density, suggesting that all individuals had a similar response to current density and that this response was relatively weak compared to between-individual differences. These results strongly suggest a silver-spoon effect with a long- lasting impact of birth environment [53]. Apparently weak individual plasticity, however, may also be due to a lack of statistical power, because a large sample size is necessary to evaluate the variance of individual-specific slopes [58] and an adequate sample size is probably even larger for a logistic mixed model. Although we detected no individual plasticity in weaning success, we did find a significant between- individual effect as well as a within-cohort effect of current density. A change in the response of a cohort without a corresponding change in the response of its individual members is likely due to selective disappearance of weaker individuals [59], as supported by the positive association of reproduction and longevity.

The PAR hypothesis was not supported in this population, in agreement with another study testing for PAR in a wild ungulate population in France [25]. Instead, the response of ewes to birth environment supports a silver-spoon effect. In a recent meta-analysis, Uller et al. [22] found only weak support for PAR but their study did not include any mammals. Wells [26] argued that PAR is unlikely to evolve in long-lived species because the stochasticity of environmental variables makes the prediction of adult environment from maternal cues highly inaccurate. In our study, the correlation between environment in the year of birth and as adult was weak for all variables tested (mean= -0.04, sd= 0.03) except for density (0.28). These weak correlations make it unlikely that a PAR strategy would be adaptive, supporting Wells' suggestion that PAR may be a rare strategy under unpredictable environment.

In conclusion, cohort effects in bighorn sheep ewes explained 5.7% and 34.2% of the variance in survival and reproduction respectively. Effects of such magnitude will inevitably have important impacts on population growth. Given the longevity of bighorn sheep, cohort effect could produce important lags in population dynamics. Our study suggests that changes in population growth are affected by complex interactions between past and present environments.

5.7 Acknowledgements

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CHAPITRE 6

MÉCANISMES MENANT AUX EFFETS COHORTE

6.1 Description de l'article et contribution

Cet article a pour but de poursuivre là où le chapitre précédent nous a laissés. Le chapitre précédent a montré que la densité à la naissance peut avoir un grand effet sur la probabilité de sevrer un jeune et sur la longévité. Mais ces effets affectent-ils la valeur adaptative ? Par quel mécanisme les conditions à la naissance influencent-elles le succès reproducteur à vie ? Est-ce par une réduction à long terme de la condition, un individu né à haute densité restant en moins bonne condition jusqu'à sa mort ? Est-ce par un délai de l'âge à la première reproduction ? Est-ce par une réduction de la longévité ? Ou peut-être est-ce un effet direct des conditions à la naissance sur la fertilité ? Cet article tente de répondre à toutes ces questions à l'aide de l'analyse de piste, une méthode statistique permettant de tester et comparer différentes hypothèses causales.

L'idée pour cet article a germé lors du cours d'analyse de piste de Bill Shipley. J'ai effectué plusieurs versions des analyses statistiques avant d'aboutir aux versions actuelles. Fanie Pelletier et Marco Festa-Bianchet ont ensuite aidé à définir toutes les implications des résultats. J'ai écrit la première version du manuscrit qui fut par la suite commenté par Fanie Pelletier et Marco Festa-Bianchet. Allison Mackay a été d'une grande aide lors de discussions très dynamiques sur la philosophie derrière les analyses de piste. Fanie Pelletier a supervisé le tout. Fanie Pelletier et Marco Festa-Bianchet ont contribué à l'interprétation des résultats et à la révision du manuscrit.

Decomposing direct and indirect effects of early-life environment on fitness of bighorn ewes

In preparation for Proceedings of the Royal Society : B

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6.2 Abstract

Cohort effects can majorly impact population dynamic by delaying the response of population growth rate to environmental variation. Cohort effects occur when a group of individuals are similarily affected by a common environment, generating differences in their short and long-term performances. The mechanisms by which environmental conditions at birth can influence future performance are difficult to study in nature because it requires data on events occurring at different life stages for the same individuals. In order to identify causal links between birth density, age at first reproduction, longevity, and lifetime reproductive success, we used path analysis with 40 years of individual-based data on bighorn sheep. Our results indicate that birth density has both direct and indirect effects on lifetime reproductive success (LRS). Most of the effects of birth density on LRS was accounted by a reduction in longevity and a direct effect of birth density on LRS. The magnitude of these effects however was modulated by adult density. Under low adult density, reduced longevity accounted for 6% of the total effect of birth density on LRS, but its effect increased to 59% when adult density was high. We also found that increasing adult density caused a decline in the proportional importance of the direct effect of birth density on LRS from 73% to 35%. Additional indirect effects of birth density on LRS were weaker than expected and included an effect through a delay of age at first reproduction accounting for 7% on average. Contrary to what was expected, the indirect effects of birth density on lifetime fitness through yearling and adult body mass were weak, accounting for only about 1.5% of the total effects of birth density on LRS. This analysis provides an in-depth view of the paths by which early-life environment interacts with adult environment to shape individuals' life-history and fitness. Our results show that the long-term consequences of a harsh early-life environment on fitness are likely to be underestimated unless individual traits and fitness components at several life stages are considered, as well as the interactions between past and present environments.

Keywords : cohort effects, silver-spoon, path analysis, fitness, delayed density-dependance

6.3 Introduction

Organisms are particularly susceptible to their environment during developmental stages [1]. Malnutrition during fetal or early life can permanently modify epigenetic, hormonal and physiological traits [2, 3]. Nutrition is also critical for proper infant development [4]. Thus, environmental conditions during early-life can have a strong long-term impacts on size [5, 6], growth [7, 8, 9], and physiology [10, 9]. The effects of early-life conditions on physiological and morphological traits can persist to adulthood and have long-term consequences on fitness [11, 12]. These effects may include changes in life-history traits. For example, environmental conditions at birth may delay sexual maturation [13] and reduce fertility [14] and longevity [15]. Alternatively, organisms may adopt alternative life-history tactics to mitigate the effects of a bad start [16, 17]. For example, reduced nutrition in utero results in faster onset of puberty in rats (*Rattus norvegicus*) [18].

In temperate species characterized by a single yearly synchronous birth pulse, all offspring born in the same year in the same area will experience equally good or bad early environments. The effects of a common environment, generally termed cohort effects, can generate differences in the long-term performance of individuals experiencing it, distinguishing them from individual born to another cohort [19]. Although cohort effects can include common conditions experienced at any given time, several studies have reported cohort effects generated through conditions during early development [19]. Early-stage cohort effects have been reported for long-term differences in size [20, 21], age at first reproduction [22], fecundity [15, 9], longevity [15, 23] and lifetime reproductive success (LRS) [24, 25].

Cohort effects can be of critical importance for ecological processes such as population dynamics [19] by affecting lifetime fitness of entire cohorts [26]. Given the large number of life-history traits that can be influenced by early environment, and the possible trade-offs between them, considering traits individually can lead to different conclusions about how cohort effects affect population dynamics [13]. For example, Beckerman et al. [13] showed that while good conditions during rearing increased fecundity in lab population of mites (*Sancassania berlesei*), they could also result in a trade-off between the number and size of eggs. Considereing either trait independently would have led to different conclusions. Similarly, short-term measures of fitness components cannot account for life-history trade-offs. As a consequence, fitness consequences of early-life conditions can become stronger as individuals are monitored over more life history stages [25]. For example, in reindeer (*Rangifer tarandus*), females born in harsh conditions reproduced at lower body mass to compensate for their reduced reproductive success late in life [27]. Our understanding of the long-term effects of birth conditions would therefore be enhanced by a clearer understanding of how early- life environment influences LRS through different life-history traits.

Silver-spoon effects, a commonly studied type of cohort effect [16], implies that individuals born in favorable conditions enjoy long-term fitness benefits compared to those born under harsh conditions, regardless of the environment they face as adults. Recent studies, however, extended this hypothesis by suggesting that silver-spoon effects may not be independent of adult environment [28]. Instead, silver-spoon effects could be less pronounced if adult environment is very favorable, because all individuals could attain a high performance. On the other hand, silver-spoon effects may be most important if the adult environment is harsh, when compensation is more difficult. An extremely adverse adult environment may also mask cohort effects if compensation is impossible and all individuals have very low fitness. To quantify cohort effects, it is therefore important to take into account potential interactions between early and adult environments. For example, in bighorn sheep (*Ovis canadensis*), year of birth alone explained 34% of variation in weaning success, but the variance explained increased to 60% when its interaction with adult density was taken into account [29].

Cohort effects have been widely studied, but only a few studies have considered more than one fitness component and even fewer have investigated the mechanisms by which cohort effects affect fitness [25]. In large vertebrates, a commonly assumed mechanism is that cohort effects have a long-lasting impact on fitness via its effect on body condition [5, 30]. For example, harsh early-life environment can reduce birth mass [31] and early growth [20], reducing juvenile body mass, which in turn results in lower adult body mass. Given that adult mass influences several fitness components, the effects of early-life environment will likely affect fitness.

Not all individuals born in harsh environment will suffer from a permanent disadvantage. Individuals born under unfavorable early environment may prolong growth in an attempt to catch-up partially or completely, but not without costs [32]. Rapid compensatory growth is often associated with reduced adult lifespan [8, 33]. As a consequence, cohort effects on fitness may persist even if differences in body conditions dissipate. Early-life conditions may also have direct effects on future performance, irrespective of adult body condition, through modifications of metabolism [2, 34], immunocompetence [9], hormonal regulation [10], or epigenetic mechanisms [35]. The long-term physiological consequences of early-life environment have attracted particular attention in humans because of their health implications [36].

In this paper, we take advantage of a unique long-term monitoring program of multiple fitness-related traits of bighorn sheep to better understand the causal mechanisms by which birth environment can impact lifetime fitness. Several environmental factors can have long-term phenotypic and fitness consequences, including weather [20], climate [23, 37] and food availability [15]. In bighorn sheep, however, the main environmental factor causing cohort effects is population density at birth [29]. Therefore, we use birth density as a proxy of early-life environment. To explore the mechanisms by which density at birth may influence LRS, we used path analysis [38], to test and compare five different hypotheses which generate 5 pairs of causal models ; each pair includes a complete version of the ecological hypothesis, and a simplified version in which non-significant paths are removed (figure A.16). The first and most direct hypothesis states that early-life environment only affects juvenile mass, which in turns affects adult mass (models 1a and 1b). This hypothesis assumes that fitness components are only affected by adult mass and adult environment and that very little compensation occurs. Thus, there is no direct link between early-life environment or early-life condition and components of LRS. The second hypothesis tests for direct effects of juvenile mass on fitness components, independent of adult mass (models 2a and 2b). If compensatory growth was costly, it would lead to a direct negative effect. Thus, for a given adult mass, individuals that were smaller as juveniles would have a lower LRS. A direct effect of juvenile mass may also reflect long-term physiological cost of deficient nutrition during early life. The third hypothesis tests for effects of early-life environment on fitness component both directly and through the correlation of juvenile mass with adult mass (models 3a and 3b). Direct effects could occur through physiological developmental differences [4], behavioral modification [10], epigenetic differences [35], or hormonal differences [39]. The fourth hypothesis is a combination of hypothesis 2 and 3, including direct effects of juvenile mass as well as direct effects of early-life environment on fitness components (model 4a and 4b). We also test a fifth and most complex hypothesiswhich states that effects of birth density could depend on adult density (model 5a and 5b). This hypothesis includes the same paths as hypothesis 4, but adds the interaction between birth and adult densities. We then explored the best causal model (not rejected by tests of d-seperation [38] and lowest AICc score) to partition the effects of density at birth on LRS along different paths allowing us to evaluate the relative importance of direct and indirect effects.

6.4 Methods

6.4.1 Study area and population

The study population is located in Alberta, Canada (52°N, 115°W, elevation : 1080 to 2170 m) and has been closely monitored since 1972 [40]. The study area covers about 38 km^2 of alpine and sub-alpine habitat approximately 30 km east of the Rocky Mountains. Ewes are marked using visual collars while lambs are marked with colored ear tags mostly within a few weeks of their birth. Re-sighting probability is over 99%, so ewes are considered dead when not seen for a year. We restricted analysis to cohorts born from 1973 to 2005, for which complete lifetime data on weaning success and survival were available for all individuals except one female born in 2004 still alive in 2015 and 31 females which were experimentally removed in 1972-1986 and 1997 [41]. Females with incomplete life-history were removed from the analysis. The population is monitored each year between late May and late September. Density was the number of females aged 2 years and older in June. Birth density was the density during the year of birth, while adult density was the mean of densities between 3 years of age and death. The risk of predation was included in the analysis as the sum of years under high predation pressure by cougar when an individual was alive. Predation of adult females is rare execpt in certain years when cougars developed specialized predation on bighorns. The risk of predation was included in the analysis as the total number of years of high predation pressure by cougars experienced by each ewe.

6.4.2 Fitness and phenotypic measurement

Fitness was defined as the lifetime reproductive success (LRS), the total number of young that survived to 1 year of age produced by a ewe during her life. We also considered two life-history traits that are tightly linked to fitness : age at first reproduction (AFR) and longevity. AFR was the age at which a female first reproduced, which was determined by observation of a nursing lamb or by evidence of lactation at capture.

Morphological measurements were taken at every capture (mean 3.2 ± 1.3 captures per ewe per year). Mass was adjusted to a common date for all individuals using a random slope approach

[42]. To include ontogenetic development, causal path diagrams included mass at different ages : early mass (June 15 the year of birth), mass at weaning (15 September of the year of birth), as a yearling (15 September at one year of age), and adult mass, which was the average age-corrected mass of female aged three years and more. By three years of age, ewes have attained about 90% of their asymptotic mass [32]. Using an average value of mass to characterize adult condition is a good proxy given the high repeatability (ICC=0.6 ; CI=0.58–0.68) of adult mass.

6.4.3 D-separation and model selection

To compare competing causal model linking birth density to fitness, we used the D-separation approach. D-separation tests causal hypothesis by testing if the implied independences are supported by the data [38]. The different biological causal model of interests were illustrated as directed acyclic graphs (DAGs, figure A.16), which represent the causal paths between variables implied by the biological hypothesis. The paths modeled in DAGs have a causal direction : mass at birth affects mass at weaning and not the other ways around. DAGs are acyclic and no feed-back loops can occur. One advantage of using D-separation rather than structural equation modeling (SEM) is that it is straightforward to include random effects and non-normal distributions. The paths between longevity and the variables affecting it were modeled using generalized linear mixed models with Poisson distribution. AFR and LRS were log transformed and modeled using Gaussian regression. All other variables naturally followed a Gaussian distribution. All models included cohort as a random effect to control for the non-independence between individuals born in the same year. R-squared of models were obtained using the method suggested by Nakagawa et al. [43]. To include the interaction between birth and adult density in the DAG (models 5a and 5b), an additional variable representing this interaction was added [38]. This variable was calculated as the product of birth density and adult density. To keep the same dataset for all models and compare them using AIC, only ewes born after 1973, that survived until 3 years of age, died before 2015 and reproduced at least once were included (N= 202). All variables were centered to the mean and scaled to one standard deviation prior to modeling to facilitate convergence.

We tested the full model for each hypothesis using the D-separation approach, then proceeded to simplify it in a backward step-wise fashion until all paths implied by the model were significant. Simplified models were also tested using the D-separation approach. First, a set of (k) mutually independent claims of independence that must be true for the structure of the hypothesized DAG to be correct is determined. Second, the probabilities (P) of these k independence claims are tested using generalized mixed model. Third, these k probabilities are used to calculate Fisher's C statistic ($-2\Sigma ln(P)$), which follows a chi-square distribution with $2k$ degrees of freedom. A D-separation test with a p-value ≤ 0.05 indicates that the proposed correlation structure of the model differs from that observed in the data, and the DAG is therefore rejected. Causal models which were not rejected were compared using AIC [44]. To be compared using AIC, DAG models must be nested, with the same number of variables but with alternative paths [44]. The interaction model, however, has an additional variable. To make models comparable, we re-fit DAGs including the interaction variable (with no link to other variables when appropriate).

6.4.4 Direct and indirect effects of early-life density on LRS

Based off the information from the best causal model, we investigated the relative importance of different direct and indirect paths linking birth density to LRS. We used the parametric models describing the different path of the best DAG to simulate LRS resulting from the observed birth densities. We then sequentially fixed part of the DAG to constant values for all paths but one to isolate the effect of birth density through that path. To fix a given path, we fixed the value of each variable composing it to its observed mean before predicting the resulting LRS. Because the best model included an interaction between birth and adult density, we repeated the process using several fixed values of adult density (0.1, 0.25, 0.5, 0.75, 0.9 percentiles). We then divided the variance in LRS produced by each path by the sum of the variance in LRS produced by all paths to obtain the proportion of the effect of birth density due to each path, given different fixed values of adult density. To calculate the standardized indirect effects from birth density to LRS through different paths, we fitted a linear regression of the previously simulated LRS as a function of birth density to quantify the effect of birth density due to each path at a given adult density.

6.5 Results

Causal hypotheses 1 to 3 were rejected (p-value ranging between <0.001 and 0.03) suggesting that both early-life density and juvenile mass have direct long-term fitness effects (table 6.1). Hypothesis 4 and 5,were not rejected p-value ranging between 0.091 and 0.664) and were therefore compared with AIC. The simplified model (figure 6.1) including the interactions between early-life density and adult density (model 5b) had the lowest AIC ; 13.9 points lower than the next best model (4b) and 57.3 points lower than the unsimplified model (5a).

Table 6.1 DAG selection table showing : Fisher's C statistic, the degrees of freedom, the resulting p-value, the AICc of the model and the marginal r^2 of the LRS model. Causal models with p-value lower than 0.05 are rejected. Illustration of the models can be found in figure S1. The best candidate model is shown in bold.

model	Fisher-C	d.f.	p-value	AICc	r^2
1a	96.00	38	< 0.001	273.3	0.515
1b	113.98	54	< 0.001	263.3	0.467
2a	52.98	20	< 0.001	268.3	0.557
2b	75.81	48	0.006	223.3	0.495
3a	58.83	30	0.001	254.2	0.612
3b	73.81	50	0.016	230.9	0.61
4a	17.18	12	0.143	252.9	0.629
4b	39.52	44	0.664	194.0	0.623
5a	28.86	20	0.091	237.3	0.637
5b	**47.07**	**48**	**0.511**	**180.1**	**0.623**

Note : different DAGs represent our 5 *a priori* hypothesis : No direct effect of birth density or juvenile mass (1a, 1b), direct effect of juvenile mass only (2a, 2b), direct effect of birth density only (3a, 3b), direct effect of both juvenille mass and birth density (4a, 4b) and direct effect of juvenile mass and interaction between birth and adult density (5a, 5b). DAGs with the suffixes a are complete models while models with the suffixes b are simplified models were non-significant effects were removed.

The best causal model explained 38% of variance in adult body mass, 37% of AFR, 36% of longevity, and 62% of LRS. It included both direct effects of birth density and yearling mass and indirect effects through adult mass (table 6.2). As expected, masses at each life-history stage were positively correlated with mass at the previous stage. Birth density had significant direct negative effects on yearling mass, longevity and LRS as well as a direct positive effect on AFR. Birth density also interacted with adult density to affect adult mass and longevity (figure 6.2). While yearling mass was an important determinant of adult mass, it also had a direct negative effect on AFR (a lower yearling mass delayed AFR) and a direct positive effect on LRS. Adult mass only had a direct effect on one fitness component, longevity. AFR and longevity were both important determinant of LRS because they determined the start and end of the reproductive lifespan of a female.

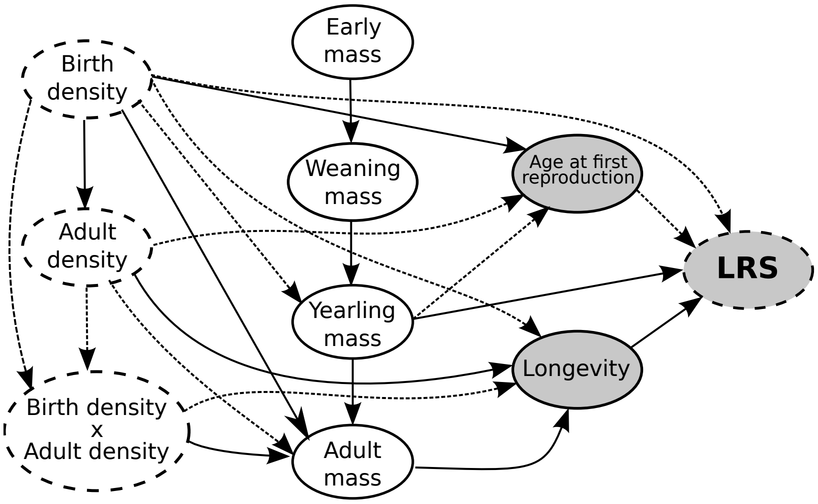

Figure 6.1 Best directed acyclic graph showing the different causal paths linking birth density to LRS. Environmental conditions are represented as circle whit black dashed border. Phenotypes at different life-stage have solid black border. Life-history traits have solid border with gray shading. Lifetime fitness (LRS) has a dashed borderwith gray shading. Dotted arrows represent negative relationship while black arrows represent positive relationship. See Table 6.2 for the strengths of the positive and negative effects.

Table 6.2 Coefficients of the parametric models composing the best candidate DAG (model 5b) which is illustrated in figure 1. Slope estimates are given along with their respective standard error and p-values. Intercepts were omitted.

Response	Predictor	Estimate	s.e.	p-value
Weaning mass	Early mass	0.901	0.045	< 0.001
Yearling mass	Weaning mass	0.46	0.072	< 0.001
	Birth density	-0.353	0.083	< 0.001
Adult density	Birth density	0.372	0.183	0.053
Adult mass	Yearling mass	0.654	0.074	< 0.001
	Adult density	-0.08	0.095	0.405
	Birth density	0.193	0.115	0.107
	Birth density x Adult density	0.354	0.099	0.001
Longevity	Adult mass	0.092	0.032	0.005
	Adult density	-0.014	0.045	0.753
	Birth density	-0.145	0.063	0.021
	Birth density x Adult density	-0.294	0.074	< 0.001
AFR	Yearling mass	-0.192	0.063	0.003
	Adult density	-0.315	0.091	0.001
	Birth density	0.49	0.111	< 0.001
LRS	Yearling mass	0.124	0.063	0.052
	Longevity	0.137	0.016	< 0.001
	Birth density	-0.341	0.069	< 0.001
	AFR	-0.187	0.071	0.009

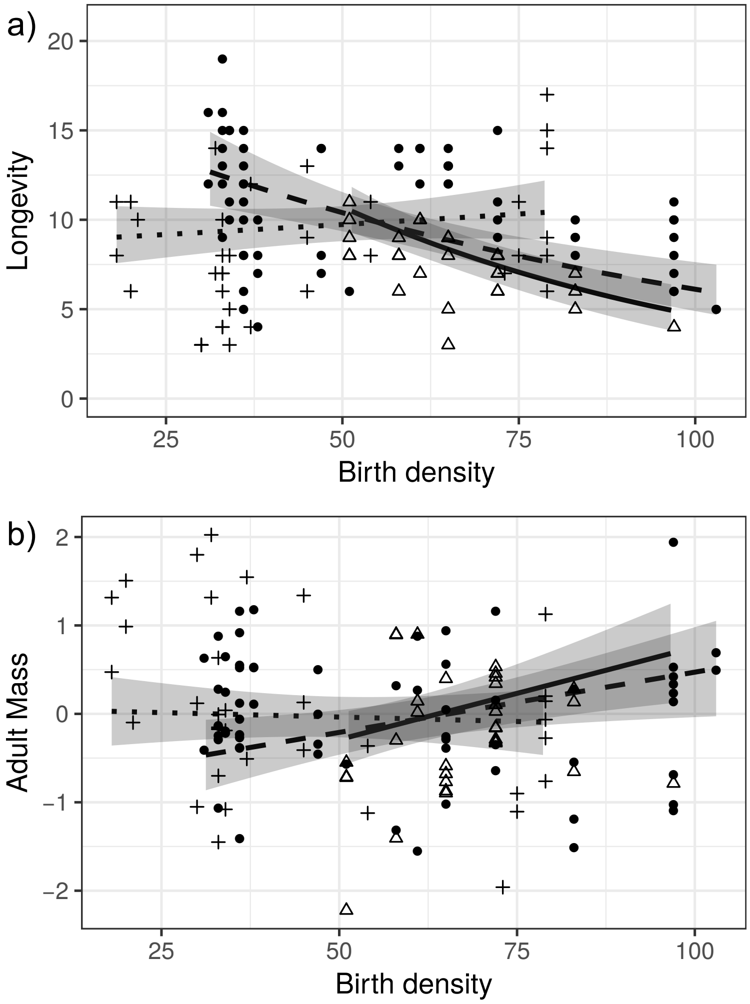

Figure 6.2 Interaction between birth and adult density on a) longevity and b) adult mass of bighorn sheep ewes on Ram Mountain, Canada. Individuals experiencing low adult density (25% percentile (48 individuals) and lower) are represented as crosses, those experiencing average adult density (25-75% percentile (48-82 individuals) as dots, and those experiencing high adult density (75% percentile (82 individuals) and more) as triangles. Model prediction (with shaded 95% CI) for adult density=48 is represented by the dotted line, for adult density=71 by the broken line and for adult density=82 by the solid line.

We then investigated the relative importance of different indirect and direct paths linking birth density to LRS. We distinguished the following paths through which birth density affected LRS : 1) a direct effect of birth density on LRS, 2) an effect going from birth density to yearling mass to LRS, 3) an effect going through AFR, 4) an effect of birth density on longevity then LRS, and 5) an effect of birth density through adult body mass, to longevity then LRS. Given that the effect of birth density on LRS through longevity depends on the density experienced as an adult, the relative proportion of the total effect of birth density on LRS through different paths also depends on adult density (table 6.3). On average, 49% of the effect of birth density passed through its effect on longevity (ranging from 3% to 73% depending on adult density). The second most important path however was the direct effect of birth density on LRS, which on average accounted for 41% of the total effect (ranging from 23% to 77%). This was followed by the effects through AFR, adult mass and yearling mass, which contributed on average 7.6%, 1.5% and 0.67% of the effect of birth density on LRS respectively. From the standardized path coefficient linking birth density and LRS (table 6.4), we obtained results conclusion in terms of relative importance of different paths. The effect through adult mass was most important at low adult density and weakest at high adult density. Longevity, however, had a strong effect on lifetime fitness both at high and low density and was weakest at an intermediate density. Overall, birth density had a negative effect on LRS which increased has adult density became higher (table 6.4).

Table 6.3 Percentage of the effect of birth density on lifetime reproductive success going through each causal path as a function of adult density in a population of bighorn sheep ewes at Ram Mountain, Alberta, Canada. The 0.1, 0.25, 0.5, 0.75 and 0.9 percentile of adult densities are displayed.

Adult density	Direct	Yearling mass	AFR	Longevity	Adult mass
10%	23.41	0.39	4.44	68.59	3.17
25%	76.87	1.27	14.56	3.33	3.97
50%	48.99	0.81	9.28	40.40	0.52
75%	30.67	0.51	5.81	62.96	0.07
90%	22.78	0.38	4.31	72.53	0.00

Table 6.4 Standardized path coefficients linking birth density to LRS as a function of adult density in a population of bighorn sheep ewes at Ram Mountain, Alberta, Canada. The 0.1, 0.25, 0.5, 0.75 and 0.9 percentile of adult densities are displayed.

Adult density	Full	Direct	Yearling mass	AFR	Longevity	Adult mass
10%	-0.018	-0.341	-0.044	-0.148	0.573	-0.125
25%	-0.453	-0.341	-0.044	-0.148	0.071	-0.077
50%	-0.785	-0.341	-0.044	-0.148	-0.308	-0.035
75%	-0.936	-0.341	-0.044	-0.148	-0.481	-0.016
90%	-1.033	-0.341	-0.044	-0.148	-0.595	-0.003

6.6 Discussion

Overall, we found highly significant long-term effects of birth density on life-history traits (AFR and longevity) as well as lifetime reproductive success. In addition, we found that the effects of birth density on LRS were strong but context-dependent. When adult density was low, we found no effect of birth density. This result is opposite to that predicted by the environment-matching hypothesis [16]. Our results support instead a context-dependent silver-spoon effect [28]. Our mechanistic approach provides valuable insights into the path by which these effects occur. Contrary to our initial expectations, paths via a long-term effect on adult mass account for only a minority of the effect of birth density on LRS. Most of the effect was accounted by a reduction in longevity and a direct effect of birth density on LRS. The mechanism by which this direct effect occurs, which may be physiological our behavioral, remains to be investigated.

Our starting hypothesis was that an important part of the effect of birth conditions on LRS would be mediated by a long-term effect on body mass. Contrary to our expectations, however, we found only weak effect of density at birth mediated by a long-term effect on body mass. Although this path is significant, it accounts for only a small portion ($< 8\%$) of the total effect of birth density. Several studies have quantified cohort effects on mass and assumed that this would result in fitness consequence and affect population dynamics [5, 20, 30]. Adult mass accounted for less than 8% of the effects of birth density on LRS. Thus, our study shows that simply quantifying cohort effects by their impact on mass will substantially underestimate their fitness consequences. The weaker than expected effect of adult mass occurs, in part, because differences in mass between cohorts tend to diminish over time [21]. In bighorn ewes, most of these differences in mass disappear by the time they are 5 years old [21]. Therefore, cohort differences in mass may disappear before ewes gain most of their lifetime reproductive success.

Additionally, ewes adopt a conservative reproductive strategy [41, 45, 46], and may be selected to attain a high mass before they reproduce [47], further reducing the importance of adult mass as a mechanism by which birth density will affect lifetime reproductive success. Our study therefore supports seveveral previous studies suggesting that there is no clear direct causal link between adult mass and lifetime reproductive success [48, 23, 49].

The effect of birth density on LRS acting through a direct reduction of longevity is much more important than the effect going through mass. Death, after all, is the ultimate limiting factor for lifetime reproductive success. Harsh conditions during early life have been reported to reduce the longevity by previous studies of wild ungulates [21, 49, 29]. Our results, however, suggest that this effect may depend on the interaction with adult density. The effect of birth density on longevity weakened when adult density was very low (even becoming positive at very low densities), which weakened the overall importance of this path. The proportion of the effects of birth density on LRS going through a reduced longevity varied from 3% to 73% depending on the adult density, highlighting the importance of considering potential interactions between early and adult environmental conditions. This weakening of the effect of a harsh birth environment is likely to result from viability selection, where individuals of lower mass die sooner when faced with high birth density. Survivors are therefore able to attain higher longevity and LRS when faced with a favorable environment as adults. Viability selection has been observed in several species of ungulates [21, 50].

Just as longevity determines the end of reproductive success, AFR determines its start. An important effect of density at birth on LRS via a delay in age at first reproduction was present in our system. This path accounted for an average of 8% of the total effect of birth density on LRS, making it the third most important path. This result supports previous findings that ewes will delay reproduction to ensure they attain a minimal mass before reproducing [22]. Our results, however, do not support the internal predictive adaptive response hypothesis [17] which proposes that individuals born under harsh condition should accelerate their reproductive schedule in prevision of reduced performance later in life. Contrarily, bighorn ewes born at high density reproduce later, even after accounting for yearling mass, suggesting that they may be unable to compensate for a bad start by adopting a faster life-history strategies.

Unexpectedly, we found a strong direct effect of birth density on LRS. Given that this effect is independent of both the start (AFR) and the end (longevity) of reproduction, it likely acts thought a reduction in the production of lambs that survive to 1 year. This reduction could result from either reduced fertility or reduced lamb survival. To investigate if it was due to reduced fertility, we fitted models, were lifetime reproductive success was replaced by lifetime fertility. The direct effect of birth density on fertility was not significant (p-value = 0.39) and the proportion of lactating mature ewes is always very high (average of 91.7%, ranging from 56% to 100% depending on the year), suggesting that an increase in lamb mortality was the mechanism by which early environment had a direct effect on LRS. There are several potential causes of death for bighorn lambs, including predation. The presence of a specialist cougar preying on sheep in 1997-2001 substantially reduced lamb survival [51]. The presence of a predator may also have indirect effects on lamb survival through the stress induced by its presence [52]. However, predation, meassured as the number of years spent under high predation pressure, did not have a significant effect on LRS (p-value = 0.28) and was not kept in the simplified DAG. One of the main determinants of lamb survival is mass at weaning [53] which is likely to be highly influenced by maternal care. There is evidence that on an annual basis, a ewe's probability to wean a lamb is dependent on the density at which she was born [29, 47]. Therefore, conditions at birth could have long-term effects on reproductive tactics of ewes. Ewes born at high density may invest less in each lamb. Similar effects have been observed in lab rats where pups reared in a low care environment provided less maternal care to their young [54]. Both the effects of predation and differential reproductive investment are likely to play a role in lamb survival but distinguishing them properly is difficult given that sheep- specialist cougars have only occurred in the later years of the study when ewes born at high density were reproducing.

We found no effect of birth density on early or weaning mass. While this may be taken as evidence that ewes buffer their lambs from the environment, it may also be the result from selective mortality of small lambs born under harsh conditions. Several studies on this population have found negative effects of birth density on weaning mass and winter survival [55]. Mass is a strong determinant of overwinter survival for lambs [53]. Lambs and yearlings whose mass is reduced by high density are likely to die and therefore not to appear in our sample. These light individual disappearing before they reach three years of age represent an invisible fraction [56, 57] which is not missing at random. The resulting estimates therefor are likely to be biased for the subset of individuals which was excluded from the analysis, meaning ewes which did not reached 3 years of age. The effects of birth density on early mass and weaning mass, which we were unable to detect may still be important for fitness and population dynamics, but are likely to act mostly by way of direct numerical effect rather than quality cohort effects [58].

Our integrative study reveals that cohort effects, driven by effects of early-life environment, can be an important source of inter-individual heterogeneity in life-history, morphology and lifetime fitness. Given that life-history traits and fitness can affect vital rates, these cohort effects are likely to alter population growth [59]. As a consequence, long term effects of early-life environment may generate lag in the population's response to environmental variation. Such lags can have important long-term impact on population dynamics, such as in the case of delayed density-dependence [19]. However, our analysis shows that simply including the year of birth or considering one trait is unlikely to be enough to capture the complexity of these effects. Population dynamics, in a closed population, is driven by the survival and reproduction of individuals, and both fitness components are affected by present and past environments. Models building from this fundamental unit (e.g. individuals) may be necessary to properly account for all the complexities of inter-individual heterogeneity.

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CHAPITRE 7

DISCUSSION GÉNÉRALE ET CONCLUSION

Mes travaux illustrent à quel point les différences interindividuelles peuvent avoir un impact majeur sur la valeur adaptative et la dynamique de population. Durant mon doctorat, je me suis principalement intéressé à ces différences à trois niveaux : au niveau génétique, au niveau phénotypique et au niveau des cohortes. Dans mon troisième chapitre, j'ai exploré l'importance des changements évolutifs comme source de différences interindividuelles. Mes travaux ont permis de mettre à jour de solides évidences que la chasse au trophée, par son rôle d'agent sélectif, peut mener à des changements évolutifs significatifs à l'intérieur de quelques générations seulement. Mes travaux s'inscrivent donc dans la liste grandissante d'études sur l'importance de l'Homme comme cause de changements évolutifs (Sullivan et al., 2017). Comme introduit dans le deuxième chapitre de ma thèse, les changements évolutifs en trait peuvent avoir de grands impacts sur la dynamique de population. Quantifier cet impact est cependant très difficile à faire. Mon chapitre de thèse le plus exigeant est indéniablement le chapitre 4 où j'ai tenté de quantifier l'importance des changements évolutifs et des changements plastiques sur la dynamique de population du mouflon d'Amérique. Mes travaux confirment l'importance des changements en masse pour la dynamique de population ; ceux-ci étaient tout aussi importants que les changements en densité ou en structure d'âge. Cependant, la majorité de ces changements en masse n'étaient pas génétiques. Malgré la faible importance des changements non héritables, j'ai détecté un effet significatif de la diminution génétique de la masse des brebis entre 1984 et 1997 sur le taux de croissance de la population. Mon étude vient donc combler un manque flagrant dans le domaine de la dynamique éco-évolutive.

Dans les deux derniers chapitres de ma thèse, je me suis intéressé à une autre source de différences interindividuelles, les effets cohorte. Mes travaux (chapitre 5) ont permis de quantifier les effets à long terme des conditions à la naissance sur la survie et la reproduction chez le mouflon d'Amérique ; la densité à la naissance est la principale source d'effets cohorte dans cette population. De plus, mes analyses suggèrent que malgré la présence d'une forte interaction entre les conditions à la naissance et les conditions adultes, aucun signe de réponse prédictive adaptative ne semble être présente dans cette population. Ayant déterminé que des effets cohorte sont présents, j'utilise dans mon chapitre 6 une approche mécanistique pour établir les liens entre la densité à la naissance, l'âge à la première reproduction et la longévité (deux importants traits d'histoire de vie) et le succès reproducteur à vie. Contre mes attentes, l'effet de la densité à la naissance sur le succès reproducteur à vie ne passe pas par une réduction à long terme de la masse adulte, mais plutôt par une réduction de la longévité et par un effet direct des conditions à la naissance sur la valeur adaptative.

Globalement, mes travaux montrent que considérer l'impact des différences en phénotype, en génotype et en conditions à la naissance pourrait nous aider à mieux comprendre les fluctuations chez des populations sauvages d'ongulé alpin. Les sections qui suivent détaillent les retombées scientifiques des différents sujets traités dans cette thèse, leurs limitations ainsi que les avenues de recherches futures découlant de mes travaux.

7.1 L'évolution rapide en nature

Une bonne compréhension des conséquences de la chasse sélective est critique pour une gestion appropriée des réglementations et quotas. Plusieurs études sur les pêcheries ont suggéré que l'exploitation pourrait mener à une diminution de la taille et à une maturation plus hâtive (Hutchings et Fraser, 2008 ; Heino et al., 2015). Si ces changements en trait ont une base génétique, leur retour à des niveaux naturels risque fort d'être lent, car les pressions artificielles sont en général plus fortes que les pressions naturelles (Swain et al., 2007 ; Allendorf et Hard, 2009). Ces changements évolutifs pourraient nuire à la productivité de la population (Kuparinen et al., 2014) et réduire sa capacité de rétablissement (Walsh et al., 2006), augmentant le risque d'extinction. Les changements évolutifs peuvent même avoir un effet au niveau de la communauté et de l'écosystème (voir chapitre 2). Cependant, les études quantifiant les conséquences évolutives de l'exploitation sont encore rares et controversées chez les mammifères (Coltman et al., 2003 ; Garel et al., 2007 ; Mysterud, 2011 ; Traill et al., 2014). Dans une récente méta-analyse, Darimont et al. (2009) ont recensé plus 475 taux de changements phénotypiques ; l'étude suggère que l'exploitation causait des changements phénotypiques significativement plus élevés qu'observés dans les systèmes naturels. Il faut cependant être prudent avant de conclure que les changements phénotypiques observés sont dus à des changements évolutifs (Merilä et Hendry, 2014). L'article de Coltman et al. (2003) était un exemple classique où un modèle animal avait été utilisé pour quantifier un changement évolutif chez un mammifère sauvage, à la suite d'une pression sélective anthropique. Il a d'ailleurs été cité plus de 580 fois. Cependant, il a été critiqué par rapport à l'approche statistique utilisée (Postma, 2006 ; Hadfield et al., 2010). Considérant les enjeux économiques (Foote et Wenzel, 2009) et écologiques (Allendorf et Hard, 2009) en jeu, une réanalyse était de mise.

Mes travaux ont permis de pallier aux critiques statistiques mentionnées précédemment. L'utilisation d'un modèle animal bayésien, comme suggéré par Hadfield et al. (2010), a permis de quantifier l'erreur sur les composantes aléatoires du modèle. L'année en cours ainsi que l'année de naissance ont été incluses comme variables aléatoires pour prendre en compte la variabilité environnementale (Postma, 2006). Le déclin en valeur de croisement a été comparé aux changements possibles suite à la dérive génétique (Hadfield et al., 2010). La probabilité que le déclin observé soit plus important que celui dû à la dérive était de 90,1%. Cette estimation est cependant très conservatrice. En effet, une part de la tendance temporelle en valeurs de croisement sera vraisemblablement absorbée par l'effet année. L'inclusion de l'année sous deux formes pourrait ainsi causer une sous-estimation des valeurs de croisement (Postma, 2006). L'utilisation du modèle animal bayésien permet d'obtenir des intervalles de confiance sur les valeurs de croisement, mais ceux-ci sont très larges. La distribution d'effets possibles de la dérive est elle aussi très large due à la faible taille de la population. Considérant toute cette incertitude, seul un effet très fort pouvait être détecté avec une forte probabilité. Considérant les résultats émergeant de mes travaux, une approche de précaution semble la meilleure alternative même si certains effets sont sous le seuil de 95% de certitude (Kuparinen et Festa-Bianchet, 2016).

En plus de pallier aux critiques statistiques, mes travaux ont également amené plusieurs améliorations aux travaux de Coltman et al. (2003). En bénéficiant d'une plus longue période d'étude que dans les travaux de 2003, nous avons pu utiliser le changement des réglementations de chasse de 1996 comme une expérimentation fortuite. Les deux périodes résultantes, une à forte pression de chasse et une à faible pression de chasse, nous permettent de conclure avec plus de certitude que les changements évolutifs observés sont le résultat de la chasse au trophée. Le déclin significatif des valeurs de croisement arrêtait avec le déclin de la pression de sélection. De plus, une réponse indirecte à la sélection a été observée dans d'autres mesures de cornes ; la réponse est proportionnelle à leurs corrélations génétiques avec la taille des cornes. La circonférence à la base des cornes des mâles et la longueur des cornes des femelles montraient des tendances en valeurs de croisement similaires, mais en plus faibles et non significatives, à celles de la longueur des cornes mâles. La circonférence à la base des cornes des femelles ne montrait cependant aucun changement évolutif, concordant avec sa très faible corrélation avec le trait sous sélection. Le changement des réglementations de chasse a fourni une expérimentation et la circonférence à la base des cornes des femelles a fourni un contrôle. Il aurait évidemment été bien d'avoir une forme de réplication, mais les efforts requis pour recueillir 40 ans de données phénotypiques et génotypiques rendaient la création d'un duplicata prohibitive. Une autre amélioration amenée par mes travaux est l'utilisation du second théorème de la sélection (STS) de Robertson-Price et la comparaison des prédictions qui en découlent aux changements observés en valeurs de croisement (Morrissey et al., 2010). La concordance entre la prédiction du STS et les changements observés est remarquable (figure 3.3), surtout lorsque comparée au changement prédit sous l'hypothèse de la dérive (Hadfield et al., 2010) ou de stase évolutive (Hunt, 2007). Dans leur ensemble, mes travaux apportent donc des arguments très convaincants de l'impact évolutif de la chasse au trophée dans cette population d'ongulé alpin.

Bien que la diminution évolutive en taille des cornes représente un déclin de 3 cm, le déclin phénotypique observé est d'environ 25 cm. La plasticité phénotypique joue donc un grand rôle dans le développement des cornes. Bien comprendre l'influence de l'environnement sur la variation temporelle en taille de corne mérite d'être étudié plus en profondeur. C'est ce que j'ai tenté de faire comme co-auteur dans le papier de **?**. Nos résultats suggèrent que la densité, la température au printemps et le PDO influence significativement la la croissance annuelle des cornes. La croissance annuelle à cependant une très faible héritabilité, la longueur des cornes à trois ans à donc été utilisé pour déterminer l'importance relative du climat et de l'évolution. La densité expliquait 26,5% de la variation en longueur de cornes à 3 ans. La température au printemps expliquait 0,9% alors que le PDO, en interaction avec la densité, expliquait un total de 29,4%. Pour ce qui est des changements évolutifs, ceux-ci expliquent 8,8%, suggérant que bien qu'ils ne soient pas la cause principale de changement phénotypique, ils ont tout de même une importance considérable.

Les implications de mon étude ne touchent pas seulement le mouflon, mais toutes les espèces exploitées. Le lien entre la chasse au trophée, la pression sélective anthropique et la réponse évolutive est évident dans le cas du mouflon d'Amérique. L'exploitation humaine a cependant le potentiel d'agir comme agent de sélection dans une foule de situations (Heino et al., 2015). En augmentant le taux de mortalité des gros adultes, la chasse et la pêche peuvent sélectionner des stratégies d'histoire de vie plus hâtive et une croissance réduite (Kuparinen et Festa-Bianchet, 2016). Même la chasse en apparence non sélective pourrait parfois l'être. Par exemple, la chasse pourrait contre sélectionner certains individus ayant des comportements qui augmentent leur détection par les chasseurs (Leclerc et al., 2017). Chez les guppys (*Poecilia reticulata*), les individus avec un tempérament plus audacieux sont capturés plus souvent par les trappes passives (Diaz Pauli et al., 2015). Une telle sélection pourrait mener à des changements évolutifs de traits comportementaux si ces traits ont une héritabilité suffisante. Ainsi, considérant que presque toute forme d'exploitation humaine impose une certaine forme de pression de sélection anthropique, mon étude suggère que de potentiels impacts évolutifs devraient être considérés plus souvent.

7.2 La dynamique éco-évolutive et ses défis

La conclusion principale à tirer de mon chapitre 4 est l'importance de faire la distinction entre changements évolutifs et changements plastiques quand on tente de quantifier l'importance de la dynamique éco-évolutive. La section précédente a largement élaboré autour de la difficulté de montrer qu'un changement phénotypique a une base génétique dans une population naturelle. Ceci explique probablement pourquoi si peu d'études en milieu naturel font cette distinction (Hendry, 2016a). Par exemple, plusieurs études suggèrent un impact de la dynamique éco-évolutive basé sur des changements phénotypiques (Hairston et al., 2005 ; Duckworth et Aguillon, 2015 ; Delong et al., 2016). Or, mon étude suggère que cela pourrait mener à une importante surestimation de l'importance des changements évolutifs. L'effet des changements évolutifs sur le taux de croissance de la population n'est en général que le quart de celui des changements plastiques.

Comme discuté dans le chapitre 2, les implications d'un lien Évo-à-Éco (l'évolution influence l'écologie) ne sont pas les mêmes que celles d'un lien Éco-à-Éco (l'écologie influence l'écologie) (Hendry, 2016b). Les effets (positifs ou négatifs) d'un changement évolutif auront vraisemblablement un effet à plus long terme sur la population. Comme illustré par les valeurs de croisement des cornes, le retour aux valeurs antérieures peut être lent. Si le changement évolutif a des sources anthropiques, les conséquences pourraient persister même si des actions de gestion pour freiner l'évolution non naturelle sont mises en route (Swain et al., 2007 ; Hendry, 2016a). Les changements plastiques quant à eux pourront probablement être renversés beaucoup plus facilement. Leurs conséquences sur des processus écologiques pourraient ainsi aussi être renversées.

Cela ne veut pas dire que la dynamique Éco-à-Éco n'est pas importante. Les changements en masse des brebis avaient une influence sur le taux de croissance similaire à celle des changements en structure d'âge et en densité. Ces résultats démontrent bien à quel point comprendre l'effet des différences interindividuelles est crucial pour bien prédire la dynamique de population. La survie et la reproduction des organismes sont intimement liées à leurs phénotypes et non leurs génotypes. Ces différences en valeur adaptative et en phénotype sont à la base de l'écologie évolutive (Endler, 1986). Il semble évident qu'un changement phénotypique de la population engendrera un changement dans sa dynamique (Pelletier et al., 2007a ; Schoener, 2011). Une grande majorité des modèles de dynamique de population ne considère pourtant que la densité et la démographie (un changement a cependant lieu grâce à l'arrivée des modèles de projection intégrale (Easterling et al., 2000 ; Vindenes et Langangen, 2015)). L'argument principal pour ignorer les différences phénotypiques entre individus est que leur effet devrait être minime par rapport aux effets déjà considérés (la structure d'âge, la densité et la stochasticité) (Sibly et Hone, 2002) ; la meilleure précision ne justifierait pas la complexité additionnelle. Mon chapitre 4 réfute cet argument. Les différences phénotypiques sont tout aussi importantes que les différences démographiques.

La présence d'importants changements phénotypiques due à des causes anthropiques est indéniable (Darimont et al., 2009 ; Alberti et al., 2017 ; Delong et al., 2016). Ma thèse, en quantifiant l'importance de ces changements sur la dynamique de population, est un encouragement à la création de suivis à long terme où les individus sont suivis individuellement et où des données phénotypiques sont recueillies (Clutton-Brock et Sheldon, 2010). Bien que mes travaux se soient principalement attardés à la masse, les données phénotypiques recueillies ne devraient pas s'arrêter aux traits morphologiques. L'écologie évolutive nous a appris que les traits d'histoire de vie, les traits physiologiques, les traits comportementaux peuvent tous avoir un impact sur la survie et la reproduction. Ils ont donc aussi le potentiel d'influencer la dynamique de population. Les retombés ne s'arrêtent pas à la population. Ils pourraient influencer les communautés et même les écosystèmes (voir section 2.7 et Hendry, 2016a). Les écologistes travaillant à des niveaux d'organisation différents (gènes, individus, populations, communautés et écosystèmes) ne peuvent se permettre de travailler en vase clos, car les interactions entre ces échelles ont toutes les raisons du monde d'être présentes et peuvent être importantes.

Une des difficultés qui a émergé de mes travaux est que la dynamique éco- évolutive doit non seulement gérer différentes échelles d'organisation écologique (génétique, phénotypique, populationnelle), mais aussi différentes échelles temporelles. Il a longtemps été cru que l'évolution n'était pas importante à l'échelle temporelle de l'écologie. L'observation de changements évolutifs rapides comme ceux observés dans mon chapitre 3 a mené à la naissance de l'étude de la dynamique éco-évolutive (Thompson, 1998). Une des questions clés de la dynamique éco-évolutive est de quantifier l'importance des changements évolutifs sur l'écologie. Selon Hairston et al. (2005), l'évolution peut être jugée importante si sa contribution au changement écologique (en taux de croissance de la population, par exemple) est grande par rapport aux autres facteurs qui y contribuent. Mon étude suggère cependant que cette question ignore un élément important, l'échelle temporelle à laquelle l'effet des changements évolutifs est quantifié. Les méthodes proposées par Hairston et al. (2005) puis par Ellner et al. (2011) ont été développées dans un contexte expérimental où l'échelle temporelle d'observation est évidente : la durée de l'expérimentation. En nature, plusieurs facteurs d'importance changent, à des vitesses différentes, et souvent de façon non monotone. Mon étude suggère que l'importance relative de l'évolution change elle aussi dans le temps. À très fine échelle temporelle, l'évolution a une importance relative très mineure. L'importance de l'évolution augmente cependant avec la durée de la période d'étude. Darwin avait raison en disant que l'évolution dépendait de l'accumulation d'une grande quantité de petits changements (Darwin, 1859). Similairement, l'importance de ces changements évolutifs dépend de l'accumulation d'une grande quantité de petits changements. La question que l'on devrait se poser n'est ainsi peut-être pas qu'elle est l'importance des changements évolutifs par rapport à d'autres changements écologiques, mais à quelle échelle temporelle est-elle aussi grande que l'importance des changements écologiques. À l'inverse des changements évolutifs, les changements plastiques, par leur nature même, peuvent causer des modifications rapides du phénotype et ainsi avoir une influence importante sur des processus écologiques même pour une courte période d'observation (Forsman, 2015). Il y a cependant probablement des limites aux changements plastiques (Auld et al., 2010). Nous pourrions donc nous attendre à ce que l'importance relative des changements plastiques diminue avec la durée d'observation... à moins que la plasticité elle-même évolue (Hendry, 2016b).

La quantification d'un effet significatif, quoique faible, des changements évolutifs en masse sur le taux de croissance de la population est une contribution intéressante de mes travaux de doctorat au domaine de la dynamique éco-évolutive. Il existe encore peu d'exemples d'effets Évo-à-Éco en nature chez les mammifères (Hendry, 2016a). En utilisant la méthode la plus efficace à ce jour pour partitionner les changements évolutifs et plastiques (van Benthem et al., 2016), mon étude suggère que les effets Évo-à-Éco ont le potentiel d'être importants. Il est d'autant plus intéressant que cet effet de l'évolution a conduit à une réduction du taux de croissance de la population. La diminution des valeurs de croisement de la masse suggère qu'il pourrait y avoir une pression de sélection qui induit une réduction de la valeur adaptative moyenne des femelles. Cette réduction en valeur adaptative peut sembler contre-intuitive. Il faut cependant considérer la masse dans le contexte de ses corrélations génétiques. La corrélation génétique entre la masse des femelles et la longueur des cornes des mâles est de 0,43 (Poissant et al., 2012). La forte pression de sélection artificielle induite par la chasse sur les cornes des mâles pourrait ainsi avoir mené à un changement néfaste en masse chez les femelles. Mon étude pourrait ainsi suggérer des conséquences indirectes de la chasse au trophée sur la dynamique de population via des changements évolutifs.

Mon approche a cependant plusieurs limitations. Premièrement, les modèles animaux utilisés sont très conservateurs. Comme mentionné précédemment, contrôler pour l'année en cours et l'année de naissance réduit notre puissance pour détecter des changements évolutifs et pourrait donc possiblement sous- estimer leur contribution (Postma, 2006). Une deuxième faiblesse est liée à l'approche Geber (Ellner et al., 2011). Cette analyse est rétrospective en ce sens qu'elle dépend entièrement des variations observées pour quantifier l'importance relative des changements évolutifs, des changements plastiques, des changements en densité, des changements en structure d'âge et des changements en PDO. C'est ce qui génère cette immense variabilité en taille d'effet visible sous la forme des intervalles de confiance de la figure 4.4. Plusieurs approches alternatives existent, mais elles ont toutes certaines limites. Une approche prometteuse est basée sur la contribution individuelle au taux de croissance de la population (Coulson et al., 2006). Cette contribution peut ensuite être mise en relation avec le phénotype ou le génotype, et la dynamique de la population sans changement évolutif peut être simulée. Cette analyse est cependant également rétrospective, ce qui réduit la généralisabilité des résultats qui en découlent. Les modèles de projection intégrale (IPM) sont une autre approche qui est de plus en plus utilisée en dynamique éco-évolutive (Smallegange et Coulson, 2013), mais leur robustesse pour la quantification de processus évolutifs reste controversée (van Benthem et al., 2016 ; Janeiro et al., 2017) ; mais voir Vindenes et Langangen (2015). L'approche la plus flexible pour étudier la dynamique éco-évolutive est probablement celle du modèle à base individuelle (Grimm et Railsback, 2005), qui permet de tenir compte des différences individuelles et changements temporels en génotype, des différences en phénotype qui en découlent et des conséquences sur la valeur adaptative et le taux de croissance de la population. Ces modèles se sont montrés très utiles pour quantifier les conséquences des changements évolutifs (Kuparinen et al., 2014 ; Eikeset et al., 2016). Ces modèles à base individuelle sont cependant difficiles à construire et à paramétriser. De plus, les simplifications faites durant leur construction rendent leur extrapolation aux populations naturelles à considérer avec précaution. À ce jour, aucune de ces approches n'est parfaite, mais les avancées qu'elles apportent sont considérables.

Les résultats obtenus dans mon étude avec l'approche Geber varient beaucoup selon la période d'observation considérée, ce qui met en doute leur généralisabilité. Il serait donc d'un grand intérêt de répliquer cette analyse avec une gamme d'autres traits. Un premier candidat intéressant serait la longueur des cornes des mâles. Contrairement aux valeurs de croisement de la masse des femelles, un fort déclin génétique de ce trait a été observé (Pigeon et al., 2016). Bien que l'influence de ce trait sur la dynamique de population soit probablement moins importante que celle de la masse, de récentes études suggèrent que ces effets pourraient tout de même être présents. Par exemple, le phénotype du père semble influencer l'allocation d'énergie aux agneaux et leur viabilité, et ce, de façon sexe-spécifique (Martin et al., 2014 ; Douhard et al., 2016a). Étudier un trait avec un fort changement évolutif et une grande importance pour la survie et la reproduction serait bien sûr idéal, mais les traits avec un fort impact sur la valeur adaptative sont probablement déjà proches de leur valeur optimale et ils évoluent donc probablement moins. Cependant, la valeur optimale d'un trait peut changer si les pressions de sélection sont modifiées (par un changement de l'environnement par exemple). Des traits influencés par les changements climatiques, comme des traits phénologiques par exemple, seraient donc très intéressants à étudier car les changements environnementaux en cours poussent possiblement leur valeur optimale loin de leurs valeurs historiques. L'étude de la dynamique éco-évolutive est un domaine encore en développement (Hendry, 2016a) et il serait judicieux de tester non seulement d'autres traits, mais aussi d'autres populations et d'autres espèces avant de tirer des généralités par rapport à l'importance des interactions Evo-à-Eco.

7.3 Les causes environnementales des effets cohorte

L'importance des effets cohorte en dynamique de population est connue depuis longtemps (Leslie, 1959), mais l'intérêt pour celle-ci a récemment été ranimé (Beckerman et al., 2002). Cet intérêt découle sans doute de l'intérêt accru pour les différences individuelles (Hamel et al., 2009a), mais aussi des apports de la biologie développementale et de la médecine (Bateson et al., 2004). Des études épidémiologiques ont mis en évidence l'importance des conditions pré- et néonatales sur le risque de pathologie à l'âge adulte (Desai et Hales, 1997). Le concept d'un avantage adaptatif dépendant du contexte adulte pour un phénotype économique (« thrifty phenotype ») a également attiré l'attention des écologistes évolutifs (Wells, 2007a). Le modèle relié à ce concept ayant reçu le plus d'attention est celui de la réponse prédictive-adaptative. Ce modèle a cependant peu été testé en nature.

Une des contributions de ma thèse a donc été de vérifier la présence de réponse prédictive-adaptative chez le mouflon d'Amérique. Bien que j'aie testé un grand nombre de variables environnementales, aucun signe de réponse prédictive-adaptative n'a été détectée. Mes travaux s'ajoutent ainsi à une lignée d'études réfutant ce modèle aussi bien au niveau théorique (Wells, 2007b), qu'en populations animales (Douhard et al., 2013 ; Workman et al., 2016 ; Lea et al., 2015) et qu'en population humaine (Hayward et Lummaa, 2013). Les études suggérant des contraintes imposées par l'environnement, c'est-à-dire des effets cuillère d'argent, semblent être plus communes. Comme argumenté par Wells (2007b), le modèle de la réponse prédictive-adaptative dépend d'une corrélation entre les conditions environnementales à la naissance et les conditions environnementales adultes, ce qui risque peu d'arriver pour des espèces longévives.

Un modèle similaire à celui de la réponse prédictive-adaptative a cependant récemment été développé (Nettle et al., 2013) : la réponse prédictive-adaptative interne. Ce modèle théorique est basé sur l'abondance d'études montrant des effets cuillère d'argent par rapport à la survie. En effet, plusieurs études, dont la mienne, documentent une longévité réduite à la suite de conditions défavorables à la naissance. Selon la réponse prédictive-adaptative interne, les organismes pourraient prévoir cette longévité réduite. Il serait alors adaptatif d'adopter une stratégie d'histoire de vie plus rapide de façon à augmenter les chances d'avoir une opportunité de reproduction avant sa fin (Nettle et Bateson, 2015). Par exemple, chez les rennes (*Rangifer tarandus platyrhynchus*), les femelles de 2 à 6 ans nées dans de mauvaises conditions se reproduisent à une masse inférieure à celles nées dans de bonnes conditions, mais subissent une diminution considérable de leur succès reproducteur après 6 ans (Douhard et al., 2016c). Les taux de croissance asymptotiques basés sur les taux démographiques des femelles nées dans de mauvaises conditions et nées dans de bonnes conditions étaient cependant équivalents, suggérant que cette stratégie d'histoire de vie permettrait aux femelles de mauvaises cohortes d'atteindre une valeur adaptative équivalente (Douhard et al., 2016c). À Ram Mountain, mon étude a montré que la densité à la naissance avait un effet marginal sur la survie annuelle et causait une diminution significative de la longévité. Une stratégie d'histoire de vie plus rapide tel que prédit par la réponse prédictive-adaptative interne serait donc adaptative. Mon chapitre 6 suggère cependant que les brebis nées à haute densité retardent leur âge à la première reproduction et ont un succès reproducteur à vie inférieur à celle nées à faible densité, contredisant encore les prédictions de la réponse prédictive-adaptative interne.

Une autre contribution de mon chapitre 5 est de soulever l'importance des effets cuillère d'argent contexte dépendants. La majorité de la littérature concerne l'effet cuillère d'argent classique, où les conditions à la naissance influencent la performance à long terme peu importe les conditions adultes rencontrées (Monaghan, 2008). Ignorer l'importance des conditions adultes mène cependant à un biais important dans la détection et la quantification des effets cohorte (Engqvist et Reinhold, 2016). Il est particulièrement intéressant d'explorer les causes et mécanismes qui pourraient mener à une réponse différente selon les conditions adultes. Les individus nés dans des conditions favorables ont un avantage et sont plus résistants à l'adversité future alors que les individus nés dans de mauvaises conditions subissent les pleines conséquences de cette adversité. Cette capacité de résister aux conditions défavorables adultes pourrait avoir plusieurs sources. Par exemple, les individus nés à faible densité pourraient être en meilleure condition à la base (les agneaux nés à faible densité sont plus gros au sevrage) (Feder et al., 2008) et ainsi piger dans leurs réserves pour faire face à un environnement défavorable. De mauvaises conditions environnementales à la naissance peuvent aussi contraindre la plasticité. Nussey et al. (2005) a montré que la plasticité des femelles cerf rouge nées à haute densité était significativement plus faible. Les individus nés à forte densité n'ont peut-être pas la plasticité nécessaire pour répondre adéquatement à un environnement adulte de mauvaise qualité. L'interaction entre les conditions à la naissance et adulte que j'ai observée peut également être considérée d'un autre point de vue. Les individus nés dans de mauvaises conditions pourraient être incapables de compensation si les conditions restent contraignantes. Par exemple, une croissance compensatoire a été observée chez le mouflon (Marcil-Ferland et al., 2013). Bien que la croissance compensatoire semble avoir des coûts (Marcil-Ferland et al., 2013), ceux-ci pourraient être réduits si les conditions adultes sont favorables. Établir clairement le mécanisme réduisant l'importance des effets cohorte sous de bonnes conditions adultes nécessitera cependant des analyses plus approfondies que celles faites dans cette thèse.

Le cinquième chapitre de ma thèse ne visait pas seulement à quantifier l'importance des effets cohorte, mais aussi à déterminer quelles variables environnementales en étaient la cause. Mes analyses suggèrent que seule la densité a un effet détectable à long terme. Cependant, comme dans la plupart des études sur l'impact des conditions environnementales, mon approche était quelque peu exploratoire. Quantifier l'environnement n'est pas une mince affaire (Krebs et Berteaux, 2006). Le nombre de variables caractérisant un milieu à un moment donné est infini. La principale limite est donc plus pratique que théorique, elle est déterminée par les variables ayant été mesurées. Dans mon cas, elle se limitait à la température, les précipitations, la densité et le PDO. Il est facile d'imaginer que des effets cohorte causés par d'autres variables non mesurées pourraient exister. Par exemple, il aurait été fort intéressant d'avoir une mesure des ressources alimentaires disponibles. Le *Normalized Difference Vegetation Index* est couramment utilisé comme index de ressources alimentaires disponibles (Pettorelli et al., 2005 ; Hamel et al., 2009b), mais il n'était malheureusement pas disponible pour l'entièreté de la période d'étude. L'influence de l'environnement n'est pas seulement déterminée par certaines variables environnementales, mais aussi par la période où celles-ci sont mesurées. Par exemple, la température au printemps influence la croissance des cornes, mais ce n'est pas le cas de la température en hiver (Douhard et al., 2017) . Mes analyses ont été basées sur des périodes biologiquement sensées, mais qui restent quelque peu arbitraires. Il est ainsi légitime de se demander si l'absence d'effet météorologique découle d'une absence d'effet biologique ou d'une mauvaise spécification des périodes (van de Pol et al., 2016). Cette crainte est d'autant plus légitime que le développement fœtal et ses effets à long terme peuvent être très dépendants de la période où la perturbation est survenue. Le développement des différents organes et systèmes ne se fait pas de façon uniforme et synchronisée durant la gestation. Le moment de la perturbation durant la gestation peut ainsi influencer ses conséquences (Symonds et al., 2007). Par exemple, l'exposition de femmes dans leur premier trimestre de grossesse à la famine a augmenté les risques de maladies cardio-vasculaires de leurs enfants alors que les femmes exposées à la famine durant leur deuxième trimestre de grossesse avaient des enfants avec un risque accru de maladies rénales (Symonds et al., 2007). L'influence à long terme des conditions à la naissance est probablement tout aussi dépendante de la période chez la population que j'ai étudiée. Une approche alternative pour éviter le biais dû à la sélection de saisons est d'utiliser une analyse par fenêtres glissantes. C'est ce que van de Pol et al. (2016) ont récemment suggéré comme approche. Cette approche nécessite cependant une très grande taille d'échantillon et souffre d'un risque accru d'erreur de type I. De plus, cette nouvelle méthode ne considère pas que ces effets environnementaux puissent être dépendants du contexte. La cause principale d'effets cohorte à Ram Mountain, la densité à la naissance, n'aurait ainsi peut-être même pas été détectée.

7.4 Une approche mécanistique des conséquences des conditions à la naissance

Le dernier chapitre de ma thèse utilise une approche plus mécanistique pour explorer comment les conditions à la naissance peuvent influencer le succès reproducteur à vie via différents traits d'histoire de vie. Comme mentionné précédemment, les effets cohorte peuvent avoir une importance cruciale sur la dynamique de la population (Beckerman et al., 2002). Cet effet passe par une modification à long terme du phénotype et des traits d'histoire de vie. Ces différences interindividuelles sont d'importants déterminants des taux vitaux et ont donc un impact sur la dynamique de la population. Compte tenu du grand nombre de traits d'histoire de la vie qui peuvent être influencés par l'environnement précoce et des compromis possibles entre ces traits d'histoire de vie, une bonne estimation des effets cohorte et de leurs conséquences nécessite de considérer plusieurs traits d'histoire de vie ainsi que leurs interactions (Beckerman et al., 2002 ; van de Pol et al., 2006 ; Panagakis et al., 2017). C'est ce que j'ai tenté de faire à l'aide d'une analyse de piste.

Mon analyse suggère qu'une des pistes les plus importantes par lesquelles la densité à la naissance influence le succès reproducteur à vie est un effet direct, indépendant de l'âge à la première reproduction, de la longévité et de la masse adulte. Ces effets directs sont très intrigants, notamment parce qu'ils supposent des implications au niveau physiologique de l'individu. En écologie, contrairement aux sciences médicales, de tels mécanismes sont difficilement étudiés. Ces mécanismes physiologiques pourraient être au niveau hormonal, au niveau métabolique ou encore au niveau épigénétique. Toutefois, les possibilités d'explorer plus en détail ces pistes de réflexion sont très limitées dans le système d'étude. On peut cependant préciser la source de l'effet obtenu. La fertilité des brebis adultes est très élevée, et ce, de façon indépendante des conditions à la naissance. L'effet sur le succès reproducteur à vie doit donc passer par la survie des agneaux. Un important déterminant de la survie des agneaux est la quantité de soins prodigués par la mère (Festa-Bianchet, 1988 ; Théoret-Gosselin et al., 2015). Les conditions à la naissance (et en gestation) sont connues pour influencer à long terme l'axe hypothalamique pituitaire surrénal (le système produisant les hormones de stress) (Monaghan et Haussmann, 2015) qui régule, entre autres, les compromis entre la survie et la reproduction (Cabezas et al., 2007 ; Bonier et al., 2009 ; Ouyang et al., 2011). Une forte densité à la naissance aurait pu « programmer » les brebis avec une stratégie plus conservatrice (Kapoor et Matthews, 2005 ; Weinstock, 2008 ; Glover et al., 2010), au détriment de la survie de leur agneau. Par exemple, les rates (*Rattus norvegicus*) élevées dans un environnement de qualité inférieure prodiguent moins de soins maternels (Cameron et al., 2008). De tels effets maternels pourraient potentiellement même mener à des conséquences transgénérationnelles des conditions à la naissance (Burton et Metcalfe, 2014). Plus d'études détaillées sur les effets maternels seront cependant nécessaires pour déterminer leur importance sous différents contextes de densité à la naissance.

L'analyse des impacts à long terme de la densité sur la population de mouflons de Ram Mountain souffre d'un facteur limitant important. L'historique de la population (Figure 5.1) illustre clairement qu'une seule période de haute densité a été observée durant le suivi de cette population. Il en résulte qu'un nombre très limité de cohortes étant nées à la haute densité et ayant été sous haute densité en tant qu'adultes est disponible (les cohortes de 1988 à 1994). De plus, ces cohortes sont temporellement regroupées. De manière similaire, seules les cohortes de 1975 à 1983 sont nées à faible densité et ont vécu à haute densité. Ce genre de problème est inhérent à l'étude des séries temporelles de courte durée. Il rend, entre autres, l'estimation des interactions entre environnement à la naissance et environnement adulte très difficile à faire sans manipulation expérimentale (Uller et al., 2013). La présence de plusieurs cycles de haute densité aurait sans doute permis une inférence plus robuste de l'effet de la densité à la naissance et de son interaction avec la densité adulte sur l'histoire de vie et le succès reproducteur. Il est cependant rare dans le cas d'espèces longévives, comme le mouflon, de pouvoir suivre une population assez longtemps pour être témoin de toutes les combinaisons possibles de densité à la naissance et de densité adulte.

À Ram Mountain, quand les conditions adultes sont bonnes, tous les individus performent bien. Cette interaction entre la densité à la naissance et la densité adulte semble diminuer l'hétérogénéité interindividuelle. Les effets cohorte observés pourraient tout de même avoir une grande influence sur la dynamique de population. Un effet à long terme des conditions à la naissance pourrait causer un délai dans la réponse d'une population aux variations environnementales (Beckerman et al., 2002), ce qui engendre dans plusieurs cas une augmentation de la variabilité (Benton et al., 2001). Les effets cohorte observés pourraient d'ailleurs avoir contribué aux délais du rétablissement de la population de Ram Mountain après son effondrement de 1992-1999. La nature contexte-dépendante des effets cohorte observés rend cependant sa modélisation plus difficile. Les effets cohorte indépendants des conditions adultes peuvent être modélisés relativement aisément en incluant un terme de densité dépendance retardée (Brigatti et al., 2016) ou d'un effet de l'environnement à la naissance dans le cas d'une population structurée en âge (Leslie, 1959). La présence d'une interaction avec l'environnement adulte implique qu'un simple délai constant ou l'inclusion de l'année de naissance pourrait être insuffisant pour capturer toute la subtilité de ces effets (De Roos et Persson, 2005 ; Benton, 2012). Des modèles suivant chaque individu avec son environnement présent ainsi que son histoire pourraient être nécessaires.

7.5 Conclusion

L'objectif de mon doctorat était d'explorer les causes et les conséquences des différences interindividuelles aussi bien au niveau génétique, au niveau des traits individuels, qu'au niveau de la cohorte. Mes travaux suggèrent que les sources de ces différences sont multiples. J'ai montré que la chasse au trophée pouvait causer des changements temporels en valeur génétique. J'ai également montré que les différences entre cohortes en probabilité annuelle de sevrer un agneau étaient causées par une interaction synergique entre la densité à la naissance et la densité adulte. Il en va de même pour des différences individuelles en masse adulte et en longévité. Mes travaux suggèrent également que ces différences interindividuelles ont de grandes conséquences, influençant la survie, la reproduction, le succès reproducteur à vie ainsi que le taux de croissance de la population. L'ensemble de mes travaux a ainsi permis de combler quelques lacunes dans notre compréhension des interactions unissant le génotype, l'individu, la cohorte, la population et son environnement. Ces interactions sont cependant complexes et nous sommes encore loin de saisir toutes leurs subtilités. Les résultats que j'ai obtenus montrent clairement que des suivis écologiques de longue durée suivant chaque individu, de sa génétique à son environnement, seront nécessaires pour comprendre comment ces différents niveaux d'organisation biologique fluctuent, et interagissent les uns avec les autres dans une dynamique éco-évolutive.

ANNEXE A

ANNEXES

A.1 Annexes Chapitre 3

Intense selective hunting leads to artificial evolution in horn size

Supplementary material

Gabriel Pigeon, Marco Festa-Bianchet, David W. Coltman and Fanie Pelletier

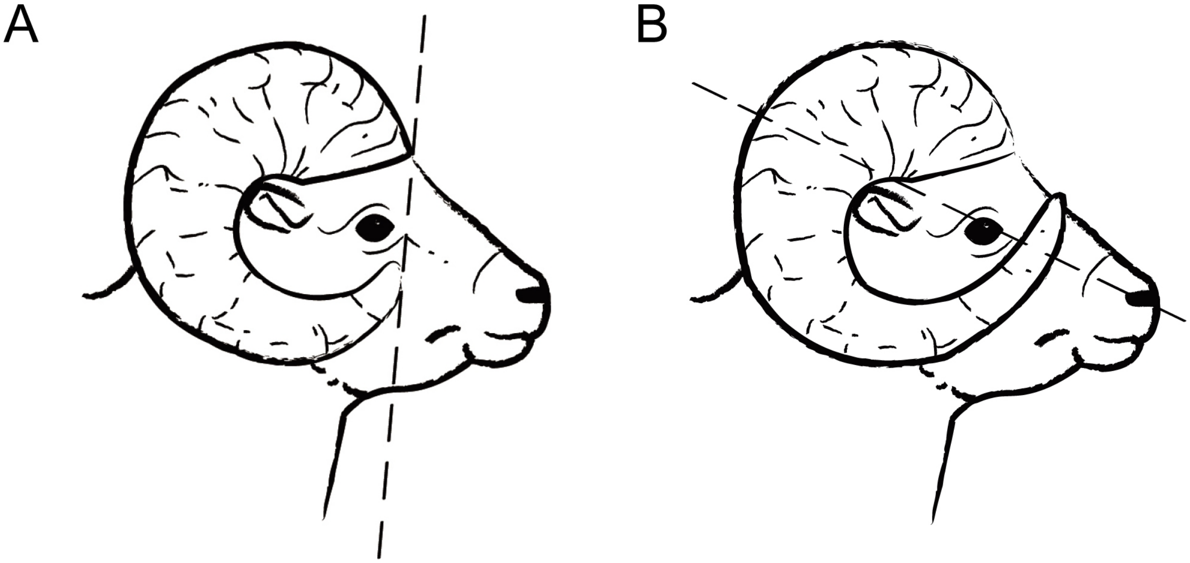

Figure A.1 Harvest regulation guideline for bighorn sheep in Alberta, Canada. A) Minimum horn size for rams harvested under 4/5 regulation. B) Minimum size for rams harvested under full curl regulation.

A.1.1 Multivariate model

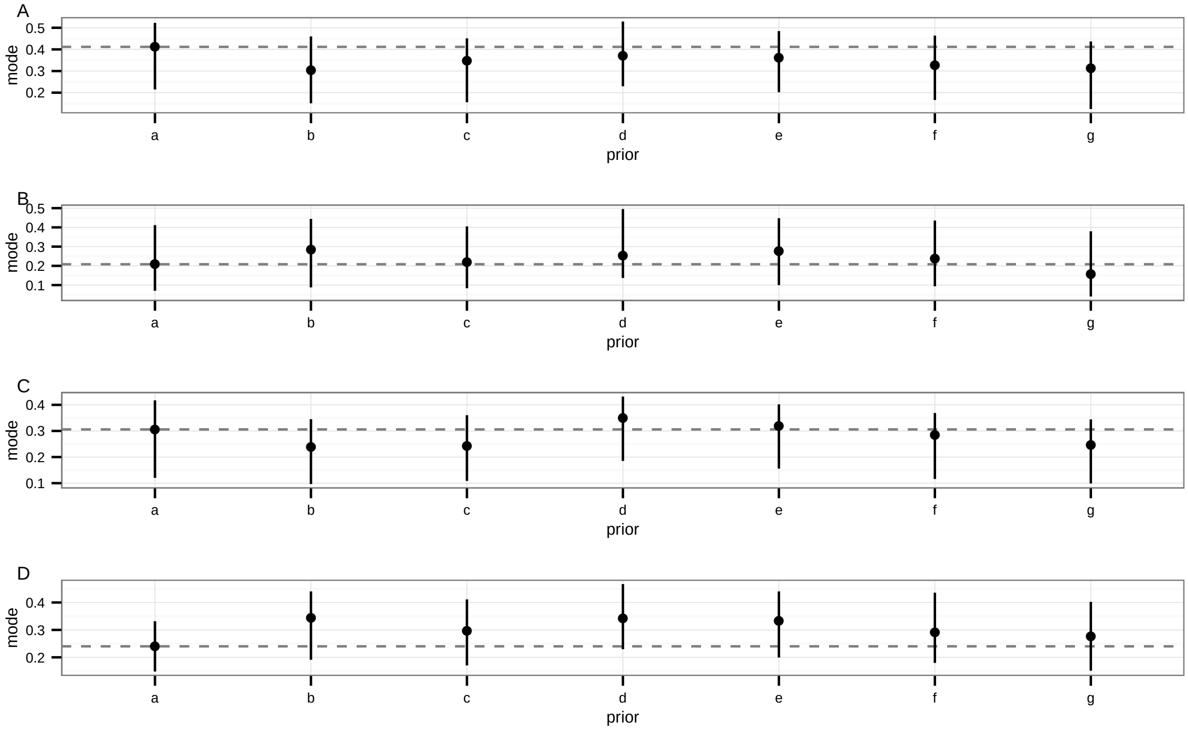

Figure A.2 Results of the sensitivity analysis showing the posterior mode with 95% Bayesian posterior interval of highest density of heritability for the multivariate animal model of A) male horn length, B) female horn length, C) male horn base and D) female horn base. Prior *a* is a flat uninformative prior with low degree of belief (nu=1.002). Priors *b* to *h* are informative (nu=2). Prior *b* used the value of h^2 reported by Poissant et al. (2012). Prior *c* assigned the variance equally between all variance components. Prior *d*, *e*, *f* and *g* assigned a varying proportion of the phenotypic variance to additive genetic effects (70%, 50%, 25%, 10% respectively). Dotted horizontal line shows the mode of prior *a*.

A.1.2 Male only univariate model

The "male-only model" animal models were first fitted using only male phenotype. Phenotypic variance was partitioned into its components, including additive genetic variance, using a univariate animal model for each trait. The models also included sheep identity, year of measurement and cohort as random effects to assess the amount of variance due to permanent, yearly and year of birth environmental effects. Maternal identity was not included in the model since the exclusion of lambs and yearlings minimized maternal effects. Age (categorical) was included as a fixed effect.

Table A.1 Summary of results for the univariate animal models with data on males only. The table shows heritability and the 95% Bayesian posterior interval of highest density for male-only univariate models of horn length and horn base. The slope of the decline (ße) in estimated breeding values through time, the probability that this decline is steeper than 0 (Pr[ße<0]) and the probability that this decline is steeper than expected by drift alone (Pr[ße<ßr]) are shown for the period subject to hunting (before 1996, hunted) and after the change in hunting regulation (after 1996, post-hunt).

	Heritability		Hunted			Post-hunt		
	h^2	CI	ße	Pr[ße<0]	Pr[ße<ßr]	ße	Pr[ße<0]	Pr[ße<ßr]
Male horn length	0.380	(0.188-0.549)	-0.082	0.946	0.874	0.023	0.620	0.560
Male horn base	0.324	(0.068-0.426)	-0.009	0.716	0.629	0.023	0.750	0.637

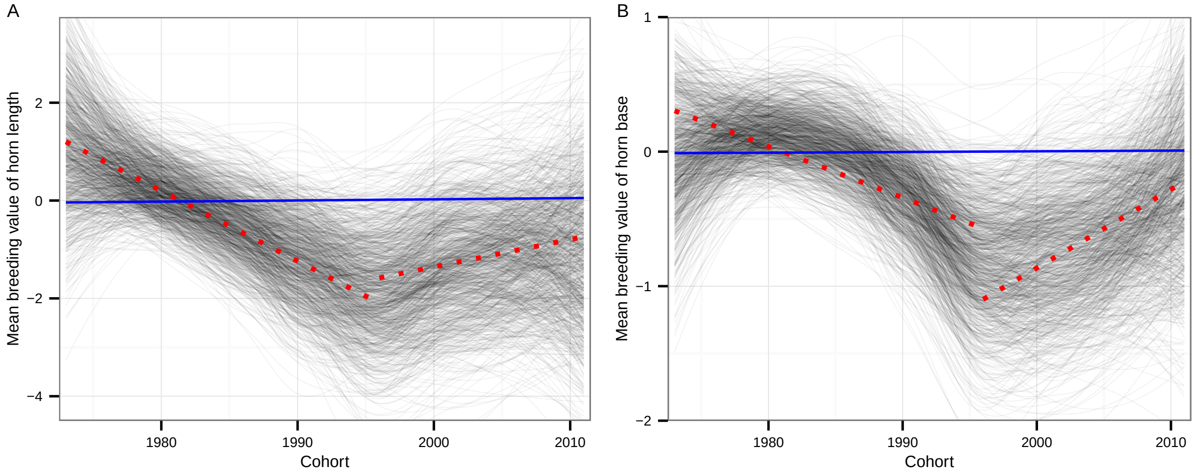

Figure A.3 Changes in mean breeding value for cohorts of bighorn rams born at Ram Mountain between 1973 and 2011, according to male-only univariate models. Panels present the breeding values of A) horn length and B) horn base. Each grey line represents the average estimated breeding value through time for one iteration of the MCMC chain of the animal model using loess. Red dashed lines represent the posterior mean trend using linear regression for the hunted and non-hunted period. Blue line represents the average response expected by drift alone..

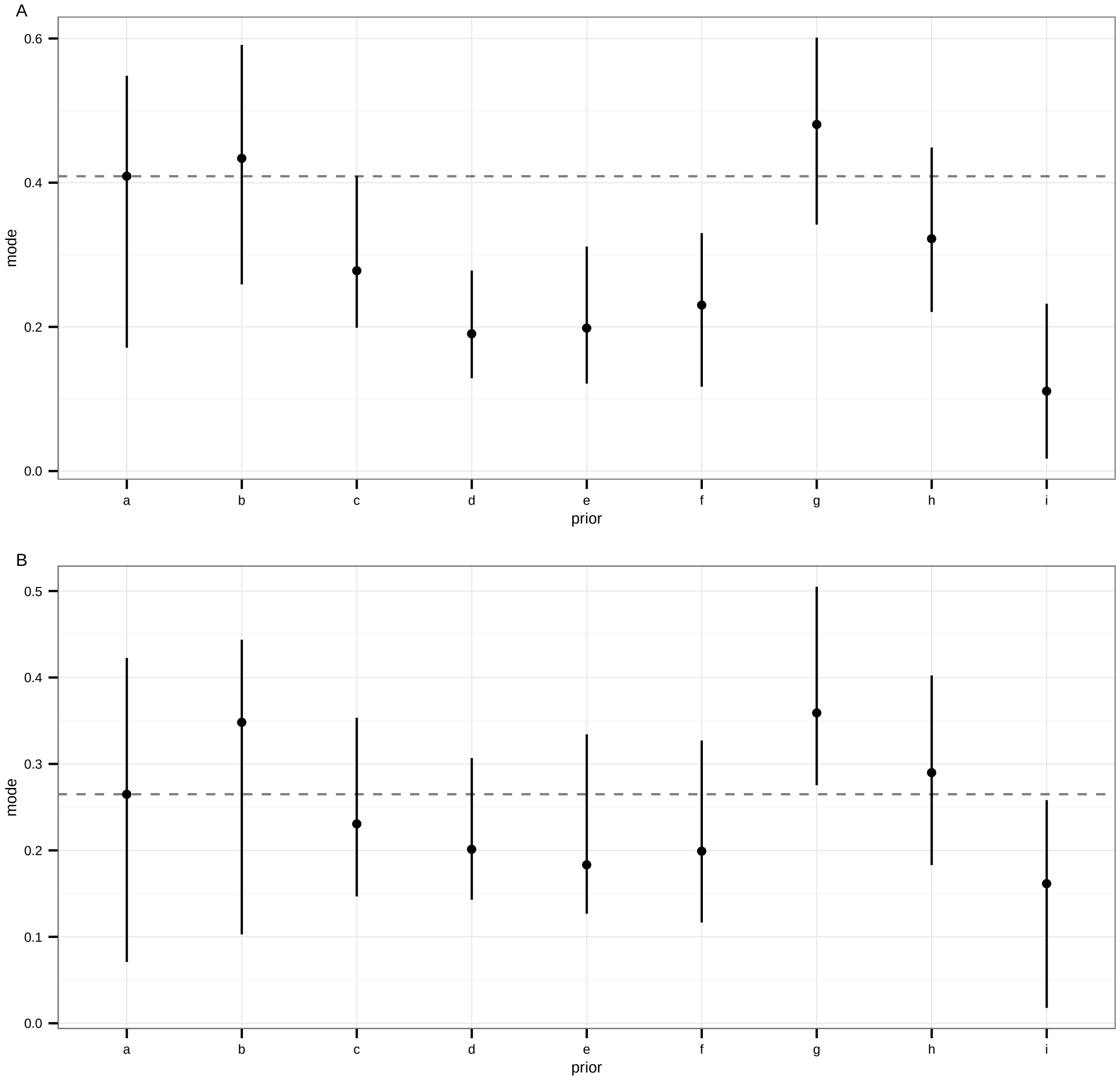

Figure A.4 Results of the sensitivity analysis of the male-only univariate models showing the posterior mode with 95% Bayesian posterior intervals of highest density of heritability for the animal model of A) male horn length B) male horn base. Prior *a* is the parameter expanded prior used in further analyses and the horizontal dashed line shows the posterior mode. Prior *b* is a flat uninformative prior with low degree of belief (V=1, nu=0.002). Priors *c* to *i* are informative (nu=2). Prior *c* assigned the variance according to the posterior modes obtained from a preliminary analysis. Priors *d* and *e* used the values of h^2 reported in Coltman et al (2005) and Poissant et al. (2012). Prior *f* assigned the variance equally between all variance components. Priors *g*, *h* and *i* assigned a large (96%), medium (60%) and low (1%) proportion of the phenotypic variance to additive genetic effects. Dotted horizontal line shows the mode of prior *a*.

A.1.3 Two-sex univariate model

We next fitted a “two-sex” univariate animal model including informative phenotypic information for males and females. This approach increases statistical power, revealing trends for females, which are not under direct artificial selection. Our modeling approach was similar to that described above. Given the high intersexual genetic correlation for horn length (1.00 ; Poissant et al. 2012), these traits can be considered the same for both sexes. Model structure was the same as described above, but also included fixed effects of sex and its interaction with age. For horn base, the intersexual genetic correlation is weak ; we thus partitioned male and female horn base variance in separate models. These models were parameterised exactly as described for the models including only male phenotype.

Table A.2 Summary of the results with the two-sex univariate animal models. The table shows heritability and the 95% Bayesian posterior interval of highest density for horn length, male horn base and female horn base. The slope of the decline (ße) in estimated breeding values through time, the probability that this decline is steeper than 0 (Pr[ße<0]) and the probability that this decline is steeper than expected by drift alone (Pr[ße<ßr]) are shown for the period subject to intense hunting (before 1996, hunted) and after the change in hunting regulation (after 1996, post-hunt).

		Heritability		Hunted			Post-hunt		
	Sex	h^2	CI	ße	Pr[ße<0]	Pr[ße<ßr]	ße	Pr[ße<0]	Pr[ße<ßr]
Horn length	M	0.367	(0.170-0.531)	-0.117	1.000	0.985	0.032	0.685	0.560
	F			0.003	0.491	0.503	0.015	0.587	0.543
Horn base	M	0.324	(0.068-0.426)	-0.111	0.745	0.745	0.023	0.750	0.637
Horn base	F	0.324	(0.080-0.486)	-0.001	0.582	0.582	0.004	0.636	0.555

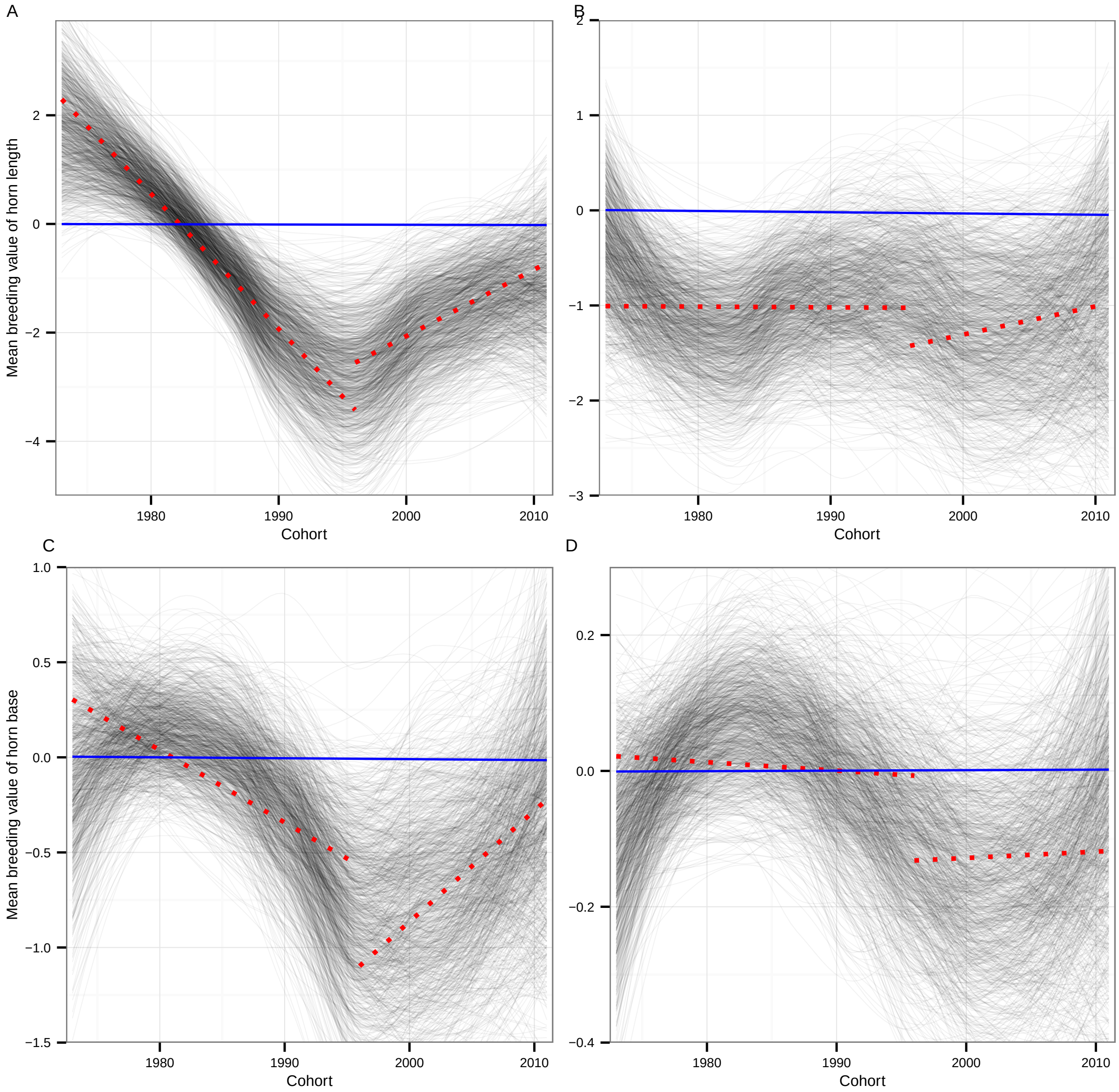

Figure A.5 Changes in mean breeding value for bighorn sheep cohorts born at Ram Mountain between 1973 and 2011, according to two-sex univariate models. Panels present the breeding values of A-B) horn length and C-D) horn base. The left column shows result for males and the right column shows result for the females. Each grey line represents the average estimated breeding value through time for one iteration of the MCMC chain of the animal model using loess. Red dashed lines represent the posterior mean trend using linear regression for the hunted and non-hunted period. Blue line represents the average response expected by drift alone.

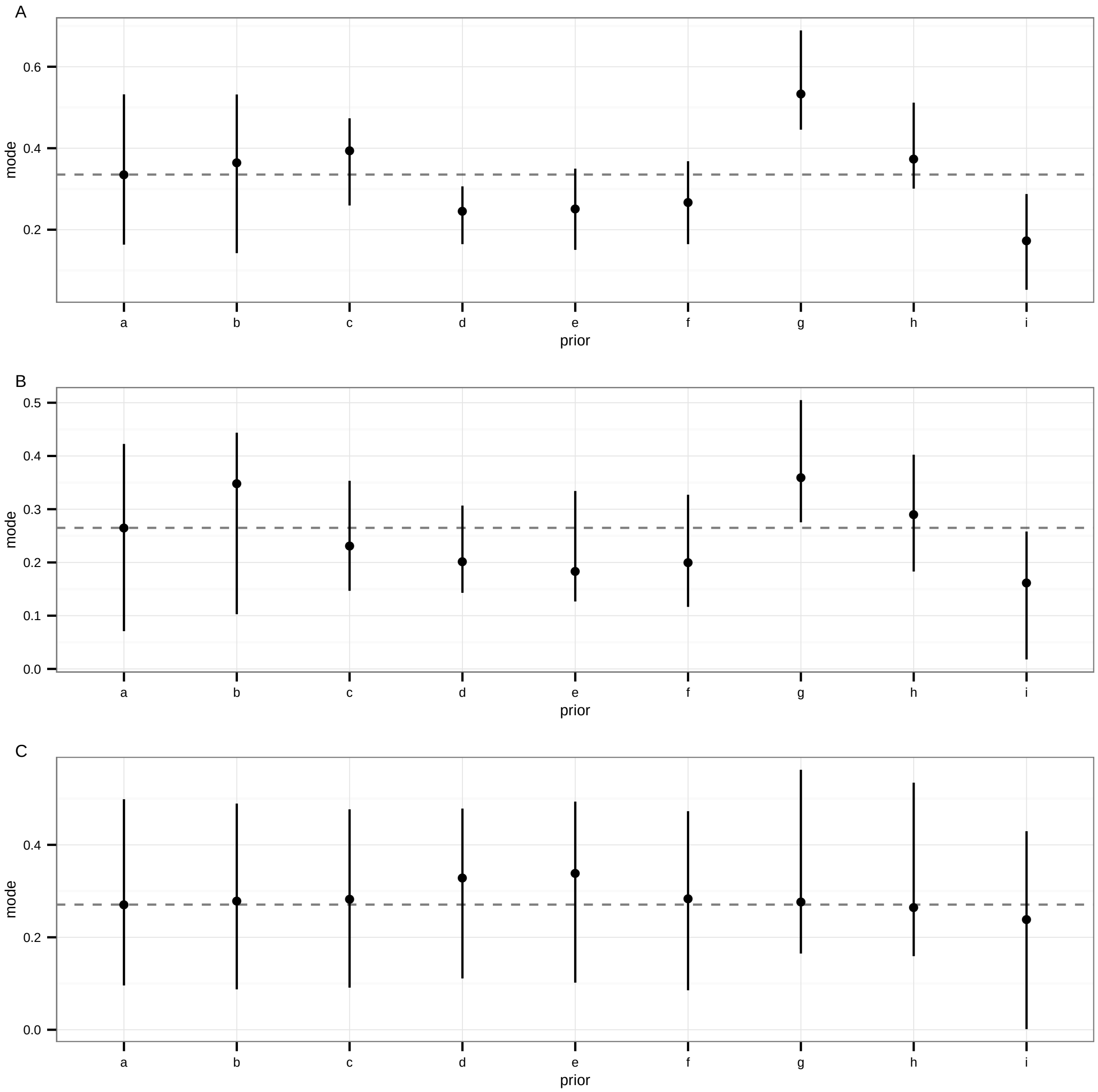

Figure A.6 Results of the sensitivity analysis of the two-sex univariate models showing the posterior mode with 95% Bayesian posterior intervals of highest density of heritability for the animal model of A) horn length, B) male horn base and C) female horn base. Prior *a* is the parameter expanded prior used in further analyses and the horizontal dashed line shows the posterior mode. Prior *b* is a flat uninformative prior with low degree of belief (V=1, nu=0.002). Priors *c* to *i* are informative (nu=2). Prior *c* assigned the variance according to the posterior modes obtained from a preliminary analysis. Priors *d* and *e* used the values of h^2 reported in Coltman et al (2005) and Poissant et al. (2012). Prior *f* assigned the variance equally between all variance components. Priors *g*, *h* and *i* assigned a large (96%), medium (60%) and low (1%) proportion of the phenotypic variance to additive genetic effects. Dotted horizontal line shows the mode of prior *a*.

A.2 Annexes Chapitre 4

The effects of genetic and plastic changes in body mass on population dynamics change over time in a large herbivore

Supplementary material

Gabriel Pigeon,Thomas H. G. Ezard, Marco Festa-Bianchet, David W. Coltman and Fanie Pelletier

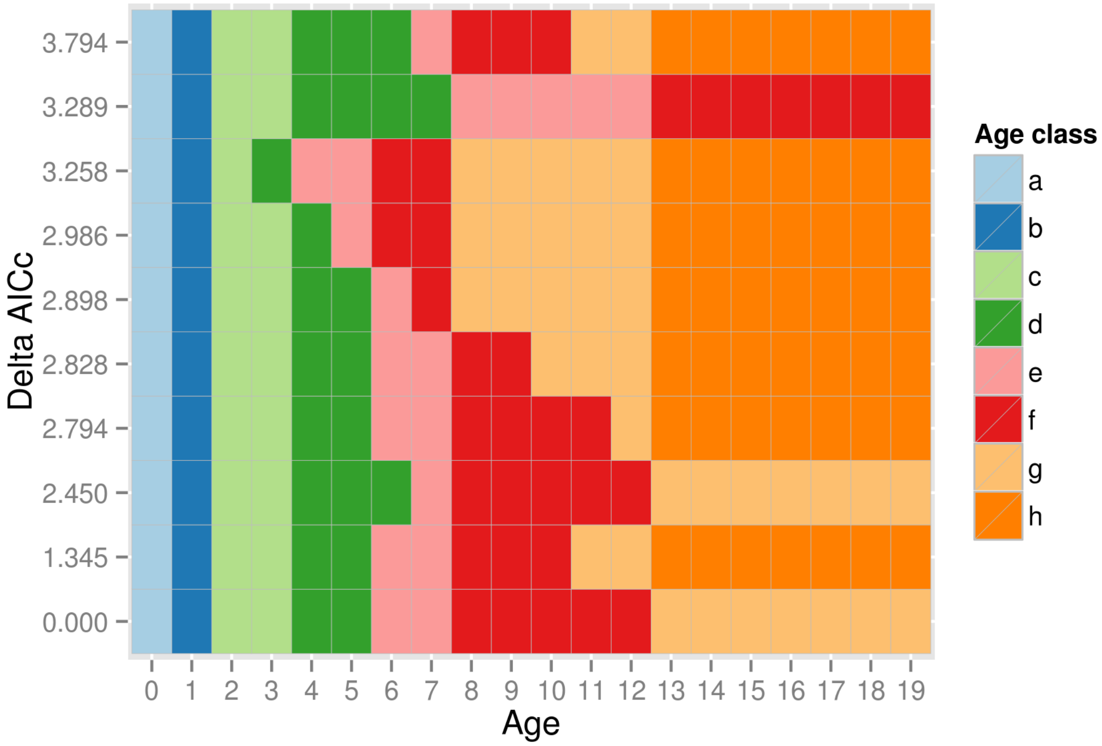

Figure A.7 Delta AICc of models using different age classes to partition the effects of age on survival and reproduction of bighorn sheep. The selected model with 7 age classes is along the bottom. Models with a Delta AICc lower than 4 are shown.

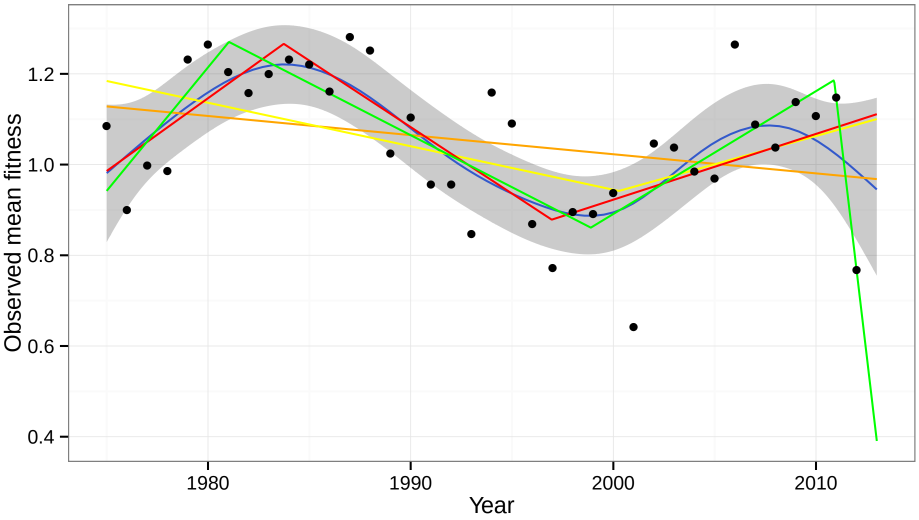

Figure A.8 Segmented linear regression and generalised additive regression of mean annual population growth rate as a function of time for the Ram Mountain bighorn sheep population. Grey ribbon represents the 95% CI for the additive model. The segmented linear regressions range from 0 to 3 inflexion points.

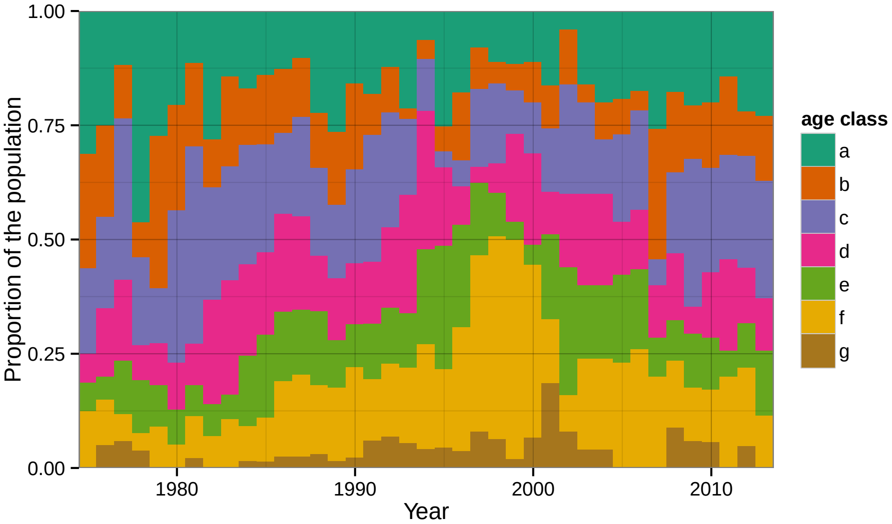

Figure A.9 Proportion of each age class present in the female population of bighorn sheep at Ram Mountain each year between 1975 and 2013. See Fig. S1 for a definition of the age classes.

Table A.3 Parameter estimates (and standard error) for 18 candidate generalized mixed models of survival with DeltaAICc<4. K is the number of parameters estimated by the models. NA represent models were this parameter was not included.

Model	MS1	MS2	MS3	MS4	MS5	MS6	MS7	MS8	MS9	MS10	MS11	MS12	MS13	MS14	MS15	MS16	MS17	MS18
ΔAICc	0	0.15	0.33	0.83	1.77	1.92	2.03	2.06	2.1	2.34	2.62	2.71	2.81	3.03	3.22	3.81	3.83	3.85
K	19	17	18	18	20	18	20	18	19	19	19	19	19	20	21	21	20	19
Intercept	0.65 (0.18)	0.42 (0.14)	0.46 (0.14)	0.56 (0.18)	0.67 (0.19)	0.44 (0.14)	0.65 (0.19)	0.42 (0.14)	0.48 (0.14)	0.46 (0.14)	0.58 (0.18)	0.32 (0.16)	0.55 (0.18)	0.36 (0.16)	0.55 (0.21)	0.67 (0.19)	0.45 (0.21)	0.44 (0.14)
Age.b	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.27 (0.20)	1.26 (0.20)	1.27 (0.20)	1.26 (0.20)	1.26 (0.20)	1.27 (0.20)	1.26 (0.20)	1.27 (0.20)
Age.c	2.23 (0.22)	2.22 (0.22)	2.22 (0.22)	2.23 (0.22)	2.23 (0.22)	2.22 (0.22)	2.23 (0.22)	2.22 (0.22)	2.23 (0.22)	2.22 (0.22)	2.23 (0.22)	2.22 (0.22)	2.22 (0.22)	2.22 (0.22)	2.23 (0.22)	2.23 (0.22)	2.22 (0.22)	2.22 (0.22)
Age.d	2.45 (0.25)	2.43 (0.25)	2.44 (0.25)	2.44 (0.25)	2.45 (0.25)	2.43 (0.25)	2.45 (0.25)	2.43 (0.25)	2.44 (0.25)	2.44 (0.25)	2.44 (0.25)	2.42 (0.25)	2.43 (0.25)	2.43 (0.25)	2.44 (0.25)	2.45 (0.25)	2.43 (0.25)	2.43 (0.25)
Age.e	1.82 (0.22)	1.81 (0.22)	1.81 (0.22)	1.81 (0.22)	1.82 (0.22)	1.81 (0.22)	1.82 (0.22)	1.81 (0.22)	1.82 (0.22)	1.81 (0.22)	1.81 (0.22)	1.80 (0.22)	1.81 (0.22)	1.81 (0.22)	1.82 (0.22)	1.82 (0.22)	1.81 (0.22)	1.81 (0.22)
Age.f	1.20 (0.18)	1.18 (0.17)	1.20 (0.18)	1.18 (0.17)	1.21 (0.18)	1.18 (0.17)	1.20 (0.18)	1.18 (0.17)	1.21 (0.18)	1.20 (0.18)	1.18 (0.17)	1.18 (0.17)	1.18 (0.17)	1.20 (0.18)	1.20 (0.18)	1.21 (0.18)	1.17 (0.17)	1.18 (0.17)
Age.g	0.37 (0.26)	0.33 (0.26)	0.35 (0.26)	0.33 (0.26)	0.37 (0.26)	0.33 (0.26)	0.37 (0.26)	0.33 (0.26)	0.36 (0.26)	0.35 (0.26)	0.34 (0.26)	0.32 (0.26)	0.33 (0.26)	0.35 (0.26)	0.37 (0.26)	0.37 (0.26)	0.33 (0.26)	0.33 (0.26)
Dens	-0.45 (0.14)	-0.39 (0.14)	-0.41 (0.13)	-0.42 (0.14)	-0.45 (0.14)	-0.39 (0.14)	-0.45 (0.14)	-0.40 (0.14)	-0.41 (0.14)	-0.41 (0.14)	-0.42 (0.14)	-0.39 (0.14)	-0.42 (0.14)	-0.41 (0.13)	-0.44 (0.14)	-0.45 (0.14)	-0.41 (0.14)	-0.40 (0.14)
Mass	0.36 (0.07)	0.38 (0.07)	0.37 (0.07)	0.38 (0.07)	0.35 (0.07)	0.37 (0.07)	0.36 (0.07)	0.38 (0.07)	0.36 (0.07)	0.37 (0.07)	0.37 (0.07)	0.39 (0.07)	0.38 (0.07)	0.37 (0.07)	0.36 (0.07)	0.35 (0.07)	0.38 (0.07)	0.37 (0.07)
Age.b :Dens	0.30 (0.20)	0.31 (0.21)	0.30 (0.21)	0.31 (0.21)	0.30 (0.21)	0.32 (0.21)	0.30 (0.20)	0.31 (0.21)	0.31 (0.21)	0.31 (0.21)	0.32 (0.21)	0.32 (0.21)	0.31 (0.21)	0.31 (0.21)	0.30 (0.21)	0.30 (0.21)	0.31 (0.21)	0.32 (0.21)
Age.c :Dens	0.64 (0.21)	0.65 (0.21)	0.64 (0.21)	0.65 (0.21)	0.64 (0.21)	0.65 (0.21)	0.64 (0.21)	0.65 (0.21)	0.64 (0.21)	0.64 (0.21)	0.65 (0.21)	0.65 (0.21)	0.65 (0.21)	0.64 (0.21)	0.64 (0.21)	0.64 (0.21)	0.65 (0.21)	0.65 (0.21)
Age.d :Dens	0.68 (0.24)	0.69 (0.24)	0.68 (0.25)	0.69 (0.24)	0.68 (0.24)	0.69 (0.24)	0.68 (0.24)	0.69 (0.24)	0.68 (0.25)	0.68 (0.25)	0.69 (0.24)	0.69 (0.24)	0.69 (0.24)	0.68 (0.25)	0.68 (0.24)	0.68 (0.24)	0.69 (0.24)	0.69 (0.24)
Age.e :Dens	0.72 (0.22)	0.75 (0.22)	0.74 (0.22)	0.74 (0.22)	0.72 (0.22)	0.75 (0.22)	0.72 (0.22)	0.75 (0.22)	0.73 (0.22)	0.74 (0.22)	0.74 (0.22)	0.75 (0.22)	0.74 (0.22)	0.74 (0.22)	0.72 (0.22)	0.71 (0.22)	0.74 (0.22)	0.75 (0.22)
Age.f :Dens	0.38 (0.18)	0.40 (0.18)	0.38 (0.18)	0.40 (0.18)	0.38 (0.18)	0.40 (0.18)	0.38 (0.18)	0.40 (0.18)	0.38 (0.18)	0.38 (0.18)	0.40 (0.18)	0.40 (0.18)	0.40 (0.18)	0.38 (0.18)	0.37 (0.18)	0.38 (0.18)	0.40 (0.18)	0.40 (0.18)
Age.g :Dens	0.69 (0.24)	0.71 (0.24)	0.69 (0.25)	0.72 (0.24)	0.69 (0.24)	0.72 (0.25)	0.69 (0.24)	0.71 (0.24)	0.69 (0.25)	0.69 (0.25)	0.72 (0.24)	0.72 (0.24)	0.72 (0.24)	0.69 (0.25)	0.69 (0.24)	0.69 (0.24)	0.72 (0.24)	0.72 (0.25)
Predation	-0.49 (0.28)	NA	-0.39 (0.28)	NA	-0.49 (0.28)	NA	-0.49 (0.28)	NA	-0.39 (0.28)	-0.38 (0.28)	NA	NA	NA	-0.38 (0.28)	-0.47 (0.28)	-0.49 (0.29)	NA	NA
$Dens^2$	-0.18 (0.12)	NA	NA	-0.14 (0.12)	-0.18 (0.12)	NA	-0.18 (0.12)	NA	NA	NA	-0.14 (0.12)	NA	-0.14 (0.12)	NA	-0.16 (0.12)	-0.18 (0.12)	-0.11 (0.12)	NA
PDO	NA	NA	NA	NA	NA	NA	-0.01 (0.11)	0.04 (0.11)	NA	0.02 (0.11)	NA	0.01 (0.11)	0.03 (0.11)	-0.01 (0.11)	-0.03 (0.11)	-0.01 (0.11)	0.00 (0.11)	0.04 (0.11)
$Mass^2$	NA	NA	NA	NA	-0.02 (0.04)	-0.02 (0.04)	NA	NA	-0.02 (0.04)	NA	-0.02 (0.04)	NA	NA	NA	NA	-0.02 (0.04)	NA	-0.02 (0.04)
PDO^2	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	0.14 (0.12)	NA	0.13 (0.11)	0.10 (0.11)	NA	0.12 (0.12)	NA

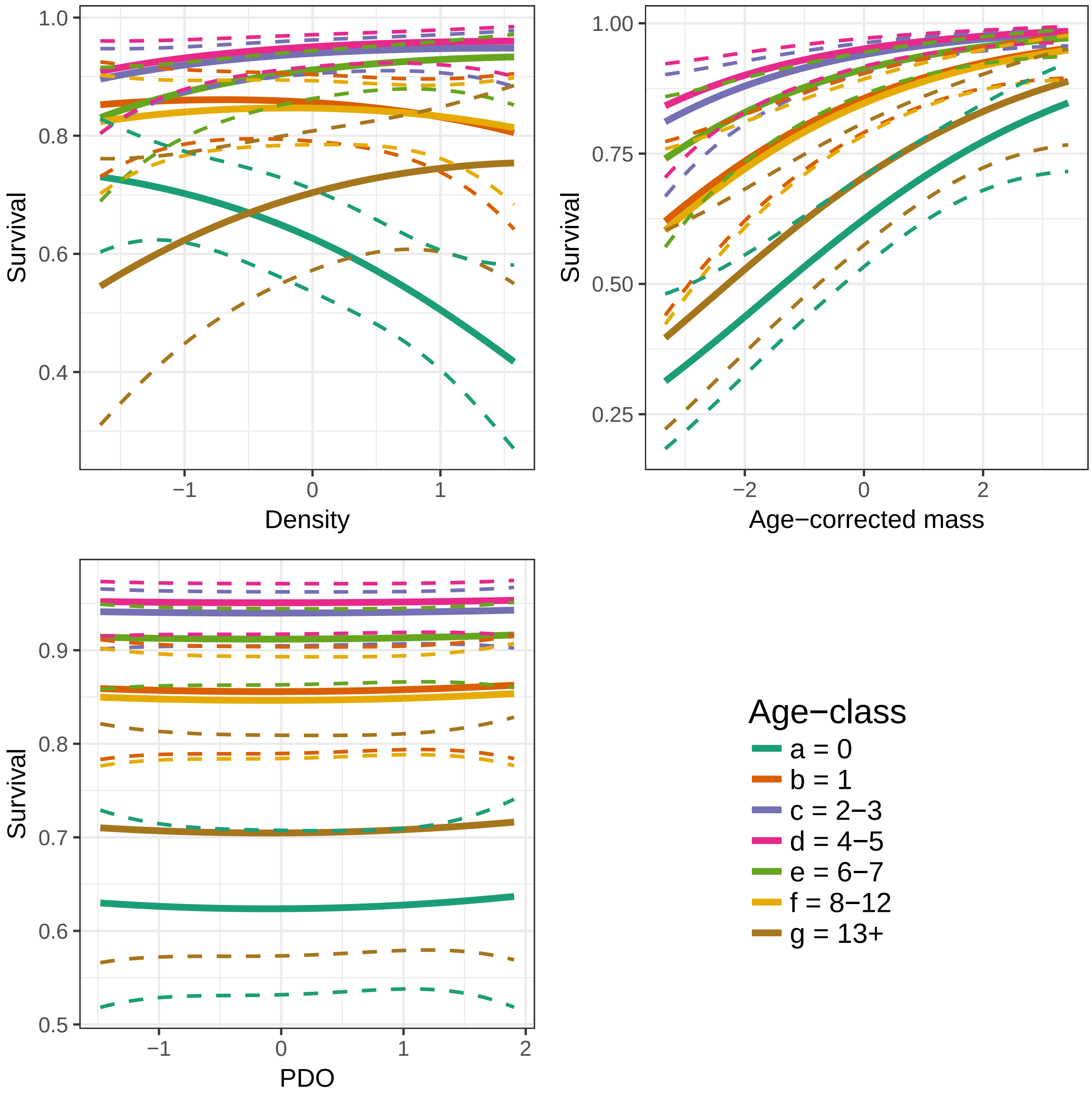

Figure A.10 Model averaged prediction of female bighorn survival as a function of scaled density, age-corrected mass and PDO for each age-class.

Table A.4 Parameter estimates (and standard error) for 11 candidate generalized mixed models of recruitment with DeltaAICc<4. K is the number of parameters estimated by the models.

Model	MR1	MR2	MR3	MR4	MR5	MR6	MR7	MR8	MR9	MR10	MR11
ΔAICc	0	1.6	1.65	1.76	1.85	2.78	3.02	3.32	3.37	3.5	3.88
K	22	23	17	23	24	21	18	24	25	18	19
Intercept	-4.62 (0.75)	-4.63 (0.75)	-4.33 (0.63)	-4.58 (0.75)	-4.77 (0.76)	-4.95 (0.73)	-4.36 (0.64)	-4.60 (0.75)	-4.78 (0.76)	-4.31 (0.63)	-4.47 (0.64)
Age.c	4.61 (0.73)	4.66 (0.74)	4.35 (0.61)	4.61 (0.73)	4.62 (0.73)	4.59 (0.73)	4.41 (0.62)	4.66 (0.74)	4.67 (0.74)	4.35 (0.61)	4.36 (0.61)
Age.d	5.55 (0.74)	5.59 (0.74)	5.27 (0.61)	5.54 (0.73)	5.55 (0.73)	5.52 (0.73)	5.33 (0.63)	5.59 (0.74)	5.60 (0.74)	5.27 (0.61)	5.27 (0.61)
Age.e	5.30 (0.74)	5.35 (0.75)	5.00 (0.61)	5.30 (0.74)	5.31 (0.74)	5.27 (0.73)	5.06 (0.63)	5.34 (0.74)	5.36 (0.74)	5.00 (0.61)	5.00 (0.61)
Age.f	4.99 (0.74)	5.03 (0.74)	4.71 (0.61)	4.98 (0.73)	4.99 (0.73)	4.96 (0.73)	4.77 (0.62)	5.03 (0.74)	5.04 (0.74)	4.71 (0.61)	4.71 (0.61)
Age.g	3.70 (0.79)	3.74 (0.80)	3.45 (0.67)	3.70 (0.79)	3.71 (0.79)	3.66 (0.79)	3.50 (0.68)	3.73 (0.79)	3.75 (0.79)	3.44 (0.67)	3.45 (0.67)
Dens	-0.86 (0.53)	-0.85 (0.53)	-0.36 (0.13)	-0.85 (0.52)	-0.85 (0.52)	-0.71 (0.51)	-0.37 (0.13)	-0.85 (0.52)	-0.84 (0.52)	-0.36 (0.13)	-0.34 (0.13)
Predation	-1.32 (0.36)	-1.33 (0.36)	-1.34 (0.36)	-1.35 (0.37)	-1.34 (0.36)	-1.15 (0.38)	-1.35 (0.36)	-1.36 (0.37)	-1.35 (0.36)	-1.36 (0.36)	-1.35 (0.36)
Mass	1.97 (0.48)	2.03 (0.49)	1.98 (0.47)	1.97 (0.48)	1.99 (0.48)	2.00 (0.48)	2.05 (0.48)	2.04 (0.49)	2.06 (0.49)	1.98 (0.47)	1.99 (0.46)
Age.c :Mass	-1.39 (0.50)	-1.45 (0.51)	-1.35 (0.48)	-1.39 (0.49)	-1.40 (0.49)	-1.42 (0.50)	-1.42 (0.49)	-1.45 (0.51)	-1.46 (0.51)	-1.35 (0.48)	-1.36 (0.48)
Age.d :Mass	-1.51 (0.50)	-1.58 (0.51)	-1.53 (0.48)	-1.52 (0.49)	-1.53 (0.49)	-1.55 (0.50)	-1.61 (0.50)	-1.59 (0.51)	-1.61 (0.51)	-1.54 (0.48)	-1.55 (0.48)
Age.e :Mass	-1.59 (0.50)	-1.66 (0.51)	-1.60 (0.49)	-1.60 (0.50)	-1.61 (0.50)	-1.62 (0.50)	-1.67 (0.50)	-1.67 (0.51)	-1.68 (0.51)	-1.60 (0.48)	-1.61 (0.48)
Age.f :Mass	-1.48 (0.49)	-1.54 (0.50)	-1.51 (0.48)	-1.48 (0.49)	-1.50 (0.49)	-1.51 (0.50)	-1.59 (0.49)	-1.55 (0.50)	-1.56 (0.50)	-1.52 (0.48)	-1.53 (0.48)
Age.g :Mass	-1.20 (0.57)	-1.26 (0.58)	-1.22 (0.56)	-1.21 (0.57)	-1.22 (0.57)	-1.22 (0.58)	-1.28 (0.57)	-1.27 (0.58)	-1.29 (0.58)	-1.23 (0.56)	-1.24 (0.56)
Dens^2	-0.34 (0.15)	-0.34 (0.15)	-0.32 (0.15)	-0.35 (0.15)	-0.32 (0.15)	NA	-0.32 (0.15)	-0.35 (0.15)	-0.32 (0.15)	-0.33 (0.15)	-0.30 (0.15)
Age.c :Dens	0.20 (0.53)	0.19 (0.53)	NA	0.19 (0.52)	0.20 (0.52)	0.13 (0.52)	NA	0.18 (0.52)	0.18 (0.52)	NA	NA
Age.d :Dens	0.59 (0.53)	0.57 (0.53)	NA	0.58 (0.53)	0.60 (0.53)	0.51 (0.52)	NA	0.57 (0.53)	0.58 (0.53)	NA	NA
Age.e :Dens	0.48 (0.53)	0.46 (0.54)	NA	0.47 (0.53)	0.48 (0.53)	0.41 (0.52)	NA	0.46 (0.53)	0.47 (0.53)	NA	NA
Age.f :Dens	0.75 (0.53)	0.74 (0.53)	NA	0.75 (0.53)	0.76 (0.53)	0.68 (0.52)	NA	0.73 (0.53)	0.74 (0.53)	NA	NA
Age.g :Dens	0.80 (0.60)	0.79 (0.60)	NA	0.80 (0.59)	0.81 (0.59)	0.71 (0.59)	NA	0.79 (0.60)	0.80 (0.59)	NA	NA
PDO	NA	NA	NA	-0.07 (0.13)	-0.12 (0.13)	NA	NA	-0.08 (0.13)	-0.12 (0.13)	-0.06 (0.13)	-0.10 (0.13)
Mass^2	NA	-0.03 (0.05)	NA	NA	NA	NA	-0.04 (0.05)	-0.03 (0.05)	-0.04 (0.05)	NA	NA
PDO^2	NA	NA	NA	NA	0.19 (0.13)	NA	NA	NA	0.19 (0.13)	NA	0.17 (0.13)

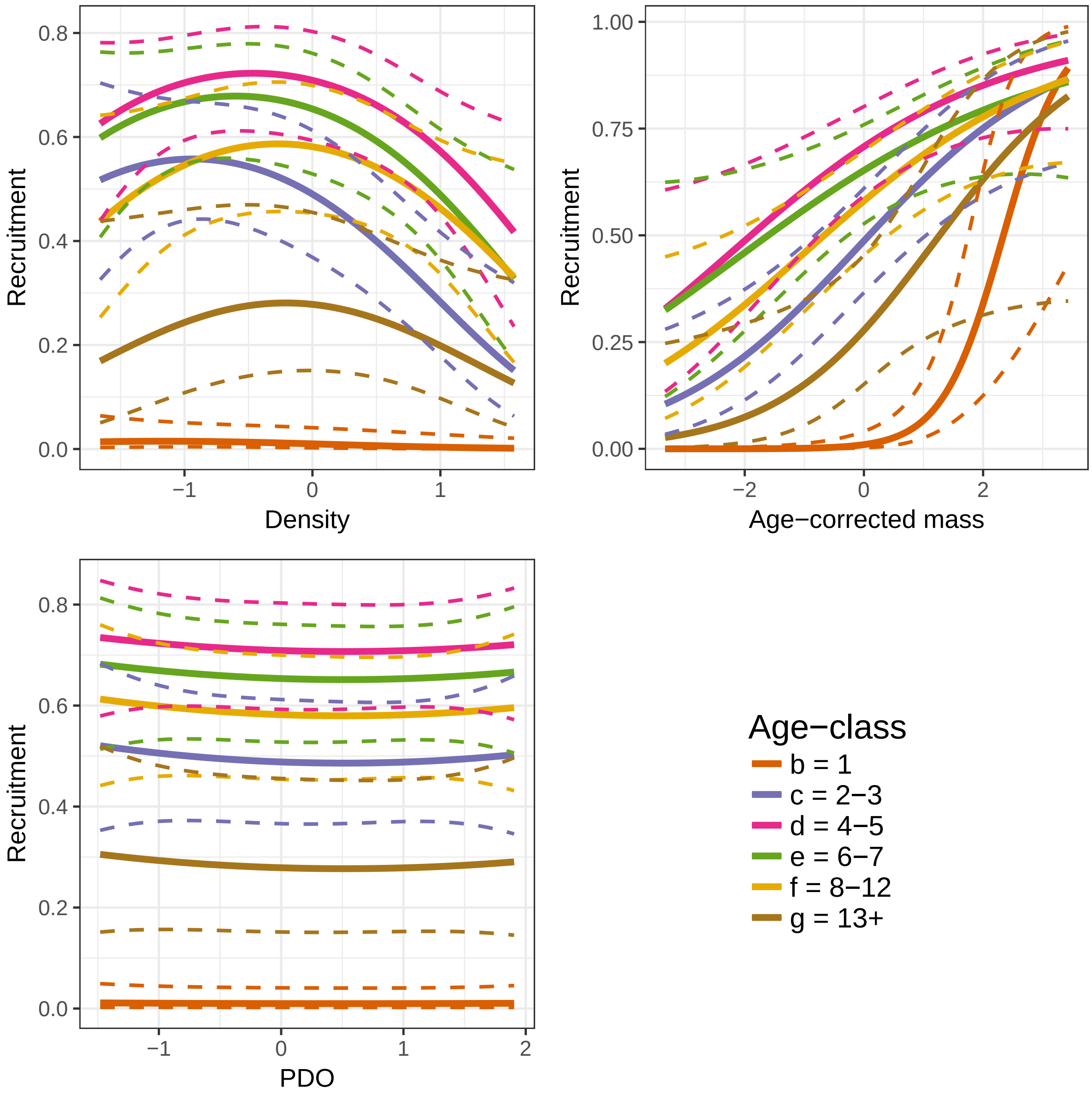

Figure A.11 Model averaged prediction of female bighorn recruitment as a function of scaled density, age-corrected mass and PDO for each age-class.

Table A.5 Temporal trends in mass of female bighorn sheep body mass for each period and age class. The slope from a linear regression of mean mass as a function of yr (β) is given followed by the 95% confidence interval on the slope.

Period	Age-class	β	95% HDP interval		P-value
1975 to 1984	0	0.072	-0.045	0.189	0.195
	1	-0.04	-0.156	0.076	0.453
	2-3	0.008	-0.111	0.126	0.884
	4-5	-0.002	-0.150	0.146	0.975
	6-7	-0.016	-0.198	0.167	0.849
	8-12	-0.002	-0.181	0.177	0.983
	13+	0.001	-0.321	0.323	0.991
1984 to 1997	0	-0.127	-0.196	-0.057	0.002
	1	-0.113	-0.181	-0.045	0.004
	2-3	-0.079	-0.140	-0.017	0.016
	4-5	0.014	-0.059	0.087	0.689
	6-7	-0.050	-0.105	0.006	0.076
	8-12	-0.066	-0.138	0.006	0.068
	13+	-0.030	-0.107	0.048	0.419
1997 to 2012	0	0.084	0.022	0.147	0.012
	1	0.080	0.028	0.132	0.005
	2-3	0.071	0.010	0.132	0.026
	4-5	0.046	-0.048	0.139	0.313
	6-7	0.122	0.038	0.207	0.008
	8-12	0.130	0.058	0.202	0.002
	13+	0.087	-0.017	0.191	0.091

Table A.6 Variance components and heritability of female body mass in bighorn sheep at Ram Mountain, Canada, according to a bivariate animal model. The posterior mode of the proportion of phenotypic variance explained by each component is followed by the 95% highest posterior density interval.

	Posterior mean	95% HDP interval	
h^2	0.224	0.143	0.343
ID	0.167	0.106	0.279
Cohort	0.112	0.054	0.185
Year	0.174	0.106	0.249

Table A.7 Temporal trends in estimated breeding value of female bighorn sheep body mass for each period and age class. The slope from a linear regression of mean annual EBV as a function of yr (β) is given followed by the 95% highest posterior density interval (HPD) and the probability that this slope is lower than 0 ; a value of over 0.95 signifying a significant decrease and a value lower than 0.05 a significant increase (with alpha levels of 0.05).

Period	Age-class	β	95% HDP interval		Pr[β<0]
	0	0.012	-0.027	0.055	0.278
	1	-0.005	-0.048	0.034	0.585
1975	2-3	-0.024	-0.066	0.020	0.850
to	4-5	-0.027	-0.084	0.033	0.810
1984	6-7	0.012	-0.047	0.086	0.371
	8-12	0.046	-0.031	0.136	0.138
	13+	0.033	-0.081	0.143	0.289
	0	-0.003	-0.021	0.015	0.612
	1	-0.001	-0.020	0.020	0.550
1984	2-3	0.001	-0.023	0.025	0.462
to	4-5	0.010	-0.015	0.036	0.197
1997	6-7	-0.007	-0.027	0.013	0.748
	8-12	-0.011	-0.036	0.009	0.832
	13+	0.001	-0.040	0.050	0.472
	0	-0.003	-0.026	0.021	0.573
	1	0.000	-0.024	0.026	0.494
1997	2-3	0.008	-0.014	0.032	0.241
to	4-5	0.001	-0.026	0.031	0.466
2012	6-7	0.012	-0.019	0.037	0.209
	8-12	0.036	0.007	0.060	0.003
	13+	0.037	0.000	0.079	0.030

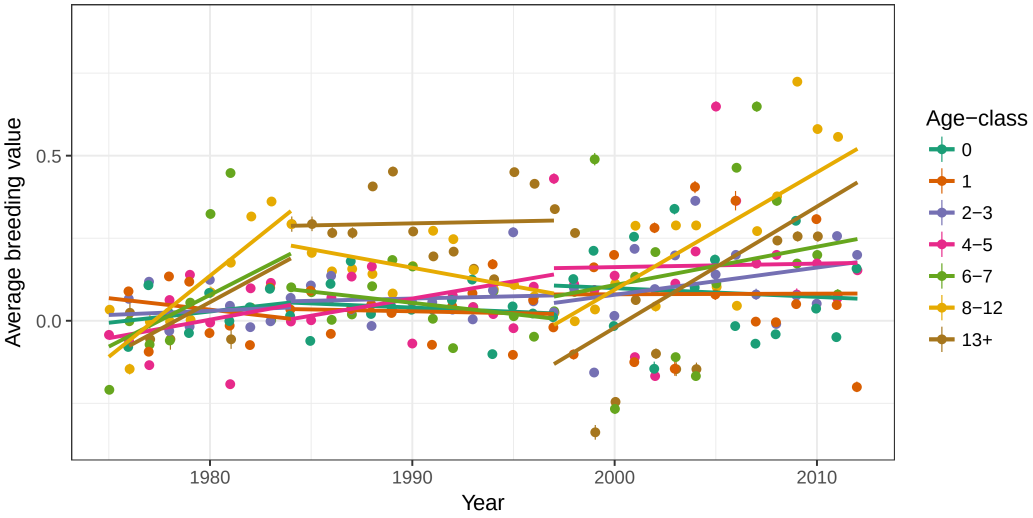

Figure A.12 Temporal change in mean breeding value of female mass within each age-class between 1975 and 2012.

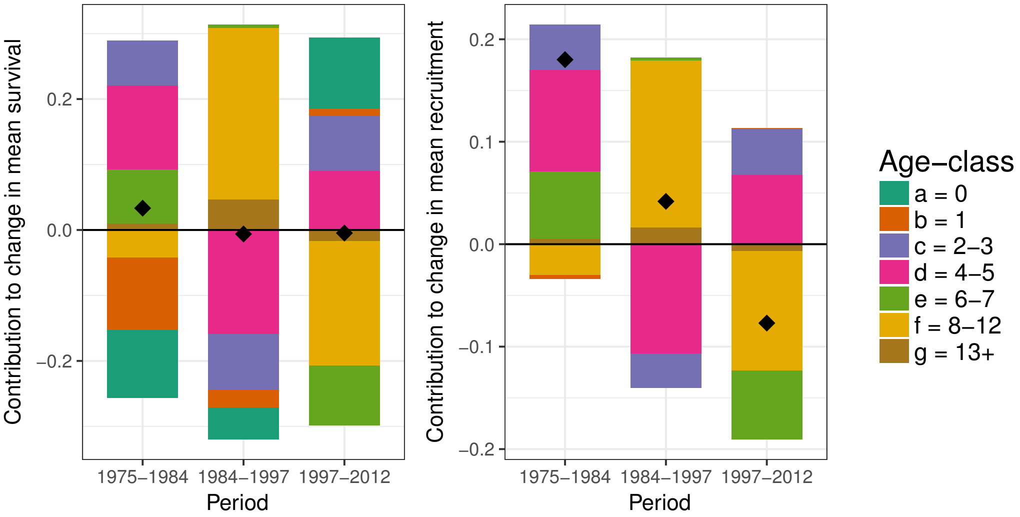

Figure A.13 Contribution of change in proportion of each age class to the change in survival and recruitment. The height of a box represents the contribution (approximately $\Delta Prop * \bar{s}$ and $\Delta Prop * \bar{r}$). Boxes under the 0 line represent negative contributions, while boxes above the 0 represent positive contribution. The small black diamonds represent the sum of these contributions ; the total effect of change in age-structure on population mean survival and recruitment.

Table A.8 Table showing the probability that the absolute effects of a change in given factor (ECO : heritable change in trait, Evo : non-heritable change in trait, Age-structure, Density and PDO) on survival is bigger than half the effect on recruitment. A value lower than 0.05 suggests a significantly larger effect through recruitment while a value larger than 0.95 suggests a significantly larger effect through survival.

Period	Eco	Evo	Age-structure	Density	PDO
1 :1975-1984	0.546	0.368	0.000	0.405	0.647
2 :1983-1997	0.910	0.380	0.004	0.000	0.497
3 :1997-2012	0.909	0.527	0.001	0.243	0.464

Table A.9 Coefficient estimates of a linear regression of the annual effects of non-heritable change on population growth rate as a function of change in density. R-squared of the models was 0.009.

	Estimate	SE	t-value	P-value
Intercept	0	0.006	0.029	0.977
Change in density	-0.013	0.023	-0.55	0.586

A.3 Annexes Chapitre 5

Long-term fitness consequences of early environment in a long-lived ungulate

Supplementary material

Gabriel Pigeon, Marco Festa-Bianchet and Fanie Pelletier

Table A.10 Statistics used to test the effect of birth environment covariates on the weaning success of bighorn ewes at Ram Mountain from 1973 to 2014. Fcst/co/t (degrees of freedom) is the statistic from the ANODEV method. P-value is its associated P-value. Adj.P-value is the P-value corrected for multiple testing using the Benjamini & Hochberg method. R2 describes the proportion of the variance between cohorts explained by the covariate. Delta AICc refers to the difference between the AICc of the model including the covariate and the base model (a negative value indicates a better model than the base model). Interactions with density are noted as " * density", quadratic effects of variables are noted as "(quad)" and models with interactions between early and current environment are noted as "Int".

Environmental Covariate	Fcst/co/t	P-value	adj.P-value	R2	Delta AICc
density (PAR)	36.334	0.000	0.000	0.556	-32.297
density (quad)	8.930	0.001	0.030	0.381	-29.789
density	14.157	0.001	0.030	0.321	-26.436
temp.spring (PAR)	6.258	0.018	0.429	0.177	-13.669
precip.fall (PAR)	4.464	0.043	0.815	0.133	-9.482
precip.winter.aft (quad)	1.970	0.158	0.825	0.120	-6.580
precip.winter.bef (quad)	1.807	0.182	0.825	0.111	-5.800
precip.spring (quad)	1.693	0.202	0.825	0.105	-5.244
precip.winter.aft * density	1.628	0.214	0.825	0.104	-2.243
temp.spring * density	1.606	0.219	0.825	0.103	-2.166
precip.spring	3.396	0.075	0.825	0.102	-7.009
temp.winter.aft * density	1.546	0.231	0.825	0.099	-1.959
temp.winter.bef * density	0.901	0.418	0.927	0.060	0.393
temp.fall * density	0.899	0.418	0.927	0.060	0.401
precip.spring * density	0.835	0.444	0.927	0.056	0.643
precip.summer (quad)	0.828	0.447	0.927	0.054	-0.760
precip.summer	1.569	0.220	0.825	0.050	-2.397
precip.summer (PAR)	1.507	0.229	0.825	0.049	-2.125
temp.winter.aft (quad)	0.592	0.560	0.927	0.039	0.549
temp.winter.aft	1.221	0.278	0.901	0.039	-1.457

Table A.11 Table A.3 continued. Statistics used to test the effect of birth environment covariates on the weaning success of bighorn ewes at Ram Mountain from 1973 to 2014. Fcst/co/t (degrees of freedom) is the statistic from the ANODEV method. P-value is its associated P-value. Adj.P-value is the P-value corrected for multiple testing using the Benjamini & Hochberg method. R2 describes the proportion of the variance between cohorts explained by the covariate. Delta AICc refers to the difference between the AICc of the model including the covariate and the base model (a negative value indicates a better model than the base model). Interactions with density are noted as “ * density”, quadratic effects of variables are noted as “(quad)” and models with interactions between early and current environment are noted as “Int”.

Environmental Covariate	Fcst/co/t	P-value	adj.P-value	R2	Delta AICc
precip.fall (quad)	0.574	0.570	0.927	0.038	0.656
precip.summer * density	0.517	0.602	0.927	0.036	1.890
PDO * density	0.503	0.610	0.927	0.035	1.945
temp.winter.bef (quad)	0.518	0.601	0.927	0.034	0.974
temp.winter.bef	1.048	0.314	0.927	0.034	-0.981
precip.fall	0.980	0.330	0.927	0.032	-0.792
temp.summer * density	0.450	0.642	0.927	0.031	2.161
precip.winter.bef	0.958	0.336	0.927	0.031	-0.731
temp.summer (quad)	0.458	0.637	0.927	0.031	1.316
precip.fall * density	0.400	0.674	0.927	0.028	2.364
temp.spring (quad)	0.399	0.675	0.927	0.027	1.656
temp.winter.bef	0.675	0.418	0.927	0.023	0.075
temp.fall (quad)	0.259	0.774	0.954	0.018	2.477
temp.fall	0.523	0.475	0.927	0.017	0.495
precip.winter.bef * density	0.215	0.808	0.954	0.015	3.125
PDO (quad)	0.212	0.811	0.954	0.014	2.756
temp.winter.aft (PAR)	0.403	0.531	0.927	0.014	0.847
temp.summer	0.361	0.552	0.927	0.012	0.959
PDO	0.360	0.553	0.927	0.012	0.963
precip.spring (PAR)	0.249	0.622	0.927	0.009	1.333
precip.winter.aft	0.164	0.688	0.927	0.005	1.531
precip.winter.aft (PAR)	0.149	0.702	0.930	0.005	1.554
PDO (PAR)	0.090	0.766	0.954	0.003	1.741
precip.winter.bef (PAR)	0.089	0.768	0.954	0.003	1.746
temp.spring	0.029	0.867	0.954	0.001	1.930
temp.summer (PAR)	0.018	0.896	0.954	0.001	1.965
temp.fall (PAR)	0.005	0.942	0.963	0.000	2.004

Table A.12 Statistics used to test the effect of birth environment covariates on bighorn ewe survival from 1973 to 2014 using logistic mixed models. Fcst/co/t (degrees of freedom) is the statistic from the ANODEV method. Adj.P-value is the P-value corrected for multiple testing using the Benjamini & Hochberg method. R 2 is the proportion of the variance between cohorts explained by the covariate. Delta AICc refers to the difference between the AICc of the model including the covariate and the base model (a negative value indicates a better model than the base model). Interactions with density are noted as " * density", quadratic effects of variables are noted as "(quad)" and models with interactions between early and current environment are noted as "Int".

Environmental Covariate	Fcst/co/t	P-value	adj.P-value	R2	Delta AICc
birth.precip.winter.aft (quad)	2.858	0.074	0.825	0.165	-2.803
birth.temp.winter.aft * density	2.182	0.132	0.825	0.135	-1.040
birth.temp.summer (quad)	2.144	0.135	0.825	0.129	-1.316
birth.precip.spring (quad)	1.660	0.208	0.825	0.103	-0.232
density (quad)	1.632	0.213	0.825	0.101	-0.167
birth.temp.winter.aft (quad)	1.552	0.229	0.825	0.097	0.020
density	3.073	0.090	0.825	0.093	-1.842
precip.winter.aft (PAR)	2.807	0.105	0.825	0.088	-1.534
birth.temp.winter.aft	2.705	0.110	0.825	0.083	-1.419
birth.precip.winter.bef (quad)	0.994	0.382	0.927	0.064	1.370
birth.precip.spring	1.957	0.172	0.825	0.061	-0.527
birth.temp.summer * density	0.837	0.444	0.927	0.056	1.915
birth.precip.summer * density	0.777	0.470	0.927	0.053	2.059
birth.temp.summer	1.636	0.211	0.825	0.052	-0.132
birth.precip.winter.aft * density	0.738	0.487	0.927	0.050	2.153
birth.precip.winter.bef	1.571	0.220	0.825	0.050	-0.051
temp.fall (PAR)	1.420	0.243	0.825	0.047	0.072
precip.winter.bef (PAR)	1.403	0.246	0.825	0.046	0.175
birth.temp.fall * density	0.652	0.529	0.927	0.044	2.363
birth.pdo.annual * density	0.588	0.562	0.927	0.040	2.520
birth.precip.winter.bef * density	0.536	0.591	0.927	0.037	2.649
birth.precip.spring * density	0.513	0.604	0.927	0.035	2.707

Table A.13 Table A.4 continued. Statistics used to test the effect of birth environment covariates on bighorn ewe survival from 1973 to 2014 using logistic mixed models. Fcst/co/t (degrees of freedom) is the statistic from the ANODEV method. Adj.P-value is the P-value corrected for multiple testing using the Benjamini & Hochberg method. R2 is the proportion of the variance between cohorts explained by the covariate. Delta AICc refers to the difference between the AICc of the model including the covariate and the base model (a negative value indicates a better model than the base model). Interactions with density are noted as " * density", quadratic effects of variables are noted as "(quad)" and models with interactions between early and current environment are noted as "Int".

Environmental Covariate	Fcst/co/t	P-value	adj.P-value	R2	Delta AICc
temp.winter.bef (PAR)	0.860	0.361	0.927	0.029	0.821
birth.precip.summer (quad)	0.376	0.690	0.927	0.025	2.985
birth.precip.winter.aft	0.613	0.440	0.927	0.020	1.183
precip.summer (PAR)	0.564	0.459	0.927	0.019	1.230
birth.precip.fall * density	0.249	0.781	0.954	0.017	3.379
birth.precip.summer	0.490	0.489	0.927	0.016	1.348
precip.fall (PAR)	0.436	0.514	0.927	0.015	1.421
birth.precip.fall (quad)	0.184	0.833	0.954	0.013	3.513
birth.precip.fall	0.365	0.550	0.927	0.012	1.516
birth.temp.spring * density	0.162	0.851	0.954	0.011	3.607
birth.temp.fall (quad)	0.137	0.872	0.954	0.009	3.643
fem (PAR)	0.254	0.618	0.927	0.009	1.697
birth.temp.spring (quad)	0.111	0.895	0.954	0.008	3.717
birth.pdo.annual (quad)	0.102	0.903	0.954	0.007	3.743
birth.pdo.annual	0.184	0.671	0.927	0.006	1.763
temp.summer (PAR)	0.169	0.684	0.927	0.006	1.799
birth.temp.winter.bef * density	0.068	0.934	0.963	0.005	3.856
temp.spring (PAR)	0.086	0.772	0.954	0.003	1.898
precip.spring (PAR)	0.073	0.788	0.954	0.003	1.923
birth.temp.winter.bef (quad)	0.035	0.966	0.968	0.002	3.934
temp.winter.aft (PAR)	0.048	0.828	0.954	0.002	1.957
birth.temp.fall	0.046	0.831	0.954	0.002	1.951
birth.temp.spring	0.017	0.899	0.954	0.001	1.992
birth.temp.winter.bef	0.010	0.923	0.963	0.000	2.002
pdo.annual (PAR)	0.002	0.968	0.968	0.000	2.018

Table A.14 Statistics used to test the effect of birth environment covariates on bighorn ewe survival from 1973 to 2014 using logistic mixed models. Fcst/co/t (degrees of freedom) is the statistic from the ANODEV method. Adj.P-value is the P-value corrected for multiple testing using the Benjamini & Hochberg method. R2 is the proportion of the variance between cohorts explained by the covariate. Delta AICc refers to the difference between the AICc of the model including the covariate and the base model (a negative value indicates a better model than the base model). Interactions with density are noted as " * density", quadratic effects of variables are noted as "(quad)" and models with interactions between early and current environment are noted as "Int".

Environmental Covariate	Fcst/co/t	P-value	R2	Delta AICc
density	11.157	0.002	0.271	-14.188
density (quad)	5.585	0.009	0.278	-12.600
precip.spring	4.774	0.037	0.137	-6.197
precip.spring (quad)	2.638	0.089	0.154	-5.185
precip.winter.aft (quad)	2.303	0.118	0.137	-4.178
temp.winter.aft	2.420	0.130	0.075	-2.456
temp.winter.aft *density	2.122	0.139	0.132	-1.717
precip.winter.aft (PAR)	2.223	0.147	0.071	-2.179
precip.winter.bef	2.007	0.167	0.063	-1.743
temp.winter.aft (quad)	1.306	0.286	0.083	-0.928
precip.winter.bef (PAR)	1.144	0.294	0.038	-0.166
precip.spring (PAR)	0.892	0.353	0.030	0.468
precip.summer *density	1.076	0.355	0.071	0.906
precip.winter.bef (quad)	1.040	0.366	0.067	0.011
temp.fall (PAR)	0.708	0.407	0.024	0.641
temp.winter.bef (PAR)	0.677	0.417	0.023	0.633
temp.fall *density	0.663	0.523	0.045	2.043
precip.summer (PAR)	0.406	0.529	0.014	1.180
precip.winter.aft *density	0.645	0.532	0.044	2.096
temp.summer (quad)	0.626	0.542	0.041	1.535
precip.fall	0.368	0.549	0.012	1.280
precip.summer (quad)	0.602	0.554	0.040	1.626
precip.winter.bef *density	0.579	0.567	0.040	2.285

Table A.15 Table A.5 continued. Statistics used to test the effect of birth environment covariates on bighorn ewe survival from 1973 to 2014 using logistic mixed models. Fcst/co/t (degrees of freedom) is the statistic from the ANODEV method. Adj.P-value is the P-value corrected for multiple testing using the Benjamini & Hochberg method. R2 is the proportion of the variance between cohorts explained by the covariate. Delta AICc refers to the difference between the AICc of the model including the covariate and the base model (a negative value indicates a better model than the base model). Interactions with density are noted as " * density", quadratic effects of variables are noted as "(quad)" and models with interactions between early and current environment are noted as "Int".

Environmental Covariate	Fcst/co/t	P-value	R2	Delta AICc
precip.spring *density	0.576	0.568	0.040	2.291
density (PAR)	0.259	0.614	0.009	1.632
precip.fall (PAR)	0.237	0.630	0.008	1.554
temp.summer	0.237	0.630	0.008	1.535
temp.summer *density	0.466	0.632	0.032	2.610
pdo.annual	0.196	0.661	0.006	1.615
temp.winter.bef	0.195	0.662	0.006	1.617
pdo.annual *density	0.415	0.664	0.029	2.758
precip.summer	0.132	0.719	0.004	1.741
pdo.annual (PAR)	0.124	0.727	0.004	1.754
precip.fall *density	0.303	0.741	0.021	3.090
temp.winter.bef (quad)	0.253	0.778	0.017	2.983
temp.fall	0.068	0.796	0.002	1.868
precip.fall (quad)	0.190	0.828	0.013	3.234
temp.spring (quad)	0.174	0.841	0.012	3.301
precip.winter.aft	0.041	0.842	0.001	1.922
temp.summer (PAR)	0.036	0.852	0.001	1.939
temp.winter.bef *density	0.130	0.878	0.009	3.610
temp.spring *density	0.130	0.879	0.009	3.612
pdo.annual (quad)	0.120	0.887	0.008	3.516
temp.winter.aft (PAR)	0.012	0.914	0.000	1.985
temp.spring (PAR)	0.010	0.921	0.000	1.987
temp.spring	0.005	0.944	0.000	1.993
temp.fall (quad)	0.035	0.966	0.002	3.864

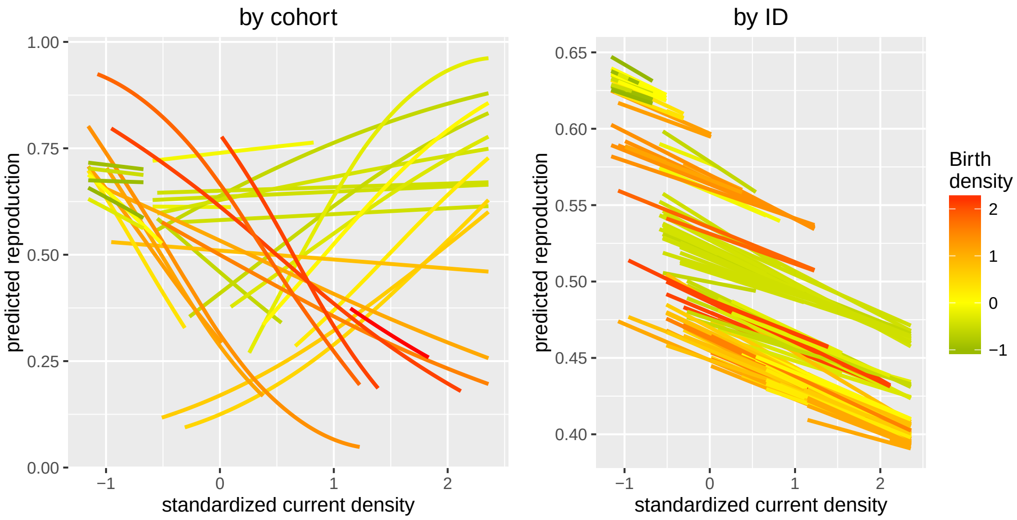

Figure A.14 Predicted reproduction of bighorn ewes by a) cohort and b) individual according to current density. Birth density is represented by the color of the curves. All density values were standardized.

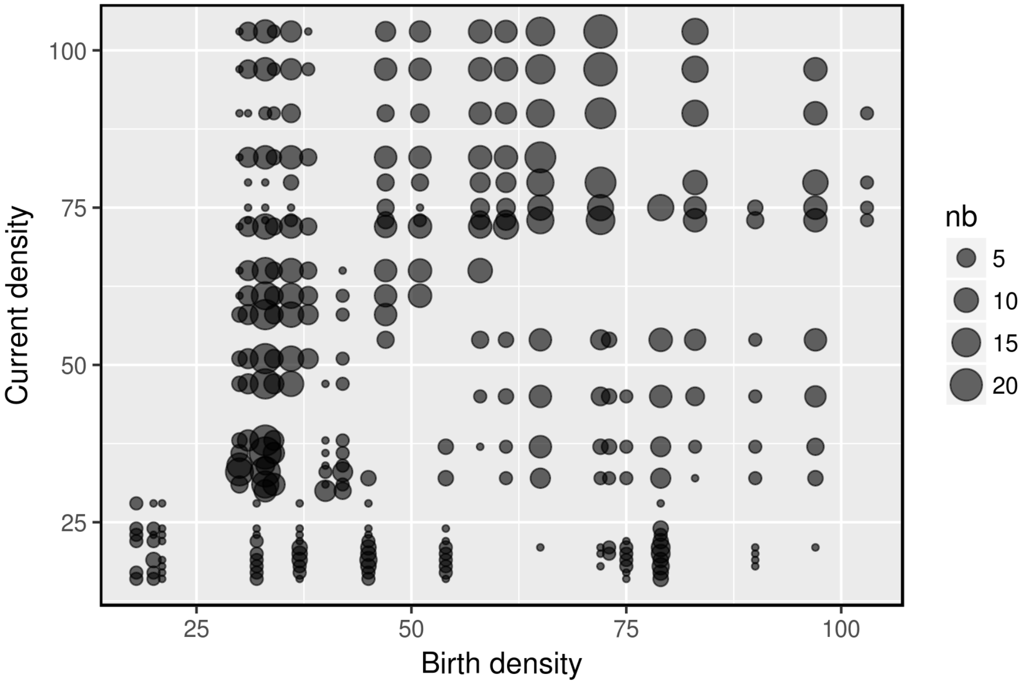

Figure A.15 Current density as a function of birth density. Each point represent a cohort during a given adult year, with size represneting the sample size.

Table A.16 Additional information about cohorts of bighorn ewes at Ram Mountain. Number of individual per cohort (N) ; length of time the cohort was present in the population in years (Present for) ; mean number of years a ewe was observed (Mean(obs/id) ; standard deviation of the number of observation per individual (Mean(obs/id)).

Cohort	N	Present for	Mean(obs/id)	Sd(obs/id)
1973	6	15	10.47	4.88
1974	7	10	5.17	3.23
1975	8	17	11.61	6.11
1976	12	10	4.35	2.84
1977	6	17	10.5	5.99
1978	11	19	12.23	4.4
1979	8	15	10.54	3.78
1980	7	13	8.75	2.53
1981	7	16	11.09	2.58
1982	11	15	10.4	2.8
1983	6	10	6.52	2.08
1984	8	14	10.85	3.08
1985	9	12	8.39	2.03
1986	10	14	9.92	2.56
1987	11	14	9.59	3.28
1988	18	14	10.05	2.83
1989	22	15	7.89	2.89
1990	12	11	7.26	1.98
1991	9	11	7.61	2.17
1992	2	5	4	0
1993	3	6	4.64	1.21
1994	4	11	7.42	3.15
1995	12	17	10.59	4.93
1996	3	7	5.4	1.24
1997	2	11	8.76	1.52
1998	3	11	8.05	2.57
1999	4	13	9	3.22
2000	6	12	7.21	4.6
2001	2	13	10	2.91
2002	1	10	9	0
2003	3	11	7.88	2.99
2004	2	10	8.12	1.02

A.4 Annexes Chapitre 6

Decomposing direct and indirect effects of early-life environment on fitness of bighorn ewes

Supplementary material

Gabriel Pigeon, Marco Festa-Bianchet and Fanie Pelletier

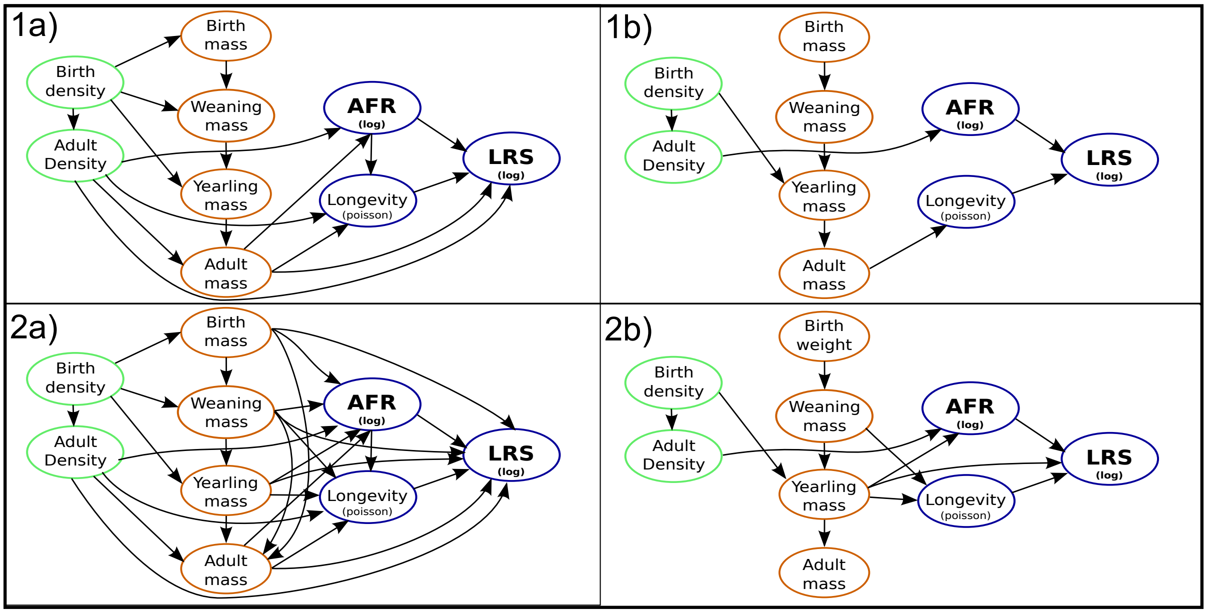

Figure A.16 DAGs representing the alternative causal hypotheses linking density at birth to LRS. Full models are in the left column while simplified models are in the righ column. Arrows represent causal link between variables. Environmental variables are in green, mass measurement are in orange, life-history traits and lifetime reproductive success are in blue.

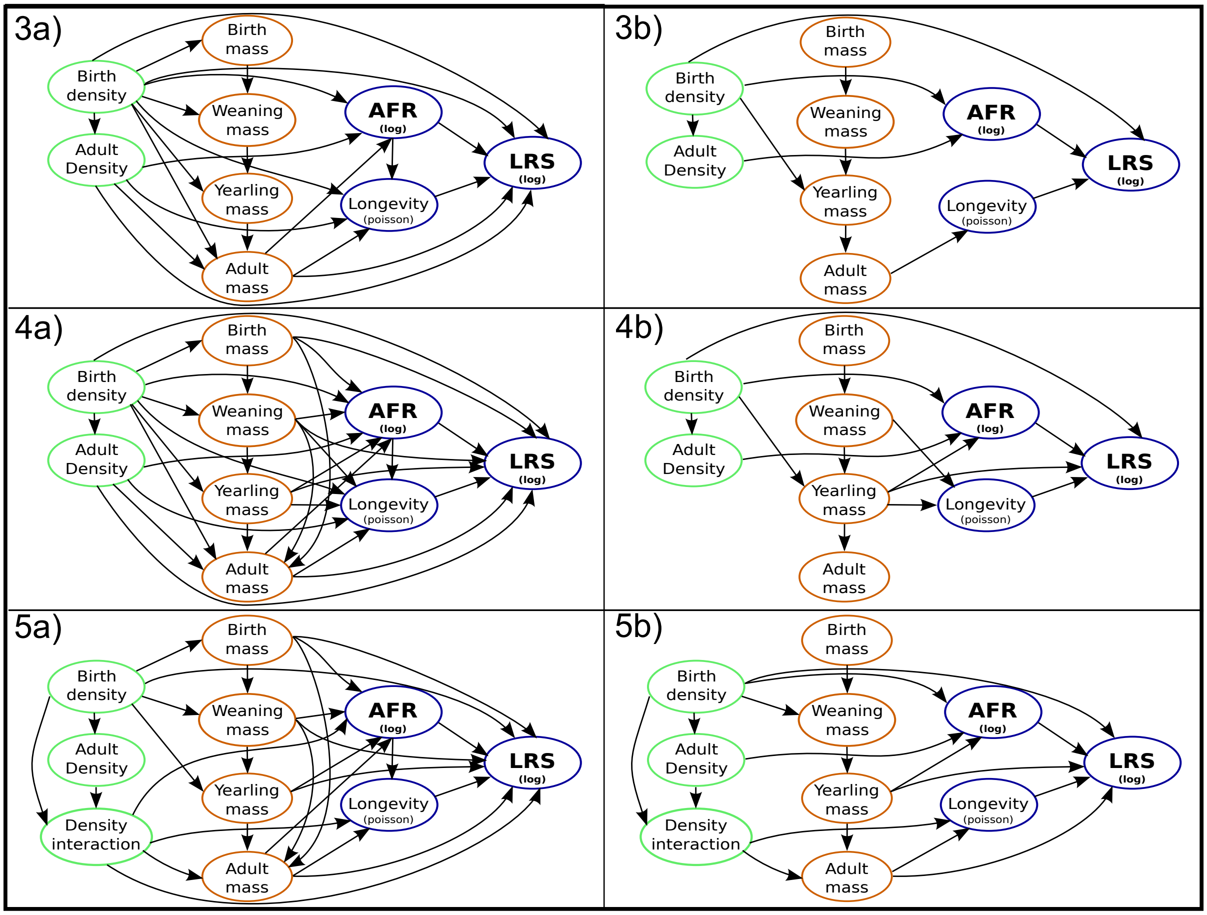

Figure A.17 Figure A.16 continued. DAGs representing the alternative causal hypotheses linking density at birth to LRS. Full models are in the left column while simplified models are in the righ column. Arrows represent causal link between variables. Environmental variables are in green, mass measurement are in orange, life-history traits and lifetime reproductive success are in blue.

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