UNIVERSITÉ DU QUÉBEC À RIMOUSKI
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INFLUENCE DU CLIMAT ET DE LA PRÉDATION SUR L'UTILISATION DE L'HABITAT ET LA SURVIE DU PORC-ÉPIC D'AMÉRIQUE

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Table des matières

Liste des tableaux

Chapitre 3

Chapitre 4

Chapitre 5

Liste des figures

Chapitre 1

Chapitre 2

Chapitre 3

Chapitre 4

Chapitre 5

Chapitre 6

Liste des annexes

Résumé

Ce travail de doctorat avait pour principal objectif de mieux comprendre les effets du climat et de la prédation sur la dynamique des populations animales, en utilisant comme modèle d'étude une population de porcs-épics d'Amérique (*Erethizon dorsatum*) située au Bas-St-Laurent, Québec, Canada. Cette population est suivie depuis mai 2000 et tous les individus trouvés sont capturés et marqués de manière permanente (à l'aide de boucles d'oreilles). La population a connu un déclin d'abondance marqué entre 2000 et 2006, déclin qui pourrait être en lien avec l'augmentation récente de l'abondance de pékans (*Martes pennanti*) dans la région. Le pékan est un prédateur efficace du porc-épic et son impact négatif sur la taille des populations de porcs-épics a déjà été signalé dans la littérature. Par ailleurs, la dynamique des populations de porcs-épics au Bas-St-Laurent semble influencée par le climat. En effet, une étude récente montre que l'abondance des porcs-épics au Bas-St-Laurent a fluctué entre 1870 et 2000 de manière cyclique, en lien avec les cycles d'activité solaire et les cycles dans certaines variables météorologiques locales.

Le calcul des taux de survie par saison (été : mai à aôut, hiver : août à mai) a permis de démontrer que les taux de survie en hiver sont plus bas et plus variables que les taux de survie en été, et qu'ils sont négativement reliés au niveau de précipitations hivernales. Par ailleurs, l'examen des causes de mortalité indique que les taux de prédation sont plus élevés les années de fortes précipitations hivernales, et que la prédation sur les adultes semble liée à la présence de neige au sol. Ces résultats suggèrent que les taux de prédation varient en fonction des conditions de neige et donc que les conditions climatiques peuvent influencer les relations prédateurs-proies.

La qualité de l'habitat qu'un animal utilise peut potentiellement influencer sa survie et son succès reproducteur. J'ai donc examiné comment les variations des conditions météorologiques et du risque de prédation influencent l'utilisation de l'habitat, et avec quelles conséquences pour la survie des individus. Nos résultats montrent que les animaux modifient leur utilisation de l'habitat en fonction du risque de prédation et des conditions météorologiques. Les individus diffèrent dans leur utilisation de l'habitat et ces différences d'utilisation de l'habitat sont liées à des différences de survie, probablement *via* des différences dans l'exposition à la prédation, principale cause de mortalité dans notre population.

Chez les espèces longévives comme le porc-épic, les fluctuations des taux de survie ont une influence importante sur la dynamique des populations. Ce travail de doctorat montre que le climat et la prédation influencent la survie chez les porcs-épics, et donc potentiellement la dynamique des populations. Il montre également que des modifications dans l'utilisation de l'habitat peuvent moduler les effets de la prédation sur la survie.

Mots-clés : écologie animale, dynamique des populations, climat, prédation, utilisation de l'habitat, survie, porc-épic, pékan

Chapitre 1 Introduction

1.1 Impact des variations climatiques sur les écosystèmes

L'augmentation des gaz à effet de serre, liée aux activités anthropiques, est une des causes du changement climatique actuel (Petit et al. 1999). Ce changement climatique s'est traduit par un réchauffement moyen des températures de 0.6 ± 0.2°C pendant le $20^{\text{ème}}$ siècle (Houghton et al. 2001). Ce réchauffement influence la structure et le fonctionnement des écosystèmes : extinction de certaines espèces, modification des aires de répartition, modification de la composition des communautés, changements dans la phénologie des évènements de reproduction ou de migration (Pounds et al. 1999, Hughes 2000, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003). En plus du réchauffement global (directionnel), différentes variations climatiques ont un impact sur les écosystèmes. Les oscillations climatiques à grande échelle d'une part, comme l'oscillation de l'Atlantique Nord (Hurrell 1995) ou l'oscillation australe dans le Pacifique Sud (Philander 1990), sont le résultat de mouvements atmosphériques et influencent les mêmes paramètres météorologiques que le réchauffement global (e.g. variations dans les températures et les précipitations). Elles ont donc certains effets semblables sur la dynamique des systèmes écologiques (Lima et al. 1999, Holmgren et al. 2001, Ottersen et al. 2001, Stenseth et al. 2003a). Les variations d'activité solaire d'autre part, influencent le climat selon différentes périodes de temps (revues dans Tsiropoula 2003, Versteegh 2005), avec là aussi des effets sur le fonctionnement des écosystèmes (Sinclair et al. 1993, Sinclair & Gosline 1997, Klvana et al. 2004, Selas et al. 2004).

Le réchauffement climatique se traduit par un changement directionnel du climat de notre planète, et semble aussi avoir un impact sur l'amplitude et la fréquence des oscillations climatiques à grande échelle (Timmermann et al. 1999, Visbeck et al. 2001, Gillett et al. 2003). Face à cette variabilité climatique croissante, comprendre les processus par lesquels le climat agit sur les écosystèmes est devenu un enjeu capital pour toute une génération d'écologistes. Bien que les effets du climat aient été bien documentés, de nombreuses incertitudes subsistent quant à la nature des liens existant entre les processus physiques et biologiques (Harrington et al. 1999). Identifier les mécanismes impliqués dans les réponses biologiques aux fluctuations climatiques est un premier pas indispensable si l'on veut prédire les effets, et possiblement s'adapter au réchauffement climatique (Berteaux et al. 2006).

1.2 Impact des variations climatiques sur les populations

Le climat est la synthèse des conditions atmosphériques dans une région donnée sur une longue période de temps. Les conditions météorologiques, par contre, qualifient l'ensemble des conditions physiques dont on peut ressentir directement les effets à un moment précis et en un point précis. À proprement parler, on ne devrait donc utiliser le mot « climat » que lorsqu'on s'intéresse aux phénomènes atmosphériques s'exprimant sur une longue période de temps ou sur une large région géographique. De nombreuses études en écologie discutent des effets du climat ou de la variation climatique sur la dynamique des populations (Albon & Clutton-Brock 1988, Lima et al. 2002a, Barbraud & Weimerskirch 2003, Krebs & Berteaux 2006). Cependant, ces travaux examinent en fait bien souvent les effets des fluctuations des conditions météorologiques et non du climat sur les populations. Pour être cohérent avec les termes employés dans la plupart des études, nous utiliserons les deux termes (i.e. climat et conditions météorologiques) de manière interchangeable dans cette thèse. On gardera cependant en mémoire les distinctions existantes.

La compréhension des effets du climat sur la dynamique des populations est une étape importante si l'on veut prévoir le devenir des espèces, des communautés, et des écosystèmes. L'étude de la dynamique des populations a pour objectif la compréhension des processus conduisant à la structure et à la taille des populations au cours du temps (Begon et al. 1996). L'abondance d'une population est déterminée par la survie, la fécondité, et les mouvements des individus (Stearns 1992, Krebs 1994). Les facteurs qui influencent les processus démographiques peuvent être classés en facteurs régulateurs (qui ramènent une population à son point d'équilibre lorsqu'elle s'en écarte) ou limitants (qui agissent sur la densité moyenne ou la densité à l'équilibre d'une population) (Krebs 1994). Les facteurs régulateurs sont par définition des facteurs dont l'effet est dépendant de la densité et sont typiquement des facteurs biotiques (compétition, prédation, parasitisme) alors que les facteurs limitants peuvent être des facteurs biotiques (généralement dépendants de la densité) ou abiotiques (généralement indépendants de la densité : climat, environnement physique ou chimique).

L'importance relative des facteurs dépendants et indépendants de la densité dans la détermination de l'abondance des populations a été longtemps discutée en écologie (e.g. Davidson & Andrewartha 1948, Nicholson 1954, Hairston et al. 1960, Douglas & Leslie 1986, Forchhammer et al. 1998, Barbraud & Weimerskirch 2003, Berryman & Lima 2006). On sait maintenant que les deux types de facteurs peuvent avoir des effets importants, et peuvent interagir pour déterminer l'abondance des populations (Saether 1997, Gaillard et al. 2000).

Le climat influence la dynamique des populations animales par des effets directs sur la physiologie des individus (coûts de thermorégulation, coûts de locomotion), ou par des effets indirects en modifiant la nature des interactions biologiques (compétition, relations prédateurs-proies, accès à la nourriture). Dans un système à trois niveaux trophiques (végétation, herbivore, carnivore, Fig. 1.1), chaque niveau peut voir son abondance modifiée par les effets du climat et de la densité, ainsi que par une modification des interactions trophiques (due par exemple à un impact du climat sur l'efficacité de chasse des prédateurs ou sur l'accessibilité de la végétation pour les herbivores). Ainsi, la survie des orignaux (*Alces alces*) à l'île *Royale* (É.U.) est plus faible les années de fort enneigement à la fois parce que la mortalité des individus âgés augmente, et parce que les loups gris (*Canis lupus*) augmentent leur efficacité de chasse (en chassant en plus grands groupes) quand la neige est profonde (Post et al. 1999b). Les interactions trophiques sont donc des voies par lesquelles les effets du climat peuvent se propager à tout un écosystème (Fig. 1.1).

Une approche souvent utilisée pour prédire les effets des changements climatiques est de modéliser le climat futur, d'en déduire la répartition de la végétation, puis la composition de la communauté animale (Schmitz 2003). Cette approche a pour inconvénient de négliger les effets potentiels du climat sur les interactions entre espèces (Davis et al. 1998, Wilmers & Post 2006, Suttle et al. 2007), et notamment sur les interactions entre prédateurs et proies qui sont sensibles aux conditions environnementales (Post et al. 1999b, Hebblewhite 2005, Lensing & Wise 2006, Wilmers et al. 2006).

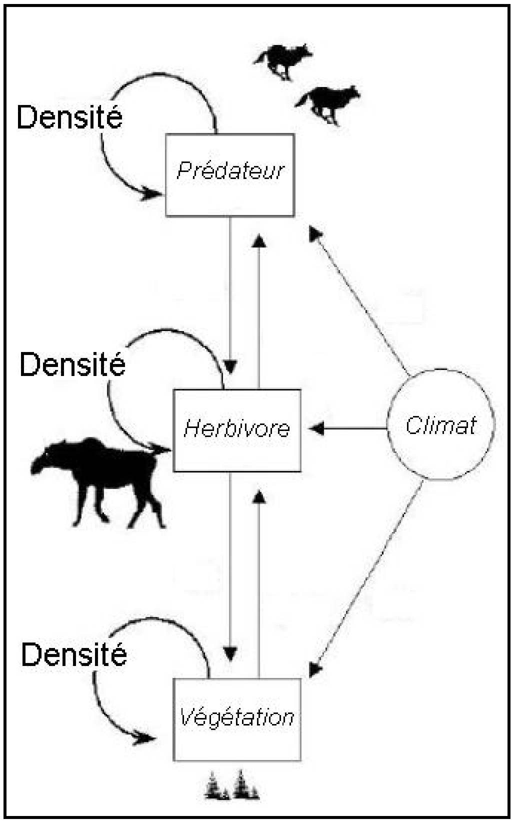

Figure 1.1 : Effets possibles du climat sur une chaîne trophique à trois niveaux, basé sur des observations empiriques des interactions entre les loups, les orignaux, les sapins baumiers, et le climat à l'île *Royale*, É.U. (tirée de Post & Forchhammer 2001). Le climat a un effet direct sur chacun des niveaux trophiques mais les interactions entre espèces peuvent aussi être influencées par les fluctuations climatiques.

1.3 Impact des variations climatiques sur les individus

La dynamique des populations animales est fonction du succès reproducteur et de la survie des individus, qui eux-mêmes dépendent de plusieurs facteurs (e.g. physiologie, comportement, conditions environnementales). Cependant, beaucoup d'études s'intéressant à la dynamique des populations sont basées sur des suivis de taille ou d'abondance de populations (e.g. Owen-Smith & Mills 2006). Pour examiner les effets du climat sur la dynamique de la population, on compare alors le taux d'accroissement de la population à un ou plusieurs facteurs climatiques (Forchhammer et al. 1998, Post & Stenseth 1998, Stenseth et al. 2002, Hebblewhite 2005). Le problème avec cette méthode est que le dénombrement des populations ne donne qu'une mesure globale de la performance de la population. Déterminer si les facteurs climatiques ont un effet positif, négatif, ou nul sur la taille des populations n'est pas suffisant pour gérer les populations (Gaillard et al. 2003). À l'inverse, les suivis basés sur les individus permettent d'identifier les mécanismes démographiques impliqués dans les changements d'abondance des populations, et constituent un premier pas vers des modèles permettant la gestion des populations. Les populations de mammifères peuvent être structurées par classe d'âge (Charlesworth 1994) et un suivi individuel à long terme permet de déterminer rigoureusement les taux de survie et de reproduction à différents stades du cycle de vie des individus (Fig. 1.2).

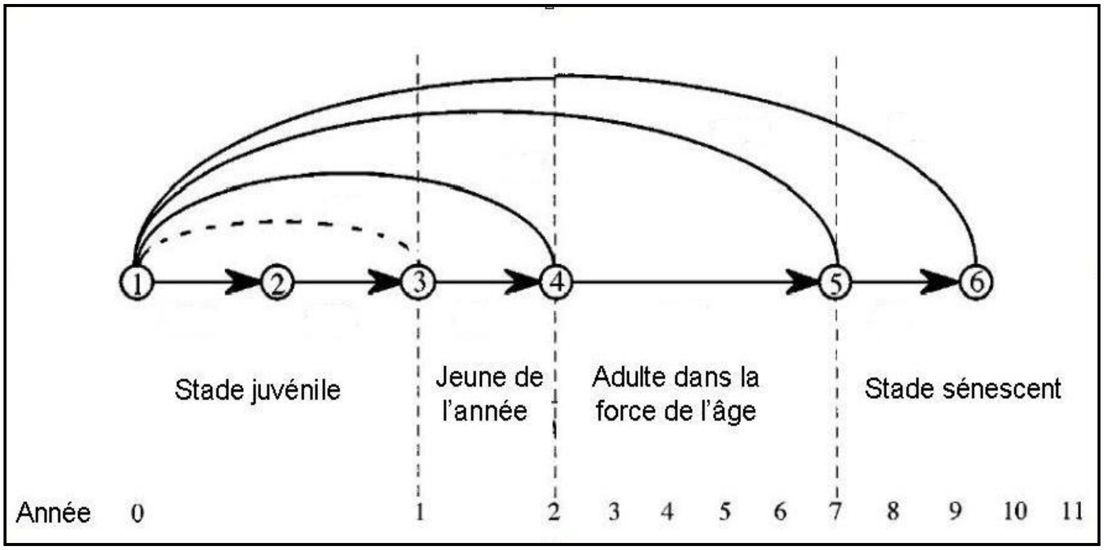

Figure 1.2 : Exemple de cycle de vie chez des herbivores de grande taille (tirée de Gaillard et al. 2000). Nombres encerclés : 1: nouveau-né, 2: jeune sevré, 3: jeune de l'année, 4: individu de deux ans (souvent l'âge de première reproduction), 5: individu « dans la force de l'âge » (*prime-age*), 6: individu sénescent. Les lignes droites indiquent la survie d'un groupe d'âge à un autre. Les lignes courbes indiquent la production de jeunes (donc la reproduction).

Les facteurs les plus importants pour la dynamique des populations peuvent varier selon les espèces considérées. En effet, puisqu'il existe des compromis d'allocation d'énergie entre la croissance, la maintenance et la reproduction (Stearns 1992), les espèces qui se reproduisent intensément (nombreuses portées, grande taille de portée) ont généralement une durée de vie courte (courte durée de génération) alors que les espèces à faible taux de reproduction (peu de portées, petite taille de portée) sont plus longévives (grande durée de génération) (Gaillard et al. 1989, Gaillard et al. 2005). Pour les espèces à durée de vie courte, ce sont les variations des taux de reproduction qui influencent le plus la dynamique des populations alors que ce sont les variations des taux de survie qui influencent le plus la dynamique des populations chez les espèces à durée de vie longue (Gaillard et al. 1989, Gaillard et al. 2005). Néanmoins, les paramètres démographiques qui influencent fortement la dynamique des populations (i.e. les paramètres à forte élasticité, Caswell 2001) sont généralement peu sensibles aux variations environnementales (Gaillard & Yoccoz 2003). Par exemple chez les herbivores de grande taille, dont la dynamique est fortement influencée par la survie et particulièrement par les taux de survie des adultes, la survie des adultes est assez stable dans le temps alors que la survie des jeunes est plus variable (Gaillard et al. 1998). Grâce à un suivi individuel à long terme, on peut déterminer quels paramètres démographiques sont sensibles aux variations environnementales (e.g. variations climatiques) et évaluer l'impact des variations observées, par exemple dans la survie juvénile, sur la dynamique de la population (e.g. Coulson et al. 2001).

1.4 Utilisation de l'habitat, climat et valeur reproductive des individus

L'utilisation de l'habitat découle d'une sélection qui devrait tendre à favoriser les habitats où la survie et la reproduction des individus seraient élevées (Levins 1968). Ainsi, les individus utilisant des habitats moins profitables devraient avoir une valeur reproductive moins bonne, c'est-à-dire laisser moins de descendants contribuant aux générations futures (Danchin et al. 2005). Alors que les patrons d'utilisation de l'habitat observés résultent de processus complexes, incluant les interactions intra et interspécifiques, la sélection du microhabitat par les individus est la base sur laquelle tous les autres processus agissent (Bowers 1995, Arakaki & Tokeshi 2005). Les individus peuvent utiliser des ressources (e.g. des microhabitats) différentes si leur efficacité d'utilisation des ressources, leurs préférences, ou leurs besoins sont différents, et reflètent une capacité morphologique, comportementale ou physiologique variable à traiter des ressources alternatives (Bolnick et al. 2003). Les différences entre individus dans l'utilisation de l'habitat peuvent alors se traduire par des différences dans la survie ou le succès reproducteur (Rosenzweig 1981, 1991, McLoughlin et al. 2005, Pettorelli et al. 2005, McLoughlin et al. 2006). Par exemple, chez le tétras pâle

(*Tympanuchus pallidicinctus*) les individus utilisant des microhabitats avec plus de couvert et un microclimat plus frais pendant l'été ont une meilleure survie que les autres (Patten et al. 2005).

Le climat se manifeste à différentes échelles de temps et d'espace. Dans le cadre de l'étude des effets du climat sur l'utilisation de l'espace par les animaux, les écologistes s'intéressent généralement à l'effet des variations climatiques saisonnières sur le comportement des animaux (e.g. migration, hibernation). Néanmoins, les animaux peuvent aussi modifier leur comportement de manière plus subtile, par exemple en modifiant les échanges thermiques avec leur environnement *via* l'utilisation de sites de repos protégés (Byman et al. 1988, Buskirk et al. 1989, Taylor & Buskirk 1994, Humphries et al. 2005), l'adoption de postures qui minimisent ou maximisent la perte de chaleur (Bakken & Gates 1975, Hayes et al. 1992, Fortin & Gauthier 2000, Bustamante et al. 2002), ou le choix de sites d'alimentation offrant des microclimats favorables (Wiersma & Piersma 1994, Brotons et al. 2000). L'utilisation d'une ou plusieurs de ces stratégies peut permettre de réduire considérablement la dépense énergétique nécessaire à maintenir une température corporelle constante (Humphries et al. 2005), ce qui peut avoir des conséquences sur la survie des individus (Sealander 1952, Bult & Lynch 1997, Soto-Gamboa et al. 1999, Merritt & Zegers 2002, Dawson et al. 2005). La manière dont les individus utilisent leur habitat peut donc moduler les effets du climat sur la probabilité de survie individuelle, et c'est pourquoi il est important de considérer les différences entre individus dans l'utilisation de l'habitat quand on s'intéresse aux effets du climat sur la dynamique des populations.

1.5 Un système sensible aux fluctuations climatiques : le porc-épic d'Amérique au Bas-St-Laurent

Chez les mammifères, les effets du climat sur la dynamique des populations ont été principalement étudiés dans des populations de petits mammifères (e.g. Lima et al. 1999, Merritt et al. 2001, Aars & Ims 2002, Lima et al. 2002b, Stenseth et al. 2003b, Korslund & Steen 2006, Saitoh et al. 2006) ou chez les herbivores de grande taille (e.g. Albon & Clutton-Brock 1988, Putman et al. 1996, Post & Stenseth 1998, Forchhammer et al. 2001, Post & Forchhammer 2002, Wang et al. 2002, Berryman & Lima 2006). Une approche couramment utilisée pour étudier les effets du climat sur la dynamique des populations est de corréler la variabilité climatique inter-annuelle avec la variabilité observée dans les paramètres démographiques. Cette approche nécessite l'utilisation de données à long terme et c'est pourquoi les données de récolte de chasse par exemple ont été largement exploitées pour traiter ces questions (Langvatn et al. 1996, Post et al. 1999a, Mysterud et al. 2000). L'un des inconvénients de cette approche à grande échelle est qu'elle se base sur des corrélations et ne démontre pas de relation de cause à effet entre les paramètres (Krebs & Berteaux 2006). Les mécanismes par lesquels le climat agit sur les populations restent flous, ce qui limite les capacités de prédiction face aux changements climatiques (Berteaux et al. 2006).

Une approche alternative est de mettre en place des études à plus petite échelle temporelle ou spatiale où l'on utilise un suivi détaillé (impliquant souvent une manipulation expérimentale de certains paramètres météorologiques) pour tenter de comprendre les relations de cause à effets entre les facteurs physiques et biologiques (Lenart et al. 2002, Suttle et al. 2007). Le problème de cette approche est que les résultats obtenus à petite échelle sont difficilement extrapolables à grande échelle (Petersen & Hastings 2001, Peters & Herrick 2004). Pour avancer dans la recherche sur le climat, Root & Schneider (1995) proposent une approche basée sur une alternance d'études à grande et petite échelles dans un cycle d'analyse qu'ils appellent le « *Strategic Cyclical Scaling* ». Dans ce cycle, les études à grande échelle permettent de générer des hypothèses, qui sont ensuite testées par des études à petite échelle. Appliquer cette méthode à différents systèmes devrait améliorer notre capacité à appréhender les conséquences écologiques des changements globaux (Root & Schneider 1995).

Klvana et al. (2004) ont récemment mis en évidence dans l'Est du Québec l'impact des variations climatiques sur un herbivore de taille moyenne : le porc-épic d'Amérique (*Erethizon dorsatum*). Ils ont utilisé les cicatrices laissées par les porcs-épics sur l'écorce des arbres, lorsqu'ils s'y alimentent pendant l'automne et l'hiver, comme indice d'abondance de porcs-épics. En datant ces cicatrices par dendrochronologie, ils ont estimé l'abondance de porcs-épics au cours des 130 dernières années. Ils montrent que l'abondance de porcs-épics a fluctué depuis 1868 suivant des cycles réguliers de 11 et 22 ans, en synchronie avec les cycles d'activité solaire, et avec les cycles dans les relevés locaux de température et précipitation (Fig. 1.3).

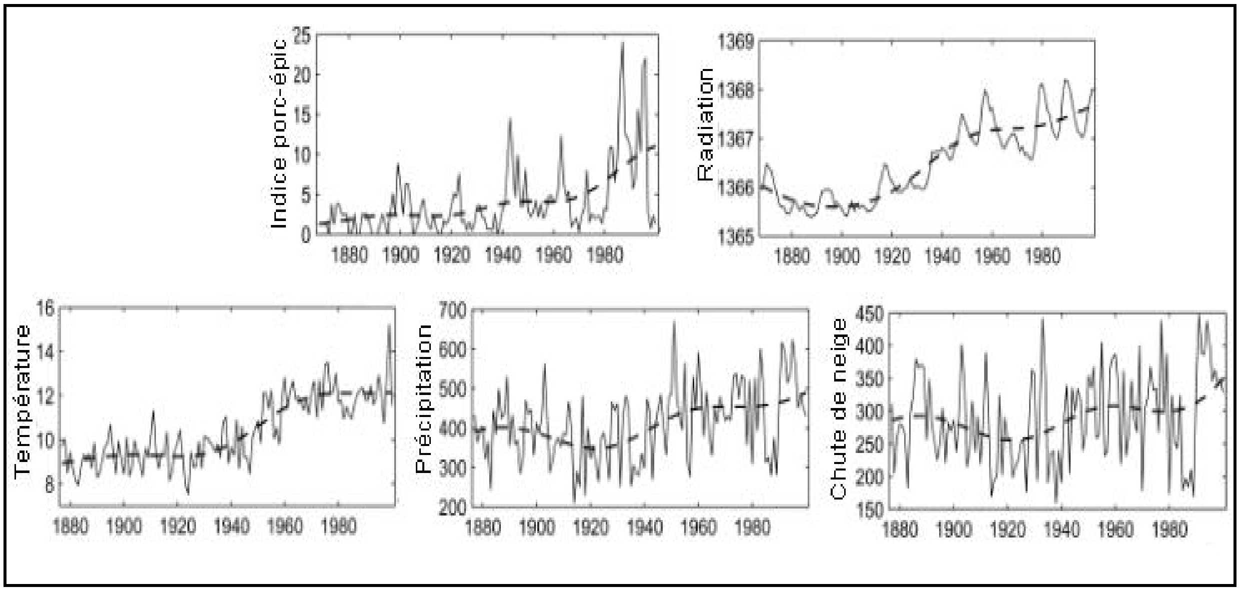

Figure 1.3 : Fluctuations dans l'indice d'abondance de porcs-épics (abondance relative de cicatrices d'une année à l'autre, moyenne sur trois sites d'échantillonnage), la radiation solaire (W/m^2), la température moyenne au printemps (Mai-Juin, °C), les précipitations hivernales totales (Novembre-Avril, en mm) et les chutes de neige (Novembre-Avril, en cm) entre 1868 (1877 pour les paramètres météorologiques) et 2000 (tirée de Klvana et al. 2004).

Cette étude, faite sur une grande échelle temporelle, permet de générer les hypothèses suivantes :

1) le cycle solaire a un impact sur certains paramètres météorologiques locaux (i.e. températures au printemps, précipitations hivernales, et chutes de neige),

2) les températures au printemps, le niveau de précipitations hivernales et les chutes de neige influencent la dynamique des populations de porcs-épics au Bas-St-Laurent.

Suivant l'approche suggérée par Root & Schneider (1995), l'un des objectifs de mon travail de doctorat a été de mettre à l'épreuve la deuxième de ces hypothèses en utilisant des données issues d'un suivi individuel fin, sur une population de porcs-épics d'Amérique au Bas-St-Laurent. Je me suis intéressée à la démographie d'une part, en étudiant les variations de survie en fonction des fluctuations dans les paramètres météorologiques, et au comportement d'autre part, en examinant comment les paramètres météorologiques influencent l'utilisation de l'habitat, et avec quelles conséquences pour la survie des individus.

1.6 La population de porcs-épics au parc national du Bic

J'ai utilisé pour ce travail de recherche une population de porcs-épics d'Amérique suivie depuis mai 2000 au parc national du Bic, dans la région du Bas-St-Laurent, au Québec (Fig. 1.4).

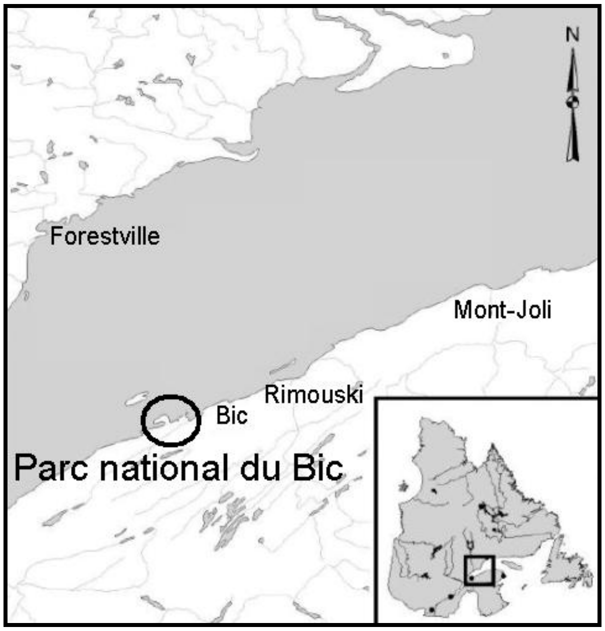

Figure 1.4 : Localisation du parc national du Bic, Bas-St-Laurent, Québec, Canada.

Le porc-épic d'Amérique est un rongeur de taille moyenne (5 à 14 Kg), assez longévif (7 à 8 ans), qui est arboricole et exclusivement herbivore (Roze 1989). Les femelles produisent généralement leur premier jeune à l'âge de deux ans et ne produisent qu'un seul jeune par an (Roze 1989, Hale & Fuller 1996). La fécondation a lieu en septembre-octobre, les femelles sont gestantes tout l'hiver, et donnent naissance à leur jeune entre la mi-mai et la fin juin (Struthers 1928). Comme pour beaucoup d'herbivores vivant en régions tempérées, l'hiver est une saison difficile pour le porc-épic puisque la quantité et la qualité nutritive de la matière végétale diminuent alors que les besoins d'énergie pour maintenir une température corporelle constante augmentent (Fournier & Thomas 1999). Les porcs-épics restent actifs en hiver mais diminuent leurs déplacements et utilisent des tanières pour se soustraire au froid

(Roze 1987). Ils perdent 10 à 40 % de leur poids et certains individus peuvent mourir par inanition si l'hiver est trop rigoureux (Sweitzer & Berger 1993). Le porc-épic d'Amérique étant longévif, la survie des adultes devrait fortement influencer la dynamique de ses populations (Gaillard et al. 1998). Une diminution de la survie des adultes pendant l'hiver pourrait donc avoir un effet important sur la taille des populations. D'autre part, comme chez d'autres herbivores longévifs, la survie des juvéniles devrait être fortement influencée par les fluctuations environnementales (Albon et al. 1987, Clutton-Brock et al. 1987, Portier et al. 1998, Milner et al. 1999, Crampe et al. 2002). Il n'existe cependant pas de données publiées pouvant confirmer cette hypothèse chez le porc-épic d'Amérique.

Dominique Berteaux a mis en place à l'été 2000 le suivi individuel d'une population de porcs-épics sur une aire d'étude d'environ 2 km^2 (Fig. 1.5) dans le secteur Est du parc national du Bic (48°20'N, 68°46'O). Le suivi est basé sur la capture d'animaux que l'on marque de manière permanente à l'aide de boucles d'oreilles (Fig. 1.6). La présence de champs au centre de l'aire d'étude (Fig. 1.5) permet une recapture facile des individus au début d'été, quand les feuilles des arbres n'ont pas encore commencé à pousser et que les porcs-épics viennent se nourrir de jeunes pousses d'herbe dans les champs. On peut également équiper les animaux d'émetteurs VHF pour ensuite les localiser par télémétrie. Les porcs-épics sont des animaux qui se déplacent relativement lentement, et passent une grande partie de leur temps immobiles dans les arbres. On peut donc se rendre jusqu'à l'animal en suivant le signal de télémétrie, ce qui permet d'accéder à des données précises concernant sa localisation et son comportement, été comme hiver (Comtois & Berteaux 2005, Morin et al. 2005).

Le parc national du Bic abritait de hautes densités de porcs-épics et la population d'étude (i.e. ensemble de porcs-épics fréquentant l'aire d'étude) comptait environ 120 individus en 2000. La population d'étude a cependant connu un déclin marqué dans les dernières années, et seulement un individu a été capturé à l'été 2006 (D. Berteaux, données non publiées, Fig. 1.7a). Des estimations de densité de porcs-épics, faites par recherche de traces en hiver le long de transects situés dans les secteurs du parc non utilisés pour les captures, montrent également un déclin très marqué ces dernières années (Y. Lemay, données non publiées, Fig. 1.7b).

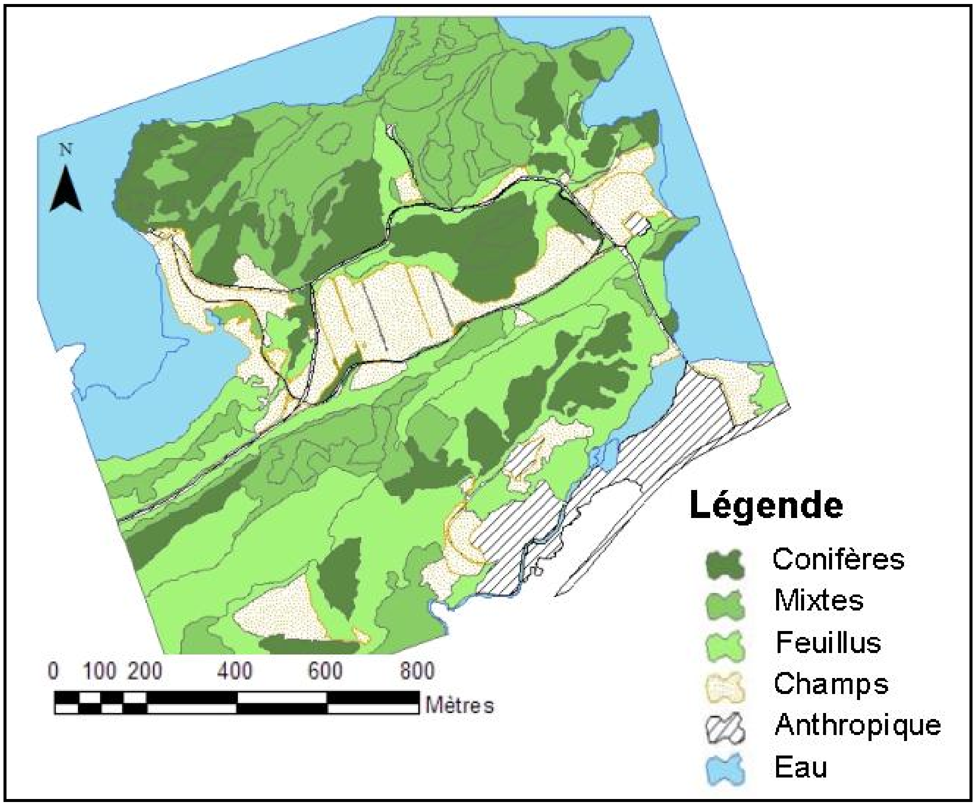

Figure 1.5 : Carte de l'aire d'étude dans le secteur Est du parc national du Bic, Québec (tirée de Morin et al. 2005). L'aire d'étude est caractérisée par une forêt boréale mixte dominée, en ordre d'importance, par : le peuplier faux-tremble (*Populus tremuloides*), le cèdre (*Thuja occidentalis*), l'épinette blanche (*Picea glauca*) et le sapin baumier (*Abies balsamea*). L'aire d'étude est fragmentée par des champs où les porcs-épics viennent se nourrir en été et où ils sont facilement capturés.

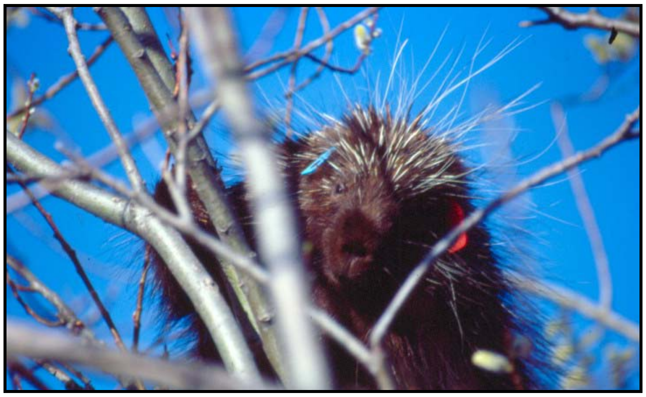

Figure 1.6 : Porc-épic d'Amérique marqué à l'aide de boucles d'oreilles de couleur. Photo par D. Berteaux.

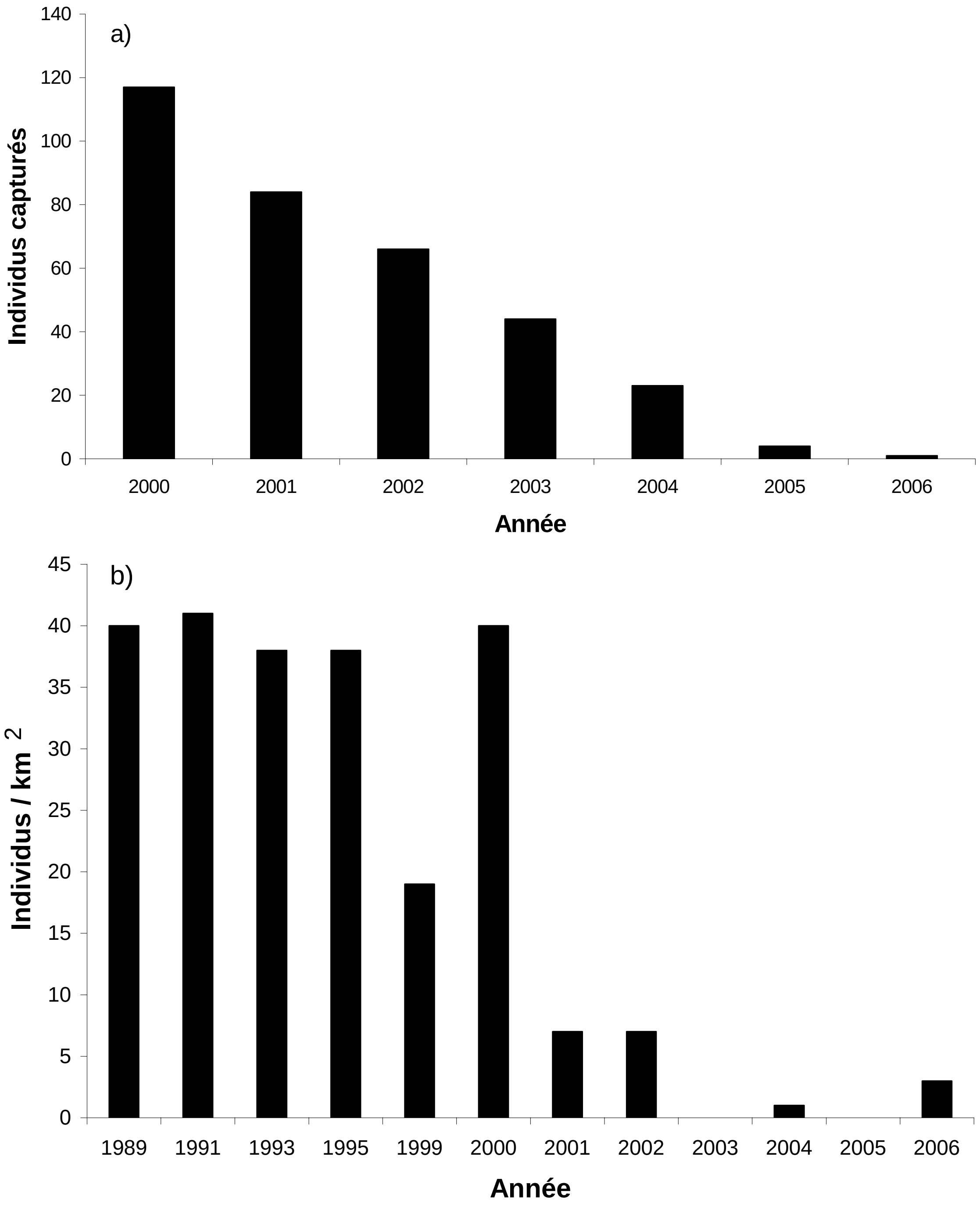

Figure 1.7 : Déclin d'abondance des porcs-épics au parc national du Bic, Québec : **a)** nombre d'individus capturés sur une aire d'étude d'environ 2 km^2 à l'Est du parc (D. Berteaux, données non publiées), **b)** estimation de densité de porcs-épics (individus/km^2) par inventaires de pistes dans trois secteurs, à l'Ouest de l'aire d'étude utilisée pour les captures de porcs-épics (Y. Lemay, données non publiées).

Le déclin d’abondance observé dans notre population d’étude ne semble donc pas lié au suivi individuel mis en place en 2000. En fait, ce déclin pourrait être lié au retour du pékan (*Martes pennanti*) dans la région (voir chap. 3). Les pékans sont des prédateurs efficaces du porc-épic (Powell & Brander 1977, Earle & Kramm 1982, Powell 1993) et leur nombre a augmenté rapidement depuis le milieu des années 1990 dans l’Est du Québec (Poulin et al. 2006). En plus de considérer les effets du climat, je me suis donc également intéressée aux impacts de la prédation sur la survie et l’utilisation de l’habitat par les porcs-épics.

1.7. Objectifs spécifiques et plan de la thèse

Le but général de ce projet est d’améliorer les connaissances des effets du climat et de la prédation sur la dynamique des populations en utilisant une espèce animale ayant été jusqu’ici peu étudiée. La survie a un effet important sur la dynamique des populations chez les espèces longévives. C’est pourquoi nous nous sommes interessés aux effets du climat et de la prédation sur la survie. La façon dont les animaux utilisent leur habitat peut faire que les individus se trouvent dans des conditions légèrement différentes face aux facteurs environnementaux (e.g. environnement thermique mais aussi risque de prédation), avec des conséquences possibles sur la survie. Ainsi, l’utilisation de l’habitat peut potentiellement moduler les effets du climat et de la prédation sur la survie, et donc sur la dynamique des populations. L’étude est basée sur un suivi individuel fin de la survie et de l’utilisation de l’habitat dans une population de porcs-épics d’Amérique. Déterminer les taux de survie est relativement simple dans la population d’étude, contrairement aux taux de reproduction qui sont difficiles à déterminer de manière fiable chez cette espèce dont les femelles cachent les jeunes à la naissance (voir chap. 2). Nous ne nous sommes pas intéressés aux taux de reproduction au cours de cette étude. Comme on l’a vu précédemment, la possibilité d’établir de manière précise la localisation des individus à l’aide de la télémétrie permet d’accéder à des données détaillées concernant leur utilisation de l’habitat. Ma thèse s’organise autour de quatre articles.

Le premier article présente les méthodes nécessaires à un suivi individuel détaillé du porc-épic d’Amérique (chap. 2). Les porcs-épics portent des épines qui rendent les manipulations et la pose d’émetteurs VHF difficiles. Au cours de l’étude de sept ans initiée par D. Berteaux, nous avons amélioré les méthodes connues pour marquer et poser des colliers émetteurs à des porcs-épics adultes. Nous avons aussi développé des méthodes pour chercher les jeunes porcs-épics (qui se cachent pendant les premières semaines suivant la naissance), les marquer et leur poser des émetteurs VHF adaptés à leur taille. Ce chapitre expose les méthodes utilisées pour le suivi de la population, et met en évidence les nouveautés apportées par rapport aux méthodes déjà publiées dans la littérature.

Le deuxième article utilise les données de capture-marquage-recapture pour calculer de manière robuste les taux de survie (chap. 3). Klvana et al. (2004) génèrent l’hypothèse que les températures au printemps, les précipitations hivernales, et les chutes de neige influencent l’abondance des porcs-épics au Bas-St-Laurent. Ce chapitre met à l’épreuve cette hypothèse en testant l’effet de ces paramètres météorologiques sur la survie. Les fluctuations climatiques pouvant modifier les interactions prédateurs-proies (Post et al. 1999b, Hebblewhite 2005) et la prédation étant un facteur important dans mon système d’étude, j’étudie également l’évolution du taux de prédation en fonction des conditions météorologiques.

Le troisième article détermine comment les porcs-épics adultes modifient leur utilisation de l’habitat en fonction des conditions environnementales au cours de l’hiver (chap. 4). J’établis tout d’abord une carte des microclimats disponibles dans l’environnement à l’aide de mannequins taxidermiques chauffés. J’examine ensuite comment les animaux naviguent sur cette carte thermique pendant la saison froide. Plus particulièrement j’étudie comment le patron d’utilisation de la tanière (e.g. temps passé en dehors de la tanière, nombre de sorties) et l’utilisation des microhabitats à l’extérieur de la tanière varient en fonction des conditions de température et de neige. À la suite de l’article, je teste si les différences entre individus dans les patrons d’activité et l’utilisation de l’habitat, se traduisent par des différences de survie.

Le quatrième et dernier article s’intéresse à l’utilisation du couvert par les jeunes porcs-épics (<3 mois) et aux conséquences de l’utilisation du couvert sur la survie au cours de leur premier été de vie (chap. 5). Chez les ongulés, les jeunes qui se cachent pour se soustraire aux prédateurs sélectionnent des habitats avec beaucoup de couvert (revue dans Mysterud & Ostbye 1999). Cependant, pendant l’été, les milieux ombragés (i.e. couverts) sont caractérisés par des conditions thermiques plus fraîches que les milieux ouverts (Demarchi & Bunnell 1993), et donc moins favorables pour des jeunes sensibles à l'hypothermie. Dans cet article, je vérifie d'abord si les jeunes porcs-épics sélectionnent des microhabitats avec beaucoup de couvert. J'examine ensuite les différences entre individus dans l'utilisation de l'habitat et les conséquences des différences interindividuelles dans l'utilisation de l'habitat sur la survie des juvéniles au cours de l'été.

Chapitre 2 Handling North American porcupines: review of existing methods and new methods to increase animal welfare

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Les études à long terme, basées sur la capture-recapture d'individus marqués au sein d'une population, permettent de calculer de manière robuste les taux de survie entre deux évènements de capture. On peut ensuite tenter d'expliquer la variabilité observée dans la survie et ainsi identifier certains des facteurs impliqués dans les fluctuations de taille des populations. Les porcs-épics sont durs à localiser dans des environnements forestiers et durs à manipuler à cause de leurs piquants. Sans doute à cause de ces difficultés, peu d'études se sont intéressées aux facteurs influençant la démographie de cet herbivore, qui peut pourtant atteindre de fortes abondances, et jouer un rôle important dans certains écosystèmes (Curtis 1941, Curtis 1944). Dominique Berteaux a mis en place à l'été 2000 un suivi individuel d'une population de porcs-épics dans le Bas-St-Laurent. Pendant sept années, nous avons amélioré les méthodes de suivi existantes et développé de nouvelles méthodes afin de limiter le dérangement des animaux et de maximiser l'efficacité du suivi. Nous détaillons ici les méthodes que nous avons utilisées en soulignant les progrès effectués par rapport aux méthodes existantes. Nous pensons que partager l'expertise acquise servira à faire progresser les standards en terme de manipulation d'animaux sauvages. Les méthodes décrites ont également permis de récolter des données précises concernant la survie et l'utilisation de l'habitat des porcs-épics, données que je mets à contribution dans le reste de mon doctorat.

2.1. Abstract

Wildlife biologists are under increased pressure to handle animals safely. Through an intensive seven-year field study of a North American porcupine (*Erethizon dorsatum*) population, we devoted considerable efforts searching, capturing, and handling large numbers of adult and juvenile individuals. Few published reports describe techniques adapted to this challenging species. We improved available techniques and developed new ones. We describe one method to search for juvenile porcupines, four new capture methods, one long-lasting marking technique, and a customized radio collar minimizing wounds to animals. The method we used to search for juveniles allowed a success rate of 47.7% (21 juveniles found around 44 females). The most efficient capture method involved using a dip net and yielded 1,026 captures (out of 1,154 captures performed during the study). We marked animals using various types of ear tags, which allowed us to identify animals from a distance and in the long term. Only 8.5% of marked individuals (n = 14 out of 165 marked individuals) lost their identity through tag loss, whereas only 3.5% of radiocollared porcupines (n = 6 out of 171 collars fitted) suffered from wounds directly attributable to radio collars. We suggest possible ways to further increase efficiency of our methods.

Key-words : capture, dip net, juvenile, marking, porcupine, Québec, telemetry

2.2. Introduction

Porcupines are present on four of the six continents, and can locally reach high densities (Roze 1989). Although they form two very distinct taxonomic groups (New World and Old Word porcupines), they share the common feature of bearing quills that impose significant challenges to anyone in need of manipulating them. Interestingly, published information on how to handle these animals is not abundant. We studied intensively a population of North American porcupines (*Erethizon dorsatum*) for seven years in Canada and were confronted with the problem of handling porcupines. Here we first review published methods to search, capture and mark North American porcupines, we then explain why some important information is lacking in the published literature, and we finally suggest four research objectives that will structure the rest of the paper.

Porcupines usually live in forests where they are difficult to locate. Hale and Fuller (1999) report low success when walking along transects to search for porcupines. Sweitzer and Berger (1997) worked in relatively open habitats and were successful at locating porcupines using trained dogs and night-vision equipment. However, by far the most efficient described technique to find porcupines involves snow tracking to locate dens where porcupines concentrate their activity in winter (Stricklan et al. 1995, Zimmerling 2005).

Capture techniques include constraining porcupines in a garbage can (Craig & Keller 1986), climbing trees to catch individuals using heavy gloves (Roze 1989, Stricklan et al. 1995), placing cage-type live traps outside occupied dens, trees or on well-used paths (Hale & Fuller 1996, Griesemer et al. 1999, Ilse & Hellgren 2001, Zimmerling & Croft 2001), netting the animal before (Zimmerling & Croft 2001, Zimmerling 2005) or after (Ilse & Hellgren 2001) chemical immobilization, and using heavy gloves after immobilizing animals in trees or dens using a jabstick (Sweitzer & Berger 1992, Griesemer et al. 1999, Ilse & Hellgren 2001) or a blow dart (Griesemer et al. 1999).

Marking techniques involve metal ear tags (Craig & Keller 1986, Zimmerling & Croft 2001) to which are sometimes attached colored plastic tags to allow identification at a distance (Sweitzer & Berger 1992, Griesemer et al. 1999), spraying tail with enamel paint (Sweitzer & Berger 1992), tattooing (Griesemer et al. 1999), fitting radio transmitter using harness and back pack (Craig & Keller 1986), or radiocollaring (e.g. Roze 1987, Sweitzer & Berger 1992, Griesemer et al. 1999, Ilse & Hellgren 2001). Flags have been attached to antennas of radio collars to ease identification of individuals at a distance (Griesemer et al. 1999).

Published techniques to search for, capture, and mark porcupines represent a fraction of those that have been tried by biologists, and method sections of publications usually do not quantify efficiency of techniques. Griesemer et al. (1999) evaluate some methods to capture and mark adult porcupines. They do not deal with juveniles, however, and some of their reported methods needed improvement. Specifically, the method they used for marking did not allow identification at a distance and was not long-lasting (25% of individuals had lost all tags 6-18 months after tagging). Also, 7% of their radio collars created wounds (Griesemer et al. (1999). The experience gained by practicing conservationists must be reported and made widely available for the field to progress (Sutherland 2006).

During our seven-year study of porcupines, we used most handling techniques described in the literature and developed new ones to increase efficiency of field work, to mark individuals durably, and to further minimize animal discomfort. Building on Hale and Fuller (1996), we also developed methods to find, mark, and radiocollar juveniles. The objectives of this paper are 1) to detail known methods to search for, capture, and mark porcupines, currently poorly described in the literature, 2) to present new techniques (including techniques suitable for working with juveniles and in the winter season), 3) to evaluate the success rate of all the methods we used, and 4) to suggest possible ways to further increase efficiency of existing methods.

2.3. Material and methods

Study area

We worked in Parc National du Bic (68º46’W, 48º21’N) on the south shore of the St. Lawrence River estuary, Québec, Canada. The study area is characterized by a rugged topography and belongs to the eastern balsam fir-yellow birch (*Betula alleghaniensis* Britt.) ecological domain, in the mid-Appalachian hills ecological region (Grondin et al. 1999). Open fields, left in fallow or used for growing barley and oats, occupy the center of the study area (see Morin et al. 2005 for details and a map).

Searching

Porcupines foraged in fields, especially in May after snow had melted but tree leaves were not yet available. We patrolled fields at night, using portable spotlights (Model Q-Beam Max Million, The Brinkmann Corporation, Dallas, TX) to locate porcupines. We also used spotlights to search for porcupines in trees. We monitored searching effort (person-hours spent patrolling) and recorded the number of porcupines captured and observed each night.

We used snow tracking in winter to find occupied dens. When porcupine densities were low, chances to find tracks were reduced, so we fitted animals with radio collars (see below) at the end of summer, in order to locate them easily in winter.

We searched for juvenile porcupines around lactating females. Females were radiocollared at the beginning of spring and regularly captured to check for lactation through manual expression of milk (Ilse & Hellgren 2001). Once a female was found to be lactating, searches started to find her juvenile. We located the female using telemetry and spent 60 minutes searching an increasingly large area around it. We searched carefully the base of trees, under dead trees or branches, in the lower branches of small trees, and in shallow dens. We used a portable flashlight to increase detection success in dark environments. When a juvenile was found, we noted the amount of time elapsed since the beginning of the search and the distance from the juvenile to its mother.

Capturing

We captured adults and juveniles from May 2000 to May 2006, at different periods of the year. We began captures using published methods, that is heavy gloves (PVC gloves fitted over leather work gloves), cage traps (82×27×33 cm, Tomahawk Live Trap Company, Tomahawk, WI), jab stick, and dip net. We sometimes climbed trees to catch an animal by hand or in a dip net. Our dip net (Fig. 2.1) consisted of a 50 cm-diameter fishing dip net fit to a 77 cm-long pole and bearing a strong 17 mm-mesh fishing net. A drawcord closed the net once an animal was caught. We also used a noose pole (4 m extension pole, Tomahawk Live Trap Company, Tomahawk, WI) to capture individuals.

We developed three techniques not described in the literature. First, when an animal was high in a tree, we agitated a 4-m long (1 cm diameter) fiberglass pole near the porcupine's head, which prompted it to come down from the tree and allowed us to catch it on the ground with a dip net. Second, if the tree was too high for the porcupine to be reached, we strapped three or four single-door cage traps (same as above) vertically around the tree trunk. Traps were placed 1.5 m above ground, so the porcupine entered one of the traps when descending the tree. We checked traps 2–12 h later. Finally, when the capture of a given individual was absolutely necessary but that individual was inaccessible in a tree, we waited silently at the base of the tree, until the porcupine came down by itself and we caught it in a dip net.

Figure 2.1 : Dip net developed to capture North American porcupines in Parc National du Bic, Québec, May 2000-May 2005. Photo by S. Descamps.

In winter, porcupines spent most of their time inside inaccessible rock dens, which are highly available in our study area (Morin et al. 2005). We placed single-door live traps baited with apples and peanut butter in porcupine paths near occupied dens. We covered traps with fabric tarps to decrease heat loss of trapped individuals. When an animal proved difficult to capture, we fitted a live trap into the entrance of the den and blocked all alternative exits. If den morphology made this operation impossible, we waited for the porcupine at the entrance of its den and caught it into a dip net. We placed movement detectors (Vigil 650X, Circuitronique Estrie, Rock Forest, Québec) outside the den several days before capture to determine the daily activity schedule of the porcupine and thus minimize waiting time.

Juveniles were captured by hand using leather gloves.

Handling

We transferred captured porcupines to a dip net for manipulations. We measured body mass using a spring scale (Pesola Macro Line 1, 2, 5, 10 or 20 kg, Pesola AG, Baar, Switzerland). To check sex and reproductive status of an individual, we twisted the net several times to restrain its movements. We determined male reproductive status from the abdominal or scrotal position of testicles, and female reproductive status by palpation and manual extraction of milk (Ilse & Hellgren 2001). We used chemical immobilization (Morin & Berteaux 2003) only when marking or collaring porcupines.

Marking

We ear-tagged porcupines with a unique combination of two color- and sign-coded plastic tags (15×45 mm, modified from Sweitzer and Berger (1992), Allflex Canada, St-Hyacinthe, Que.) to allow identification at a distance. Both tags bore the same sign but colors were independent. We attached plastic tags to the bottom part of the ear using self-piercing aluminum ear tags (tag size three, National Band and Tag Co., Newport, KY). We disinfected ears by washing the site with chlorexidine veterinary soap, rinsing with water, and applying iodine tincture before piercing. We attached tags in the cartilaginous bottom part of the ear. We attached two smaller self-piercing aluminum ear tags (tag size one, National Band and Tag Co.; hereafter called mini-tags) to the upper part of the ears. We suspected they would be lost less often than larger aluminum tags bearing plastic tags, and would therefore help to maintain identification of individuals. We tested this hypothesis by comparing loss rate of tags versus mini-tags.

Ears of juveniles were too small to support tags so we marked them using two mini-tags only. We threaded unique combinations of colored plastic-coated wires through mini-tags for identification of juveniles at a distance. Capture techniques and immobilization procedures were approved by the McGill Animal Care Committee (permit 4213), the Comité de protection des animaux de l'Université du Québec à Rimouski (permit CPA12-02-06) and the Société de la Faune et des Parcs, Gouvernement du Québec (permits 20000417-001-01-S-P to 20060501-002-01-S-F).

Collaring

We used Lotek SMRC-5RB VHF transmitters (Lotek Wireless Inc., Newmarket, Ont.) mounted on customized, home made collars (Morin et al. 2005). We did not test back pack attachment for our radio transmitters (Craig & Keller 1986) because we believed animal movements would be less constrained by collars. We first tested leather collars modified from nylon collars described in Griesemer et al. (1999). Following Sweitzer and Berger

(1992), we also tested a plastic attachment system (Fig. 2.2) that was made of a 1 mm-diameter metal wire inserted within Tygon tubing (0.63×0.95 cm [1/4×3/8 inch], VWR International, catalogue number 63014-472, Ville Mont-Royal, Que.). We fastened collars loosely enough to allow animals to gain mass (Berteaux et al. 2005), but tight enough to prevent loss and reduce chances of an animal getting hung by its collar in a tree. We attempted to capture, immobilize, and check neck condition of collared porcupines every three months.

Figure 2.2 : Tygon tubing system used to attach radio transmitter to North American porcupines in Parc National du Bic, Québec, May 2000-May 2005. Note that the metallic part (cramp) used to close the collar is visible on the picture but was inserted into the Tygon after the collar was adjusted around the porcupine's neck. Photo by S. Descamps.

We equipped juveniles captured soon after birth with Holohil VHF transmitters (model R1-2DM 7.5 g, Holohil Systems Ltd., Carp, Ont.) mounted on a metal wire inserted within clear flexible Vinyl tubing (0.31×0.47 cm [1/8×3/16 inch], United States Plastic Corp., catalogue number 59001, Lima, OH). We captured and weighed collared juveniles every week to check mass gain. Juveniles were chemically immobilized after each mass gain of 400 g to verify if size of collars needed adjustment. When juveniles reached 3 kg, we changed transmitters for larger units supported by more powerful batteries (R1-2DM 19g VHF transmitters, Holohil Systems Ltd.) and mounted on a metal wire inserted within small Tygon tubing (0.31×0.63 cm [1/8×1/4 inch], VWR International, Catalog number 63014-468).

Evaluation of our methods, and statistics

We evaluated our methods using qualitative field observations rather than quantitative data. We determined the best capturing technique as the easiest one to use and the one apparently inducing the least stress to the animal. We determined the best marking and the best collaring techniques as the longest-lasting and the one provoking the least wounds to the animals, respectively. We compared loss rates of tags versus mini-tags using a chi-square test. All quantitative results are presented as means ± SE.

2.4. Results

Searching and capturing

We searched for porcupines during 2,617 person-hours. This yielded 1,716 observations performed on 165 individuals (81 males and 84 females) that were captured 1,154 times. We made 37 captures using gloves, one using the jabstick, 1,026 using the dipnet (10 and six after waiting for the animal to come down a tree or to exit its den, respectively), 10 by climbing a tree to net the porcupine, 14 using the noose pole, 14 using a pole to drive porcupines down a tree, six using the vertical traps and 46 using traps in winter. Our dip net was easy to use and animals struggled less than when hand-captured by the tail or captured with a noose pole. The net did not induce abundant quill loss as <20 quills (out of approximately 30,000) were generally lost at each capture. Captures by hand or with a pole resulted in many more quills being lost (generally >100) so we avoided those techniques. Of the 46 captures made using traps, eight were performed with traps blocking den entrance. These eight captures resulted from about 15 capture attempts. However, five of the eight caught porcupines changed den afterwards. A few porcupines ($n < 5$) accidentally fell on the ground when we tried to capture them by climbing trees.

We searched for juveniles around 35 different mothers for a total of 44 mother-years. We found 21 juveniles and our success rate was thus 47.7%. We performed 295 searches (mean: 6.5 ± 1.0 searches per mother per year, range: 1-24 searches). We spent 282.5 hours searching for juveniles and found 7.4 juveniles per 100 hours of search. However, we found 16 and 18 of the 21 juveniles within the first three and five searches performed around their mother, respectively (Fig. 2.3a). We found 17 of the 21 juveniles within the first 30 minutes of the search (Fig. 2.3b). We could calculate distance between juvenile and mother for 19 juveniles found. Distance was ≤ 5 m for 11 juveniles, < 5m and ≤ 15 m for six juveniles, and < 15 m and ≤ 30 m for the two remaining ones.

Marking

We marked 136 adults and 29 juveniles. Color and sign-coded ear tags were readable with binoculars from 10-20 m depending on vegetation density. Juveniles never lost their mini-tags. Sixty-one of the 136 adults lost one or more aluminum tags between consecutive captures (mean time interval between consecutive captures = 61 ± 3 days) but could be retagged before they had lost all four tags. Tags were lost more often than mini-tags (79 tags vs. 35 mini-tags, $\chi^2_1 = 21.48$, $p<0.001$). On eight occasions, porcupines had lost both large aluminum tags (and therefore also plastic tags) but could still be identified by their remaining mini-tags. On 14 occasions, animals had lost all tags and were retagged with a new identity.

Collaring

We fitted 264 collars to 118 individuals for a total of 23,239 collar-days. A given collar remained on a porcupine for 88 ± 5 days (range = 1-452 days). We first used leather collars to attach radios (n = 93), but rejected them because neck quills often grew under collars, which generated abrasion and wounding (n = 22). We used the Tygon tubing attachment system for the remaining 171 collars. Only six of these 171 collars created wounding. Three porcupines died because they got hung in a tree by their collar.

Only juveniles fitted with a collar at a very young age (age ≤10 days or mass ≤600 g) needed a collar adjustment at their first collar check, that is after a 400 g mass gain since collaring. Collar size of other juveniles did not need adjustment before the second or third check, that is before their mass had increased by 800 or 1200 g since collaring.

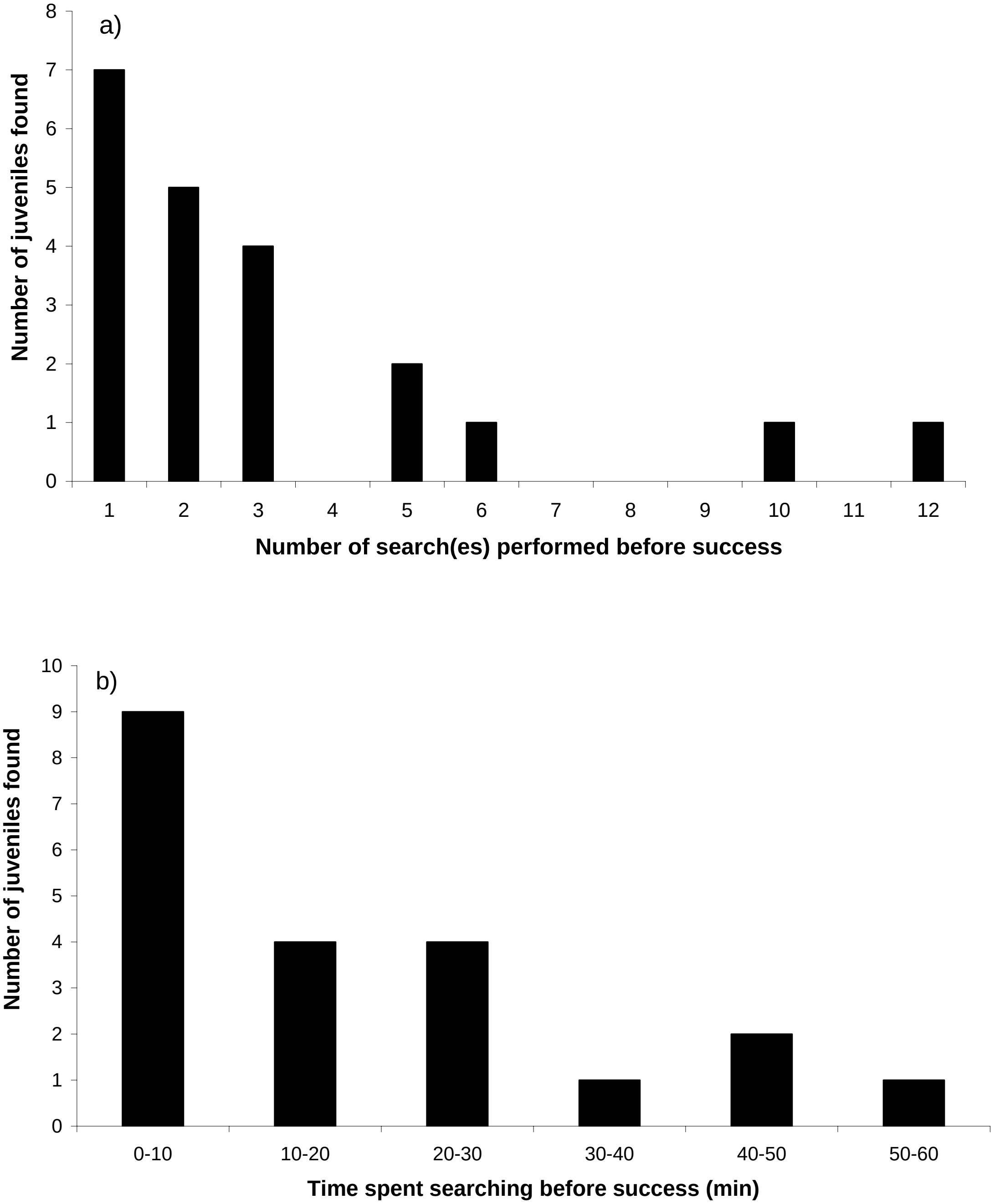

Figure 2.3 : Number of times a juvenile was found through a systematic search around a female North American porcupine in Parc National du Bic, Québec, May 2000 to May 2005, according to **a)** number of search(es) performed to find the juvenile (includes the successful search), and **b)** time spent searching (min) before finding a juvenile (only data from successful searches are shown).

2.5. Discussion

Searching

Finding adult porcupines was relatively easy in our study area in spring and at the end of autumn, when porcupines used open fields to forage. Juveniles were much more challenging to find. Had we limited to three the number of searches around each mother on a given year, and to 30 minutes the duration of each search, we would have reduced the total time spent searching to 48.1 hours and the number of juveniles found per 100 hours of search would have increased to 33 (16 juveniles found in 48.1 hours). Hale and Fuller (1996) reported 10 juveniles found after 176 one-hour searches around 23 adult females. Their overall success rate of 43.5 juveniles per 100 mothers is close to ours. Their searching method and the number of searches performed before finding each new juvenile was, however, not reported. Doing a maximum of three 30-minute searches per mother would increase search efficiency when many potential mothers are available. A greater search effort would still be useful if few adult females are known and the number of found juveniles must be maximized. We recommend investing most of the effort searching the first 15 m around the mother, especially in a dense forest habitat where searching a larger radius is not efficient.

Ascertaining the reproductive status of females around which the searches are made might increase success rate of searches. We considered a female to be lactating if some liquid could be manually extracted from nipples. This was not always reliable. For example, we made 11 unsuccessful searches around a female who later proved to be pregnant during these searches (the twelfth search yielded a newborn porcupine; see Fig. 2.3a). An alternative, probably better method to determine reproductive status consists in checking nipples after stimulation of milk release by injection of oxytocin (Roze 1989, Hale & Fuller 1996). We tried this method in the first stages of our study but abandoned it after a few unsuccessful tests. We, however, suspect that our lack of experience with porcupine handling biased negatively this early test.

Capturing

The most efficient capture method usually was the dip net. Use of a dip net had already been reported (Zimmerling & Croft 2001, Zimmerling 2005) but authors did not describe equipment nor did they evaluate method efficiency. A single experienced observer can safely record sex, reproductive status, and mass without using chemical immobilization, although we recommend an inexperienced observer to work with a helper. There is a risk of mortality when chemical immobilization is used (this study: three deaths) so we minimized its use (Morin & Berteaux 2003).

Success rate of cage traps placed on the ground varied greatly and was on average low. Some individuals never entered traps while others were trap happy. This low efficiency is surprising given the widespread use of this method (Hale & Fuller 1996, Griesemer et al. 1999, Ilse & Hellgren 2001). Baiting with peanut butter in addition to sliced apples (Griesemer et al. 1999) improved our success rate and winter trapping was more successful than summer trapping (results not shown). Blocking den entrance with a trap seemed to prompt den abandonment so this should be used as a last resort. Vertical traps placed on tree trunks were successful when the porcupine could not reach the ground by transferring into a neighboring tree.

Climbing trees to capture porcupines was commonly used in some studies (e.g. Roze 1989, Stricklan et al. 1995). We avoided this technique after a few porcupines fell from their tree, although we observed no obvious injury.

Marking

Marking was long-lasting and allowed identification at a distance. The fact that plastic tags were of different colors but displayed the same sign made visual identification much easier. We often identified animals foraging or resting in a tree without disrupting their behavior. Throughout our seven-year study, 8.5% (n = 14 out of 165) of marked animals lost their identity. This significantly improves the 25% loss of all tags reported by Griesemer et al. (1999). Attachment of tags in the cartilaginous bottom part of the ear and ear disinfection greatly minimized tag loss. Mini-tags helped avoiding identity loss of porcupines. Although more costly, Passive Integrated Transponders (PIT) have now become a better alternative to mini-tags (Schooley et al. 1993, Michard et al. 1995, Forman & Williamson 2005) so we recommend their use to prevent identity loss.

Collaring

Our leather collars induced wounds in 23.6% of cases and we abandoned them after the second year of study. We did not test the attachment systems suggested by Griesemer et al. (1999), because 66% of their machine-belting collars (n = 19 out of 29) and 7% of their tubular webbing collars (n = 1 out of 14) created wounds (Griesemer et al. (1999). Only 3.5% of our Tygon tubing collars (n = 6 out of 171) created wounds. Tygon tubing collars remained soft and flexible even at cold temperatures, which helped prevent skin abrasion. Because we tested Tygon tubing collars in all seasons, and for long time periods, we are confident that it is a suitable transmitter attachment system and recommend its use. Contact between tube and skin did not cause abrasion and growing quills easily found their way on either side of the collar.

The three instances of a porcupine getting hung by its collar in a tree occurred in winter. A similar problem was witnessed in two red squirrel studies (J. Ferron, Université du Québec à Rimouski, personal communication; S. A. Boutin, University of Alberta, personal communication). Since porcupines loose weight during winter (Roze 1984, Sweitzer & Berger 1993), collars fitted in autumn become loose as winter progresses, increasing hanging risk. However, R. A. Sweitzer (in litt.) did not report this problem with porcupines. To reduce this threat, we recommend a regular check of collars, especially at the beginning of winter when porcupines are loosing mass faster (Sweitzer & Berger 1993).

We present the first report of radio collars fitted to juvenile porcupines (≤ 1.5 kg). Radio collars are difficult to fit on juveniles because of their rapid mass gain that forces regular checks of collar size. Our description should help future investigators minimizing the number of chemical immobilizations needed for adjusting collar size. Flexible Tygon was unnecessary for newborns because collars did not face cold temperatures. When we changed collars before winter, we used Tygon tubing to prevent subsequent neck abrasion.

2.6. Conclusion

Given the unique morphology of porcupines and the scarcity of published information regarding their study techniques, our findings will complement existing knowledge and facilitate further research on this (or similar) species. The pressure on wildlife ecologists for using safe and humane techniques has never been so high (Farnsworth & Rosovsky 1993, Powell & Proulx 2003, Beier 2005, Minteer & Collins 2005). Our account should help to feed the toolbox of wildlife technicians and biologists, as well as the databases of animal care committees.

Chapitre 3 Predation as a possible mechanism relating winter weather to population dynamics in a North American porcupine population

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Dans un contexte de réchauffement climatique, comprendre les mécanismes par lesquels le climat agit sur la dynamique des populations animales est devenu un enjeu scientifique et politique important. Pour progresser dans la recherche sur les effets du climat, une méthode est d'alterner les études à grande échelle (qui permettent de générer des hypothèses) avec des études à petite échelle (pour mettre à l'épreuve ces hypothèses). Klvana et al. (2004) génèrent l'hypothèse que l'abondance des porcs-épics au Bas-St-Laurent est influencée par les variations d'activité solaire, *via* un effet sur les variables météorologiques locales. Nous utilisons ici les données de capture-recapture récoltées sur notre population d'étude (chap. 2) pour mettre à l'épreuve cette hypothèse et identifier le(s) mécanisme(s) par le(s)quel(s) l'activité solaire influence l'abondance de porcs-épics. Notre étude confirme l'existence d'une corrélation entre les variations d'activité solaire et le taux d'accroissement de la population d'étude. De plus, la radiation solaire est corrélée avec les précipitations hivernales, elles-mêmes corrélées aux variations observées dans la survie hivernale des porcs-épics (juvéniles et adultes). L'examen des causes de mortalité indique que les taux de prédation sont plus élevés les années de fortes précipitations hivernales et que la prédation sur les porcs-épics adultes semble liée à la présence de neige au sol. Les variations d'activité solaire pourraient donc affecter la taille des populations de porcs-épics par des effets en cascades sur les précipitations hivernales, les taux de survie des porcs-épics en hiver, et une fluctuation des taux de prédation en fonction des conditions de neige. Notre étude confirme l'hypothèse générée par Klvana et al. (2004) et identifie un mécanisme possible par lequel le climat hivernal pourrait affecter la dynamique des populations de porcs-épics.

3.1. Abstract

Understanding the effects of climate on population dynamics of mammals is plagued by experimental difficulties. One way to move ahead with climate research may be to alternate large and small-scale studies on a given system. In such a “cyclical scaling”, large-scale studies serve to generate hypotheses that can be challenged with small-scale studies. Klvana et al. (2004) showed that North American porcupine (*Erethizon dorsatum*) populations in eastern Québec have regularly fluctuated over the past 130 years in relation to fluctuations in the solar cycle and local weather variables. This generated the hypothesis that solar activity may affect porcupines’ abundance through effects on weather variables. We used a small-scale study to challenge this hypothesis and shed light on the mechanism(s) linking porcupine abundance to weather conditions. We started in 2000 a capture-recapture study which implied systematically searching and capturing porcupines in May and August each year. This design allowed estimating “summer” (May to August) and “winter” (August to May) survival rates between 2000 and 2005. Summer survival was high and constant over the study period (mean monthly survival: 0.86 for juveniles and 0.97 for individuals ≥1-yr-old) while winter survival was lower and variable from year to year (mean monthly survival: 0.53-0.83 for juveniles and 0.84-0.96 for individuals ≥1-yr-old). Local winter precipitation was negatively correlated to solar irradiance and explained a large part of the variation in winter survival ($r^2 = 0.87$) with winter survival being negatively influenced by winter precipitation. Predation rates were elevated in years of high winter precipitation and 95% of depredated porcupines were killed when snow was covering the ground. Predation rates thus appeared strongly related to snow conditions, and variations of predation rates according to snow conditions may explain the observed relationship between winter precipitation and survival of porcupines.

Key-words : capture-mark-recapture, climatic variations, mortality causes, predator-prey, seasonal survival

3.2. Introduction

A growing number of studies indicates that climate affects population dynamics of mammals (Krebs & Berteaux 2006). Climate can have direct effects on individuals (for example winter weather influences population dynamics through effects on locomotion (Telfer & Kelsall 1984) or thermoregulation (Cook et al. 1998)); or indirect ones by affecting species interactions. For example, deep snow may influence predator-prey relationships (Post et al. 1999b, Hebblewhite 2005) and access to food resources (Turner et al. 1994, Post & Stenseth 1999). Obviously, the different ways in which climate influences population dynamics are complex and our understanding of mechanisms linking climate to population growth rate is limited (Owen-Smith & Mills 2006). Because we can hardly manipulate climate, testing specifically for changes driven by weather variations is plagued by experimental difficulties. The two main approaches that have been used are 1) small scale studies that aim at determining mechanisms linking weather variations and changes in biological processes; and 2) large scale studies (i.e. data collected over long time periods and/or large areas) that aim at correlating the observed climatic variability with changes in ecosystem functioning. Both approaches have important drawbacks and Root and Schneider (1995) suggested alternating studies performed on large and small scales to move ahead with climate research. In such cycles of analysis, large-scale studies would generate hypotheses that would be tested using small-scale studies.

The solar cycle is known to have an impact on weather (Sinclair et al. 1993) with cascading effects on entire ecosystems (Verschuren et al. 2000, Hodell et al. 2001). For instance, the reproductive output of snowshoe hares in Yukon was found to be cyclic and highly correlated with sunspot numbers with a two years time lag (Stefan & Krebs 2001, Krebs & Berteaux 2006). Possible mechanisms involved in this relationship include an effect of solar activity on snow depth which might in turn affect food supplies (Krebs & Berteaux 2006) and lynx hunting success (Stenseth et al. 1999, 2004). North American porcupine (*Erethizon dorsatum*) populations in the Bas St. Laurent region of eastern Québec seem also to be affected by the solar cycle. Klvana et al. (2004) found that an index of porcupine abundance (porcupine feeding scars) was related to fluctuations in the solar cycle, winter precipitation, snowfall, and spring temperature over the past 130 years. As for the snowshoe hares, one possible mechanism linking solar activity to porcupine abundance could be that the solar activity affects snow conditions which may in turn affect access to food resources (Roze 1989) or hunting behaviour of predators (e.g. coyotes, Thibault & Ouellet 2005). The solar activity could also influence spring temperature which can have direct effects on thermoregulation of juvenile porcupines (Haim et al. 1992) or indirect effects on condition of individuals through an impact on vegetation growth (Albon et al. 1987, Langvatn et al. 1996, Post & Stenseth 1999). Klvana et al. (2004) did not identify the mechanism(s) linking porcupine abundance to weather conditions but their study, made on a large temporal and spatial scale, raised the hypothesis that solar activity influenced population dynamics of porcupines through an effect on local weather variables. Following the approach suggested by Root and Schneider (1995), we set up a study on a smaller temporal and spatial scale, and in the same porcupine population as in Klvana et al. (2004) to challenge this hypothesis and shed light on the mechanism(s) linking porcupine abundance to weather conditions.

We started a multi-annual capture-recapture study that allowed us to estimate annual population size, “summer” (May to August), and “winter” (August to May) survival rates separately, and to determine causes of mortality for the carcasses we found. Reliable estimates of annual survival rates have been calculated using capture-recapture designs for several mammal species (e.g. Jorgenson et al. 1997 on bighorn sheep, Bonenfant et al. 2002 on red deer, Ozgul et al. 2006 on yellow-bellied marmots, Baker & Thompson 2007 on monk seals) but calculations of seasonal survival rates from individual-based capture-recapture data are infrequent, especially in mammals (but see Lima et al. 2001 on mouse opossums, Crespin et al. 2002 on bank voles, Lima et al. 2002a on leaf-eared mouse, Sendor & Simon 2003 on pipistrelle bats). Using seasonal survival rates is crucial to understand how mortality risks faced by animals vary during their annual cycle (Gauthier et al. 2001). In particular, in our system, we were interested in distinguishing effects of spring temperature on summer and/or winter survival and in assessing differences in variability between winter and summer survival rates.

Our study, based on a small temporal and spatial scale, allowed us to test for a relationship between porcupine abundance, solar activity, and local weather, and to determine whether the effects of local weather on porcupine abundance are mediated through changes in predation risk. To do so, we tested the following predictions: first, changes in abundance of porcupines are correlated with solar activity. Second, solar activity is correlated to winter precipitation, snowfall, and spring temperature. Third, changes in winter precipitation, snowfall and spring temperature are correlated to changes in abundance of porcupines. More specifically in long-lived vertebrates, survival is the demographic parameter that has the largest influence on changes in abundance (i.e. the largest elasticity) (Gaillard et al. 2000, Saether & Bakke 2000, Eberhardt 2002). Because North American porcupines are relatively long-lived (Roze 1989), we therefore investigated the relationship between survival of porcupines and local weather with the predictions that an increase in winter precipitation and/or snowfall and a decrease in spring temperature should lead to a decrease in survival of porcupines.

Finally, in a fourth step, we investigated some potential mechanisms linking weather variables to survival of porcupines. Three non-exclusive mechanisms can be proposed, each leading to specific predictions:

1) Low spring temperatures increase starvation probability of neonates and then decrease juvenile summer survival. Young mammals are sensitive to hypothermia because of their immature thermoregulatory system (Hull 1973, Leon 1986). We therefore expected juvenile porcupines to show reduced summer survivorship in years of low spring temperature.

2) Low spring temperatures and high snowfall/winter precipitation increase winter starvation probability and then decrease winter survival. Low spring temperatures can decrease primary productivity (Langvatn et al. 1996), which could in turn reduce fall body condition and influence winter survival of herbivores (Loison & Langvatn 1998, Portier et al. 1998). In winter, the presence of snow covering the ground impedes movements of porcupines and decreases their access to food resources (Roze 1984). We therefore predicted low spring temperatures and high snowfall/winter precipitation to negatively influence winter survival rates of porcupines through increased starvation rates.

3) High snowfall and/or high winter precipitation increase winter predation probability and then decrease winter survival. In presence of snow, predators can modify their hunting behaviour so as to increase hunting efficiency on some prey (Post et al. 1999b, Jedrzejewski et al. 2002, Hebblewhite 2005) and to relieve hunting pressure on others (Lindstrom &

Hornfeldt 1994, Gese et al. 1996a, Selas & Vik 2006). Prey living above the snow surface usually suffer higher predation risk as snow deepens. We therefore expected winter predation rates on porcupines to increase in years of high snowfall/winter precipitation.

3.3. Material and methods

Study population

We worked from May 2000 to May 2006 in a ca. 2 km^2 area of Parc National du Bic (48°20'N, 68°46'W, elevation 0-150m), Québec, Canada. The study area is fragmented by abandoned and cultivated fields and characterized by a rugged topography, abundance of natural rock dens, and a mixed boreal forest. We captured porcupines in open fields during intensive capture sessions in May and August every year from 2000 to 2004 and in May only in 2005 and 2006 (Table 3.1). Each night of survey involved one to six observers (usually two) who patrolled the study area on foot or bicycle for one to nine hours (usually five). We sexed, weighed, aged (as juvenile, subadult, or adult using body mass in May, Berteaux et al. 2005), and permanently marked porcupines upon capture with metal ear tags (Berteaux et al. 2005, Morin et al. 2005). We also used telemetry to monitor individuals and fitted radio collars (Lotek SMRC-5RB VHF transmitters, Lotek Wireless Inc., Newmarket, ON, Canada, L3Y 7B5) on 97 individuals for 23576 porcupine-days (Table 3.1).

Parturition period is mid-May to late June so we considered a population-year to start in May (e.g. year 2000 extends from May 2000 to April 2001). We estimated minimum population size for a given year as the number of different individuals observed between May and April of the following year. Open fields are very attractive to porcupines for feeding in summer and porcupines were easily observed when using fields. We are therefore confident that virtually all porcupines present in the study area were captured or observed at least once each year. As a confirmation, we rarely found marked animals not observed one year and later relocated (only three and four animals, respectively in 2001 and 2002, which we added to the population size for the year that they had not been observed).

Table 3.1 : Monitoring effort according to season and year in a North American porcupine population in Parc National du Bic, Québec, May 2000-May 2006. **Survey** corresponds to the number of nights and person-hours spent searching for porcupines randomly in the study area. **Radio-tracking** corresponds to the effort made following porcupines by telemetry (number of individuals followed, proportion of the total population, and mean number of days bearing a collar)

	2000	2001	2002	2003	2004	2005	2006
Survey							
May							
nights	20*	20*	26	20	22	18	10
person-hours	150*	150*	481.3	195.2	319.1	224.7	88.0
August							
nights	15*	14	14	5	12	0	0
person-hours	100*	151.8	152.5	69.0	140.1	0	0
Radio-tracking							
Summer†							
n (proportion of males)	12 (8.3)	51 (52.9)	13 (46.2)	38 (47.4)	23 (39.1)	0	0
% of marked individuals	10.3	60.7	19.7	86.4	100	0	0
days per individual	29 ± 6	62 ± 5	62 ± 10	91 ± 7	79 ± 10	0	0
Winter†							
n (proportion of males)	21 (61.9)	0 (0)	19 (57.9)	38 (47.4)	15 (33.3)	0	0
% of marked individuals	18.0	0	28.8	86.4	65.2	0	0
days per individual	54 ± 6	0	147 ± 15	186 ± 10	162 ± 13	0	0

†Summer, May to August; Winter, September to April. *estimated minimum numbers (precise record of searching effort started in August 2001 only)

Study design

We first tested if changes in abundance of porcupines correlated with solar irradiance during the study period. Second, we tested if solar irradiance correlated with local weather variables. Then, we estimated winter and summer survival of porcupines from May 2000 to May 2005 in order to test for an effect of local weather on survival. Because time-lag effects of weather on phenotypic and demographic traits can be important (Post & Stenseth 1999, Post 2005), we investigated for a direct and for a delayed influence of environmental covariates on survival (lags 1-2 years). Finally, to determine which age-class was the most sensitive to changes in local weather, and whether changes in survival were mainly due to changes in predation or starvation rates, we examined causes of mortality according to year, season and age classes.

Relationship between abundance of porcupines and solar irradiance

We used estimates of population size to calculate population growth rate as:

$$r_t = N_{t+1} / N_t \qquad (1)$$

in which r_t is population growth rate for year t, N_t is population size in year t and N_{t+1} is population size in the following year. We used a Pearson correlation to test for an association between population growth rate and total solar irradiance monitored with absolute radiometers placed onboard satellites (daily irradiance in W/m^2 as calculated by Frohlich (2000), averaged over a year). We obtained solar irradiance data from the World Radiation Center (Physicalisch-Meteorologisches Observatorium Davos, PMOD/WRC, Switzerland, unpublished data from the VIRGO Experiment on the cooperative ESA/NASA Mission SoHO) and standardized it ((value - mean)/SD) before analyses. Solar irradiance is more likely to be a biologically and climatically explicative measure of the solar activity than the traditionally used sunspot number (Klvana et al. 2004). However, we also performed analyses using the sunspot number (obtained from the World Data Center for the Sunspot Index), given its widespread use in the ecological literature. We found similar results using either measure so results using sunspot numbers are not shown. Below we use solar activity and solar irradiance as synonyms.

Relationships between solar irradiance and local weather variables

We used Pearson correlations to test for a correlation between solar irradiance and weather variables. Based on Klvana et al. (2004), we considered three weather variables:

winter precipitation (total precipitation in mm, between November and April), snowfall (in cm, between November and April) and spring temperature (mean monthly temperature in °C, averaged over May and June). We obtained weather records from the Environment Canada weather station at Rimouski, about 20 km from our study site (48°27'N, 68°31'W). We examined relationships between solar irradiance and weather parameters for years 1998 to 2004 because we tested for effects of environmental covariates on survival with lags of up to two years (i.e. starting in 1998) and because 2004 was the last population year we used in survival analyses (see below). We standardized weather data before analyses.

Seasonal survival rates

We determined fates of porcupines through capture, visual and radio-telemetry observations (hereafter called porcupine observations). Survival analyses included only porcupines that died naturally (i.e. not from research related reasons, see below). Our dataset consisted in 82 females (12 captured for the first time as juveniles, 16 as subadults, and 54 as adults) and 77 males (16 captured for the first time as juveniles, seven as subadults, and 54 as adults). Preliminary analyses indicated that survival was similar for subadults and adults so that we only considered two age classes: juveniles and individuals ≥1-yr-old. We used methods detailed in Loison et al. (1994) to include different ages at capture in the estimation procedures. We estimated seasonal survival rates of porcupines from May 2000 to May 2005 ($k = 11$ occasions of captures). We defined as "summer survival" the survival from May-June to August and as "winter survival" the survival from August to May-June. The lengths of our "summer" and "winter" periods were thus four and eight months, respectively. We used observations from May and June to determine presence at the beginning of summer because using only May would have reduced our sample size ($n = 139$ instead of 159), especially for juveniles ($n = 18$ instead of 28). Indeed, juveniles are born at the end of May or beginning of June so that many of them were observed for the first time in June and died during their first summer (i.e. were not observed in August).

We performed survival analyses using capture-mark-recapture methods (Lebreton et al. 1992), using the program M-SURGE 1.7.1 (Choquet et al. 2004, 2005) which can take into account unequal interval lengths between capture occasions. The fit of our data to the Cormack-Jolly-Seber model was acceptable (Goodness of fit test using U-CARE 2.02 (Choquet et al. 2003, Pradel et al. 2003): $\text{Chi}^2 = 39.620$, $df = 29$, $p = 0.090$) so that we used this model as a starting point for model selection (Lebreton et al. 1992). As survival rates were the parameters of interest in our study, we first modelled sighting probabilities to have more statistical power when modeling survival (Lebreton et al. 1992). We carried out model selection following the parsimony principle based on Akaike information criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002). We considered models that were different by less than two units of AICc to be competitive to explain the data (Burnham & Anderson 2002). As it was impossible to distinguish mortality from permanent emigration, we refer to apparent rather than absolute survival. However, we believe apparent survival is close to absolute survival in our population because we only observed five marked individuals in the regularly surveyed areas adjacent to our study site.

We first tested for the effects of sex and age on survival. Indeed, North American porcupines are sexually dimorphic (male/female mass ratio in late summer = 1.22) and mammalian populations are commonly age-structured (Charlesworth 1994), so that we expected age and sex-differences in survival. Following Klvana et al. (2004), we then tested for an effect of winter precipitation, snowfall, and spring temperature on survival rates. We used standardized weather data and tested for direct and delayed (lags: 1-2 years) effects on survival.

The percentage of yearly variations in survival that is explained by an environmental covariate was calculated following Schemper (1990):

$$r^2 = \frac{Deviance(\mathrm{co}variate) - Deviance(cons\tan t)}{Deviance(year) - Deviance(cons\tan t)} \tag{2}$$

where covariate, year and constant refer to the models with covariate-dependent, time-dependent and constant survival rates.

Causes of mortality

We located dead porcupines during surveys (n = 13) or using radio-telemetry (n = 47). Since we did not perform telemetry in winter 2001 and years 2005 and 2006 (Table 3.1), we considered that searching effort was insufficient those years (n = 4 carcasses found) and excluded these periods from analyses. Three porcupines died during anaesthesia and three died when they got hung by their collar in a tree. We excluded these unnatural deaths from analyses. We therefore determined probable cause of mortality for 50 animals that died in 2000, 2002, 2003 and 2004. We classified carcasses as dead from starvation (not injured and emaciated), road kills, dead from tree fall (injured and found under a tree) or predator killed. We considered a porcupine as killed by predators either when its radio-collar was retrieved bearing visible traces of blood and its carcass could not be found (n = 8 porcupines) or when remains of skin, intestines or stomach (Sweitzer 1996) were found, along with predator signs (tracks, scats) or not (n = 20). Sweitzer (1996) used the presence of intestines or stomach on carcasses to discriminate depredated porcupines from scvavenged carcasses. In addition, we found most carcasses shortly (i.e. 1-2 days) after we determined mortality from the audible change in the telemetry signal. We are therefore confident that porcupines that we considered as killed from predators were actually depredated animals and not porcupines dead from other causes and later scavenged. Potential predators in our study site included fishers (*Martes pennanti*), coyotes (*Canis latrans*) and great horned owls (*Bubo virginianus*). We recorded predator identity when possible. We used G-tests (Sokal & Rohlf 1981) to compare the causes of mortality across years, and between age classes (two age classes were considered: juveniles and individuals ≥1-yr-old).

Predation and starvation were the two main mortality causes in our population (see Results), so we also used G-tests to examine whether proportions of juveniles and individuals ≥1-yr-old dying from predation and starvation were different between seasons (summer vs winter). Because we hypothesized that the presence of snow on the ground could affect predation and starvation rates, we further separated the winter season in two periods for analyses of causes of mortality: winter but no snow (from September to approximately mid-November), and winter with snow covering the ground (approximately from mid-November to end of April).

3.4. Results

Relationship between abundance of porcupines and solar irradiance

We observed a strong decline in abundance of all age classes in our study population, from a total of 117 individuals captured in 2000 to only one individual in 2006 (Table 3.2). Consistently, overall population growth rate was <1 in all years (i.e. the population size was decreasing) and varied from 0.72 in 2000 to 0.25 in 2005 (Table 3.2). Population growth rate was positively correlated to solar irradiance (r = 0.94, p = 0.006, n = 6).

Table 3.2 : Structure and size of a North American porcupine population followed in Parc National du Bic, Québec, May 2000-May 2006. Population growth rate was calculated as population size in year *t+1* divided by population size in year *t*

	2000	2001	2002	2003	2004	2005	2006
Juvenile males	7	1	4	3	2	0	0
Juvenile females	2	3	1	3	3	0	0
Subadult males	6	2	2	0	0	0	0
Subadult females	10	3	2	0	2	0	0
Adult males	47	38	27	17	7	1	0
Adult females	45	37	30	21	9	3	1
Total	**117**	**84**	**66**	**44**	**23**	**4**	**1**
Growth rate	**0.72**	**0.79**	**0.67**	**0.52**	**0.17**	**0.25**	

Relationships between solar irradiance and local weather variables

The solar irradiance was negatively correlated with winter precipitation (r = -0.81, p = 0.027, n = 7) but only marginally with snowfall (r = -0.71, p = 0.076, n = 7) and not at all with spring temperature (r = 0.18, p = 0.700, n = 7) (see Fig. 3.1).

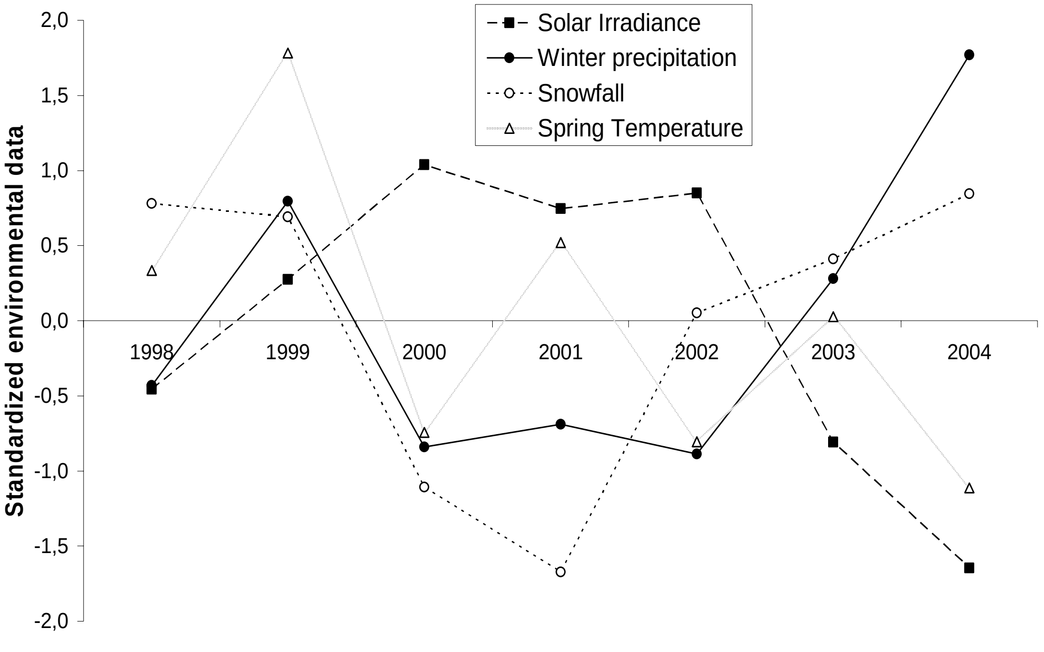

Figure 3.1 : Standardized yearly solar irradiance, winter precipitation, snowfall and spring temperature between 1998 and 2004. Solar irradiance was obtained from the PMOD/WRC (Davos, Switzerland), and weather records from the Environment Canada weather station at Rimouski, about 20 km from Parc National du Bic, Québec.

Seasonal survival rates

The selected model included capture rates that were a function of age and season, with summer capture rates dependent on telemetry effort (Table 3.3). Juveniles were less likely to be recaptured than individuals ≥1-yr-old; recapture probability in May was higher than in August (0.95 and 0.92 in May vs 0.70 and 0.63 in August for juveniles and individuals ≥1-yr-old, respectively) and recapture probability in August was higher when >50% of marked animals were followed by telemetry (i.e. in 2001, 2003 and 2004, see Table 3.1).

Table 3.3 : Model selection for sighting probabilities (p) in a population of North American porcupines, Parc National du Bic, Québec, May 2000-May 2005. We used data on 159 individuals. We considered survival rate to be time-dependent (ϕ_t) in all models and tested for an effect of sex, age (a, considering two age classes: juveniles and ≥1-yr-old), season (s), and year (y) on sighting probabilities. We tested for an effect of use of telemetry on summer sighting probability and coded 0: years when <50% of marked individuals were followed by telemetry (i.e. low telemetry effort in 2000, 2002), 1: years when >50% of marked individuals were followed by telemetry (i.e. high telemetry effort in 2001, 2003, and 2004). Model in bold represents the selected model

Biological meaning	Notation†	Deviance	np*	ΔAICc**
Sighting probability is time-dependent	p_t	807.436	19	9.710
Constant sighting probability	p	869.156	11	51.758
Sex effect	$p_{t + sex}$	807.266	21	14.817
Age effect	$p_{t + a}$	803.149	21	10.700
Additive effect of year and season + age	$p_{y + s + a}$	810.954	17	8.100
Effect of year only + age effect	$p_{y + a}$	855.595	16	50.232
Year effect in winter only + age effect	$p^U_{a}\, p^W_{y + a}$	823.468	17	20.614
Year effect in summer only + age effect	$p^U_{y + a}\, p^W_{a}$	808.259	17	5.405
Summer sighting probability dependent on telemetry + age effect	$p^U_{telem + a}\, p^W_{a}$	**810.277**	**14**	**0.000**

†U, summer; W, winter; *np, number of estimated parameters; **ΔAICc, difference in AICc with the selected model

Survival was a function of age and season, with time-dependent winter survival (Table 3.4). Juveniles exhibited lower survival than individuals ≥1-yr-old, whatever the season considered. Summer survival was high and constant over the study period (mean monthly survival ± SE: 0.86 ± 0.06 for juveniles and 0.97 ± 0.01 for individuals ≥1-yr-old) while winter survival was lower and variable from year to year (mean monthly survival: 0.53-0.83 for juveniles and 0.84-0.96 for individuals ≥1-yr-old, Fig. 3.2). Winter precipitation explained a large part ($r^2 = 0.87$, Table 3.5) of the yearly variations in winter survival (i.e. to include this covariate decreased AIC_c by 5 units, Table 3.5). Snowfall alone explained a moderate amount of variation in winter survival whereas spring temperature explained little variation (Table 3.5). Winter survival was inversely related to winter precipitation (Fig. 3.2) and, because of the inverse relationship between winter precipitation and solar irradiance, positively related to solar irradiance (Fig. 3.2). We found no evidence of a lagged effect (one and two years) of winter precipitation, snowfall, or spring temperature on winter survival (Table 3.6).

Table 3.4 : Tests of the effects of sex, age (a, considering two age classes: juveniles and ≥1-yr-old), season (s) and year (y) on seasonal survival rates (ϕ) in a population of North American porcupines, Parc National du Bic, Québec, May 2000-May 2005. We used data on 159 individuals and modeled sighting probabilities following model selected in Table 3.3. Model in bold represents the selected model

Biological meaning	Notation†	Deviance	np*	ΔAICc**
Constant survival	ϕ	840.892	5	31.841
Sex effect	$\phi_{t + sex}$	810.241	15	24.155
Age effect	$\phi_{t + a}$	791.199	15	5.113
Additive effect of year and season + age	$\phi_{y + s + a}$	799.204	11	3.557
Effect of year only + age effect	$\phi_{y + a}$	807.256	10	9.299
Year effect in summer only + age effect	$\phi^{U}_{y + a}\ \phi^{W}_{a}$	807.998	11	12.351
Year effect in winter only + age effect	$\phi^{U}_{a}\ \phi^{W}_{y + a}$	**795.637**	**11**	**0.000**

†U, summer; W, winter; *np, number of estimated parameters; **ΔAICc, difference in AICc with the selected model

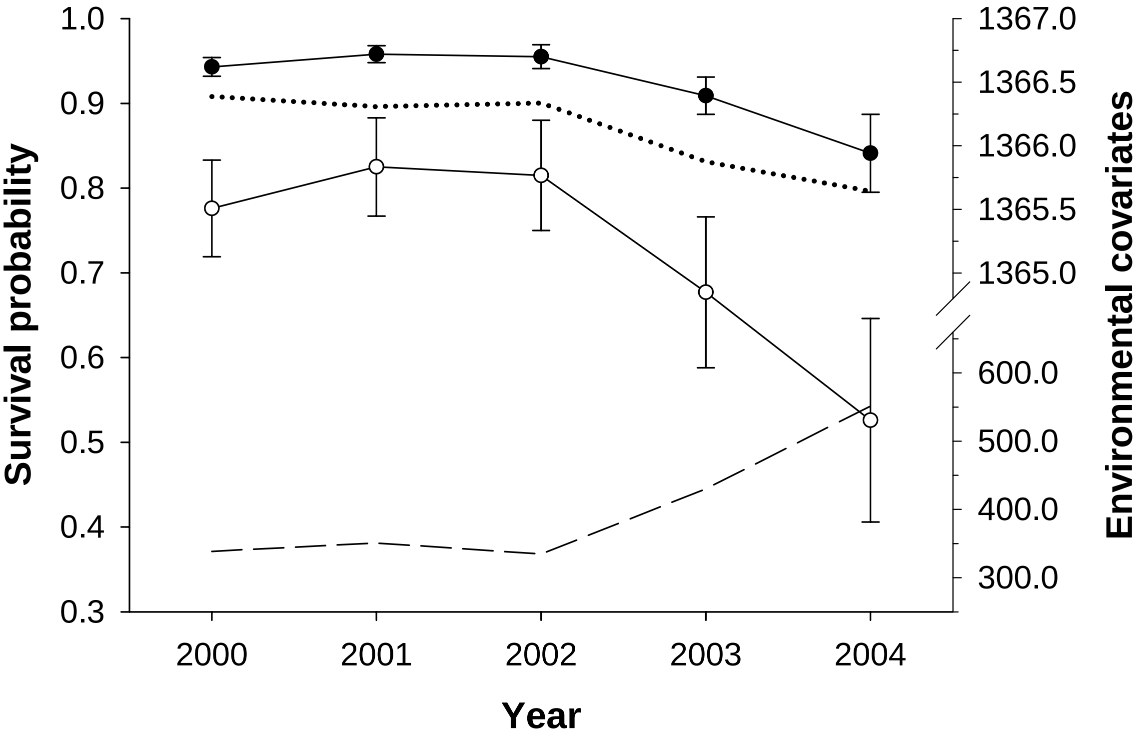

Figure 3.2 : Mean monthly survival probability between August in year *t* and May in year *t + 1* according to age (white symbols: juveniles; black symbols: individuals ≥1-yr-old) in a North American porcupine population, Parc National du Bic, Québec, August 2000-May 2005. Results correspond to estimated values (mean ± SE) from model selected in table 3.4. Secondary axis shows environmental covariates related to winter survival: dotted line corresponds to mean solar irradiance (for year *t*, in W/m^2), long-dashed line corresponds to winter precipitation recorded at Rimouski (from November, year *t* to April, year *t + 1*, in mm).

Table 3.5 : Tests of the effects of local weather variables on winter survival rates (ϕ^W) in a population of North American porcupines, Parc National du Bic, Québec, May 2000-May 2005. We used data on 159 individuals. Model in bold represents the selected model. We show the percentage of yearly variation in survival that is explained by each environmental covariate (r^2)

Biological meaning	Notation†	Deviance	np*	ΔAICc**	r^2
Year effect in winter only + age effect, *from Table 3.4*	$\phi^U{}_a\ \phi^W{}_{y+a}$	795.637	11	5.041	1
Winter survival dependent on winter precipitation + age effect	$\phi^U{}_a\ \phi^W{}_{\text{Precipitations}+a}$	**797.442**	**8**	**0.000**	**0.87**
Winter survival dependent on snowfall + age effect	$\phi^U{}_a\ \phi^W{}_{\text{Snowfall}+a}$	802.543	8	5.101	0.52
Winter survival dependent on spring temperature + age effect	$\phi^U{}_a\ \phi^W{}_{\text{Spring}+a}$	808.327	8	10.885	0.12
No yearly variation in winter survival + age effect	$\phi^U{}_a\ \phi^W{}_a$	810.049	7	10.389	0

†U, summer; W, winter; y, year; a, age modelled as two age classes (juveniles, ≥1-yr-old); *np, number of estimated parameters; **ΔAICc, difference in AICc with the selected model

Table 3.6 : Tests of lagged (one year: y-1; two years: y-2) effects of winter precipitation on winter survival rates (ϕ^W) in a population of North American porcupines, Parc National du Bic, Québec, May 2000-May 2005. We used data on 159 individuals. Model in bold represents the selected model. We also performed tests of lagged effects of snowfall and spring temperature on survival but don't show results here since no model was better than the selected model

Biological meaning	Notation†	Deviance	np*	ΔAICc**
Direct effect of precipitations + age effect, *from Table 3.5*	$\phi^U{}_a\ \phi^W{}_{\text{Precipitations}+a}$	**797.442**	**8**	**0.000**
Lagged effect of precipitations (y-1) + age effect	$\phi^U{}_a\ \phi^W{}_{\text{Precipitations (y-1)}+a}$	809.678	8	12.236
Lagged effect of precipitations (y-2) + age effect	$\phi^U{}_a\ \phi^W{}_{\text{Precipitations (y-2)}+a}$	805.747	8	8.305

†U, summer; W, winter; y, year; a, age modelled as two age classes (juveniles, ≥1-yr-old); *np, number of estimated parameters; **ΔAICc, difference in AICc with the selected model

Causes of mortality

We assigned a probable cause of mortality to 46 of the 50 porcupines examined. Predation (n = 28 [60.9%]) and starvation (n = 13 [28.3%]) were the main causes of mortality. Tree fall (n = 3) and road kill (n = 2) together represented 10.8% of the mortalities. We determined predator identity for 14 of the 28 predation events observed. Fishers were responsible for 86% (n = 12) and coyotes for 14% (n = 2) of these predations. The proportion of mortalities due to predation vs. other causes (starvation, tree fall and road kill combined) was not constant through time (G = 8.640, df = 3, p = 0.034) and increased from 40% in 2000 and 2002 to 91.7% in 2004 (Fig. 3.3). Causes of mortality did not differ between age classes (G = 1.399, df = 3, p = 0.706, Fig. 3.4).

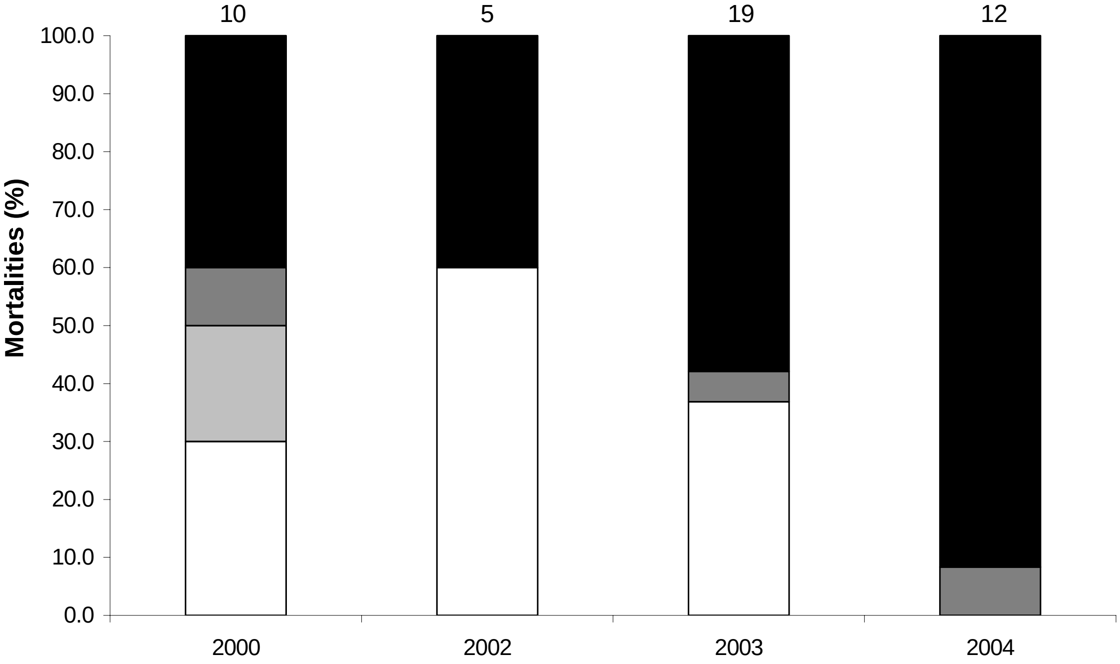

Figure 3.3 : Causes of mortality determined for carcasses found during monitoring of a North American porcupine population in Parc National du Bic, Québec, May 2000-May 2006. Percentage of carcasses dead by starvation, road kill, tree fall and predation are shown respectively in white, light grey, dark grey and black. Sample sizes for each year are indicated at the top of each bar.

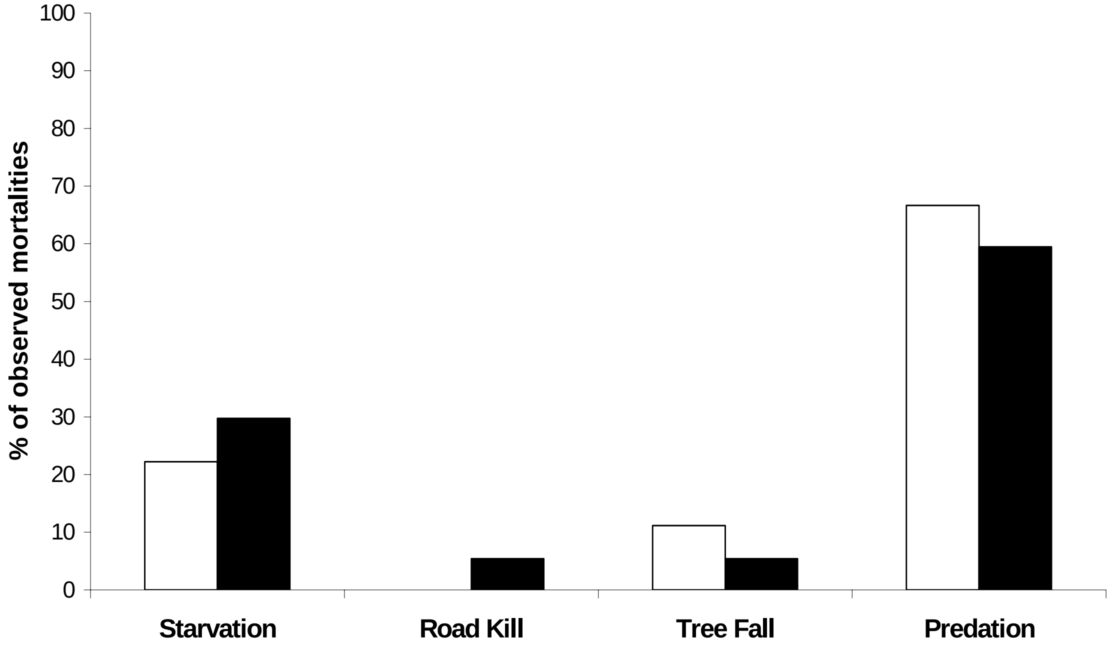

Figure 3.4 : Causes of mortality for dead juveniles (in white, n = 9) and individuals ≥1-yr-old (in black, n = 37) in North American porcupines, Parc National du Bic, Québec, May 2000-May 2006.

Among depredated animals (six juveniles, 22 individuals ≥1-yr-old), timing of death differed between age classes (G = 26.324, df = 2, p<0.001). Juveniles were killed mainly in summer (83.3% in summer vs. 16.7% in winter, Fig. 3.5a) and individuals ≥1-yr-old exclusively in winter and almost exclusively when snow was covering the ground (95.5% when snow was covering the ground, Fig. 3.5a). Among starved animals (two juveniles, 11 individuals ≥1-yr-old), timing of death did not differ between age classes (G = 0.731, df = 2, p = 0.694) with most of the starvations occurring when snow was covering the ground for both age classes (100 and 81.8% of the deaths by starvation happened when snow was present respectively for juveniles and individuals ≥1-yr-old, Fig. 3.5b).

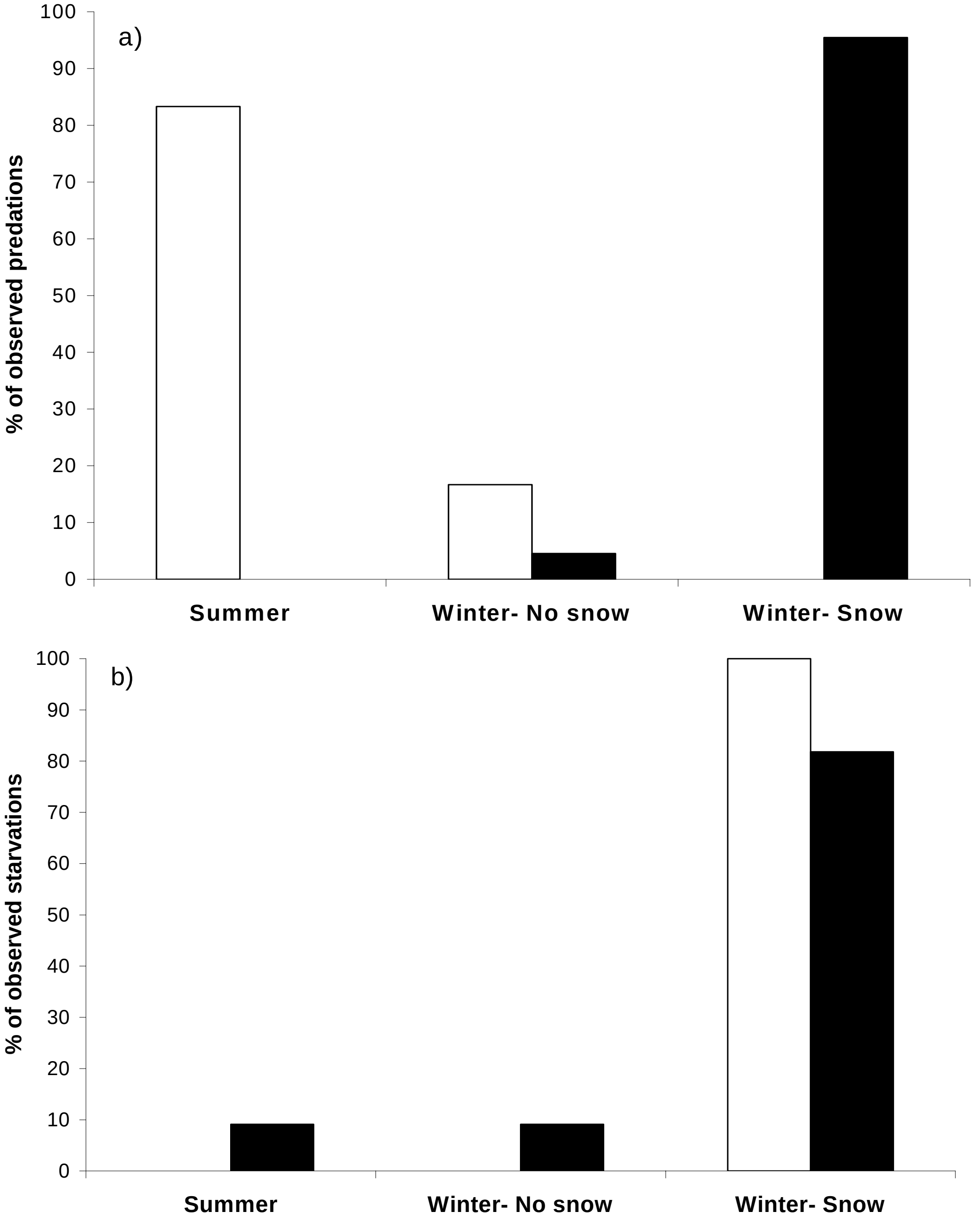

Figure 3.5 : Season of mortality for the: **a)** depredated juveniles (in white, n = 6) and individuals ≥1-yr-old (in black, n = 22), and **b)** starved juveniles (in white, n = 2) and individuals ≥1-yr-old (in black, n = 11), in North American porcupines, Parc National du Bic, Québec, May 2000-May 2006. Seasons were defined as: summer (from May to August), winter but no snow (from September to approximately mid-November), and winter with snow covering the ground (approximately from mid-November to end of April).

3.5. Discussion

Relationship between abundance of porcupines and solar irradiance

We observed a strong decline in abundance of porcupines from 2000 ongoing. Density of porcupines concomitantly dropped (from ca. 40 to ca. three animals per km^2 between 2000 and 2006, Y. Lemay UQAR, unpublished data) in other areas of the Parc National du Bic where no captures were performed so that we are confident that our study design is not responsible for the observed decline. As it was hypothesized from Klvana et al. (2004), changes in abundance of porcupines were correlated to solar irradiance at our study site. Our first prediction was therefore supported. We now discuss how solar activity could influence abundance of porcupines in eastern Québec through cascading effects on winter precipitation, winter survival rates, and predation rates on porcupines.

Relationship between solar irradiance and winter precipitation

We found that high solar activity was associated with low levels of winter precipitation. Klvana et al. (2004) also found a link between solar activity and winter precipitation when analysing weather records for the same area for the 1877-2000 time period. In their study, both time series showed regular periodicities, with a lag of four to five years between the two cycles. A significant number of studies have found correlations between solar activity and different meteorological parameters (reviews in Tsiropoula 2003, Versteegh 2005). Positive, negative or non-existent correlations have been reported between local weather and solar activity. Some were direct (e.g. Currie 1993, Lean et al. 1995) while others were delayed correlations (e.g. Perry 1994, 2006). Such conflicting evidence gives a confusing and contradictory picture of solar influences on the earth's climate. One reason for this confusion may be that solar effects on meteorological parameters differ in various geographical regions and at different time periods. Indeed, some reversals between solar activity and weather variables have been reported in the literature. We found no significant correlation between solar irradiance, snowfall and spring temperature between 1998 and 2004 while Klvana et al. (2004) found those series to remain in phase between 1877 and 2000. One explanation may be that we were faced with a breakdown of the link between solar irradiance and some local parameters. Alternatively, the statistical tool we used (i.e. direct correlations) may have been too simplistic to detect complex relationships such as those that can be inferred using wavelet analyses (Tsiropoula 2003, Klvana et al. 2004). In any case, our second prediction was at least partly supported in that we found a direct negative relationship between solar activity and winter precipitation. More generally, the impact of solar variability to our local environment will be certainly discussed for many more years until a linking mechanism is identified. However, we believe that reporting observed correlations may help understanding the existing relationships between sun and climate.

Seasonal survival rates

In long-lived vertebrate species such as porcupines, population growth rates are sensitive to survival, and especially to adult survival (Gaillard et al. 2000, Saether & Bakke 2000, Eberhardt 2002). Demographic parameters with high elasticities are expected to be canalized against environmental variations and to exhibit limited temporal variability (Gaillard & Yoccoz 2003). In populations of porcupines, adult survival is thus expected to be the life history trait least affected by local weather. On the other hand, juvenile survival has often a low elasticity but exhibits large variability, and thus can greatly affect population growth rate (Gaillard et al. 1998, Gaillard et al. 2000). Consequently, juvenile survival is expected to be a life history trait greatly affected by weather variability. We found both juvenile and adult survival rates to be variable in our population. The decline in winter adult survival over time is likely a major cause of the decline in the size of our population and our study gave us the rare opportunity to witness a population crash while documenting variations in a demographic parameter with high elasticity.

Winter is often pointed out as a critical period for herbivorous mammals because the energy demand is high while the available food is of low quality (Halfpenny & Ozanne 1989, Robbins 1993). However, reliable estimates of seasonal survival rates are rare (but see Lima et al. 2001, Crespin et al. 2002, Lima et al. 2002a, Sendor & Simon 2003) and factors affecting survival on a seasonal basis have been poorly explored. Calculating seasonal survival rates allowed us to identify winter as the most critical period of the annual cycle for the survival of porcupines. We found that winter precipitation explained a large part of the variability observed in winter survival, with low levels of winter precipitation being associated with high winter survival. Our third prediction was therefore supported in that an increase in winter precipitation led to a decrease in survival of porcupines. How winter precipitation influenced winter survival of porcupines is examined below.

Mechanism linking winter precipitation to winter survival

North American porcupines are short-limbed animals and presence of snow covering the ground greatly reduces their mobility (Roze 1984, 1987). Snow increases probability of starvation of porcupines (Sweitzer et al. 1997), possibly by increasing energy expenditure (through elevated locomotion costs) and/or decreasing energy acquisition (through a limited access to food resources). Snow may also increase porcupines' probability of death by predation either directly by reducing their escape ability (Huggard 1993) or indirectly because starved animals may be more susceptible to predators (Sweitzer 1996). Furthermore, predators may show variable hunting efficiency (Gese et al. 1996b, Thibault & Ouellet 2005) and/or may shift to more vulnerable prey (Patterson et al. 1998, Patterson & Messier 2000) according to snow conditions.

We observed higher predation rates in years with high levels of winter precipitation. We also found that predators killed adult porcupines almost exclusively when snow was covering the ground. Either because adult porcupines were more vulnerable in presence of snow cover, because predators were more efficient, or because they shifted to hunt porcupines when snow deepened, predation rates appeared strongly related to snow conditions in our system.

Fishers were the main predators of porcupines in our study area. Fishers are efficient predators of the North American porcupine (Earle & Kramm 1982, Powell 1993) and their number has been rapidly increasing in eastern Québec since the middle of the 1990s (Poulin et al. 2006). They feed primarily on snowshoe hares when available (Powell 1993, Martin 1994), but may well switch to porcupines when snow deepens. Indeed, snowshoe hares are light animals that are characterized by a low foot-load (Murray & Boutin 1991) so their sinking depth in fresh snow should increase more slowly compared to fishers' and porcupines'. In deep snow, fishers may then be unable to chase hares and therefore switch to preying on porcupines, which are a more risky (because of quills) but less energetically costly prey to run after.

Because we did not monitor predator density, we are not sure whether higher predation rates were due to an increase in predator density, to a functional response of predators to increasing snow cover, or both. However, because we found that winter precipitation was correlated with winter survival in our population, and because adult predation occurred only in the presence of snow), we believe that changes in predator efficiency, predator behaviour, or prey susceptibility are the factors most likely explaining why variations in winter precipitation influenced survival.

Interestingly, we found that winter precipitation explained more variability in porcupine survival than snowfall. We hypothesize that this occured because winter precipitation is a better indicator of snow conditions than snowfall. Winter precipitation included precipitations that occurred during winter both as rain and snow, so they may better reflect conditions of snow penetrability than snowfall alone. Snow penetrability is more likely than snowfall to influence vulnerability of porcupines to predation because it directly influences mobility of animals, and therefore escape ability (Huggard 1993). Indeed, behaviour of porcupines during winter is affected to a greater extent by variations in snow penetrability than in snowfall (G.Mabille, unpublished data). For example, animals become more diurnal when snow penetrability increases (chap. 4) while variations in snowfall have no effect on timing of activity. Similarly, hunting behaviour of fishers may also vary with snow penetrability.

3.6. Conclusion

We confirmed the hypothesis of a link between winter precipitation and abundance in a porcupine population and identified variations in predation rates as a possible mechanism relating winter weather to abundance, through effects on winter survival rates. Even though our study was not experimental, using the “strategic cyclical scaling” approach described by Root and Schneider (1995) allowed us to identify the link between weather conditions and survival, and therefore to go one step further than traditional studies of climate influences on population dynamics. Our study also adds to the existing body of evidence in support of an effect of climate on predator-prey processes and strongly emphasizes that understanding how species interactions vary according to weather conditions is crucial to properly model how communities will respond to climate change (Schmitz 2003, Wilmers & Getz 2005, Sala 2006, Suttle et al. 2007).

Chapitre 4 Navigating the thermal map : porcupines eat in the cold but rest in the warm

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(à soumettre, *Oecologia*)

Les variations temporelles et spatiales des conditions météorologiques et du risque de prédation influencent le patron d'activité et l'utilisation de l'habitat des animaux. Le risque de prédation était relativement élevé pendant notre étude et apparemment lié aux conditions de neige pendant l'hiver (chap. 3). D'autre part, les conditions thermiques constituent une contrainte potentielle pour les porcs-épics pendant l'hiver quand les températures sont plus basses que leur température critique inférieure. Les contraintes dues à l'environnement thermique et à la prédation étaient donc substantielles pendant l'hiver, et nous avons examiné l'influence de ces contraintes sur le patron d'activité et l'utilisation de l'habitat par les animaux. Les résultats montrent que les porcs-épics modifient leur patron d'utilisation de la tanière en fonction des conditions de température. L'enfoncement dans la neige, qui est possiblement lié au risque de prédation, influence également le patron d'utilisation de la tanière. Les animaux semblent utiliser leur tanière comme un refuge contre le froid et les prédateurs. Néanmoins, puisqu'ils doivent sortir pour s'alimenter, les porcs-épics font face à un compromis entre recherche de nourriture et protection contre le froid et les prédateurs. On montre qu'ils y répondent en modifiant l'intensité de l'alimentation en fonction des conditions de température. Par contre, ils ne modifient pas leur utilisation des microhabitats à l'extérieur de la tanière en fonction de la température. Ceci suggère qu'ils choisissent les microhabitats extérieurs en fonction de la qualité de la nourriture qui s'y trouve plutôt qu'en fonction des conditions thermiques. Le comportement des animaux pendant l'hiver semble donc être influencé à la fois par des contraintes liées aux conditions thermiques, au risque de prédation, et à l'acquisition de nourriture. Les différences individuelles dans l'utilisation de l'habitat sont liées à des différences de survie. Les animaux faisant le plus de sorties par jour survivent moins bien. On interprète ces différences dans la survie comme des différences dans l'exposition à la prédation, principale cause de mortalité des adultes pendant l'hiver.

4.1. Abstract

Because the climate is changing, there are now additional incentives to understand the strategies that organisms use to cope with thermal heterogeneity. The thermal environment experienced by an animal is determined by conditions of air temperature, wind, and radiation, and habitat can also mediate the thermal environment. We mapped microclimates by estimating energy expenditure in microhabitats available to North American porcupines (*Erethizon dorsatum*) in the cold Canadian winter. We then examined activity patterns and microhabitat use of free-living individuals to determine whether porcupines responded behaviourally to thermal constraints. The lower critical temperature (T_{lc}) of winter acclimatized porcupines in southern Québec lies around –2°C and individuals are exposed, during winter, to operative temperatures (T_e) that are well below T_{lc}. According to our thermal map, porcupines reduced metabolic rate by about 25% when moving from a tree to their den in cold conditions (T_e<-19.9°C). Porcupines modified their pattern of den use when T_e decreased: they reduced the time spent outside of the den, increased the number of activity bouts in a day, reduced the duration of activity bouts, and became more diurnal. Outside of the den, porcupines increased feeding intensity when T_e decreased, but did not change microhabitat use according to T_e. Rather, they used different microhabitats for different activities: they exploited open microhabitats and top of trees for feeding, and covered microhabitats and bottom of trees for resting. We suggest porcupines fed in open and arboreal microhabitats because they offered the most beneficial food, even though energy expenditure was high in these microhabitats. Finally, activity patterns varied with snow conditions. Porcupines spent less time outside and became more diurnal when snow penetrability, and therefore possibly predation risk, increased. Behaviour of porcupines during winter appears to be constrained not only by thermal conditions, but also by constraints on food acquisition and predation risk.

Key-words : behavioural thermoregulation, herbivore, heated taxidermic mount, foraging strategy

4.2. Introduction

In a context of climate change, understanding the way that variability in the thermal environment influences animal ecology becomes crucial. Thermal conditions can shape patterns of activity and habitat selection which, in turn can have fitness consequences for animals (Sealander 1952, Bult & Lynch 1997, Dawson et al. 2005). How temperature influences activity has been much studied for ectothermic reptiles and amphibians (e.g. Christian et al. 1983, Grant & Dunham 1988, Niewiarowski 2001) but comparatively less is known about the way thermal conditions affect the activity of endothermic animals. Moreover, most studies on endotherms focused on small mammals living in hot environments (see Chappell & Bartholomew 1981, Bennett et al. 1984, Vispo & Bakken 1993, Sharpe & Van Horne 1999). However, several authors have stressed the importance of collecting data in cold environments to fully understand general ecological processes (Campbell et al. 2005) and specifically the effects of temperature on activity (Sears et al. 2006). Humphries et al. (2005) recently demonstrated that behavioural thermoregulation allows huge energy savings for red squirrels (*Tamiasciurus hudsonicus*) exposed to cold temperatures and emphasized the need for further work on the impacts of cold temperatures on mammal behaviour and energetics.

In cold environments, animals can use behavioural thermoregulation to create a more favourable thermal environment. For example, they may exploit a nest or den to reduce heat loss (Prestrud 1991, Clark et al. 1997, Zimmerling 2005), show activity patterns that vary with temperature (Chappell 1981, Kortner & Geiser 2000, Humphries et al. 2005), choose specific foraging microhabitats (Wiersma & Piersma 1994, Brotons et al. 2000), and use postures promoting heat conservation (Hayes et al. 1992, Fortin & Gauthier 2000, Scantlebury et al. 2006). A significant number of studies have dealt with behavioural thermoregulation, but comprehensive studies examining several aspects of thermoregulatory behaviour in the cold are rare (but see Guthery et al. 2005). Furthermore, the existing literature often describes the thermal conditions using a general measure of air temperature (T_a) made within or close to the study site. However, the thermal environment experienced by an animal in its natural habitat may differ greatly from the overall conditions measured with

T_a, first because of the effects of wind and solar radiation on heat load (Lustick et al. 1978, Bakken 1991), and second because microclimates can be highly heterogeneous in space (Chappell et al. 1978, Sharpe & Van Horne 1999). An accurate thermal map of an animal's environment is therefore necessary to evaluate the ecological effectiveness of its thermoregulatory behaviour. Comprehensive and detailed studies are needed to understand the complex interactions existing between thermal conditions and behaviour, especially in cold environments.

The North American porcupine (*Erethizon dorsatum*) is the only arboreal folivorous mammal of the boreal forest. Porcupines stay active year round and rely on low quality food (mainly bark and leaves of conifers) during winter. The lower critical temperature (T_{lc}, temperature below which an organism increases basal metabolic rate) of winter acclimatized porcupines can vary between +10°C and –12°C, depending on the size and origin of the study animal (Irving et al. 1955, DeMatteo & Harlow 1997, Fournier & Thomas 1999). In southern Canada, T_{lc} of porcupines lie around –2°C (Fournier & Thomas 1999) and individuals are exposed, during winter, to temperatures that are well below T_{lc}. Porcupines can den to avoid the coldest temperatures, but must exit the den daily to feed. Wind speed increases with height above ground (Rosenberg 1974, Byman et al. 1988) so feeding in trees should be energy demanding. However, the tree canopy is also highly heterogeneous in terms of microhabitats available to a mid-sized mammal. How porcupines use their den and select feeding microhabitats could greatly affect their thermoregulatory costs. We used one population of free-ranging porcupines in southern Canada to investigate how thermal conditions affected their habitat use and activity patterns during winter.

Our objectives were 1) to establish a detailed map of microclimates available to porcupines, 2) to characterize activity patterns of porcupines according to the thermal environment, 3) to evaluate whether microhabitat use of porcupines was determined by thermal constraints. What makes the current report significant is that we modelled the thermal environment at a very fine scale and compared the resulting thermal map with detailed behavioural data from individually-marked, wild animals.

4.3. Material and methods

Study area and study population

We worked from 12 January to 16 April 2004 and 13 December 2004 to 19 March 2005 in a ca. 2 km^2 area of Parc National du Bic (48°20’N, 68°46’W, elevation 0-150m), Québec, Canada. The study area is fragmented by abandoned and cultivated fields, and characterized by a rugged topography, abundance of natural rock dens, and a mixed-boreal forest (see Berteaux et al. 2005, Morin et al. 2005 for details). We worked on a population of individually-marked porcupines monitored each summer since 2000. The population sometimes reached a high density (ca. 40 individuals/km^2; D. Berteaux, unpublished data), and regularly fluctuated in abundance (Klvana et al. 2004). Porcupines were at medium to low densities (ca. 15 to 2 individuals/km^2) during this study.

Study design

We proceeded in three steps. First, we measured air temperature inside dens, and air temperature (T_a), wind speed, and net radiation at an automated weather station located in the study area. We did not measure wind and solar radiation inside dens as they were negligible.

Second, we characterized the “thermal quality” of microhabitats available to porcupines using heated taxidermic mounts. Use of heated mounts to estimate the metabolic heat production of free-living animals has been much debated (Walsberg & Wolf 1996, Larochelle 1998, Fortin 2001, Dzialowski 2005) but they remain a useful tool to compare thermal effects across a range of complex natural environments. We measured operative temperature (T_e) 0.3 m above ground (i.e. at porcupine’s height) as a general measure of the thermal environment prevailing in the stand. T_e incorporates the effects of T_a, convection, conduction, and radiation into a single variable (Winslow et al. 1937, Bakken & Gates 1975). We then placed mounts in different microhabitats and compared power consumption between microhabitats for a range of T_e measured in the stand. We considered one microhabitat to be of good “thermal quality” (i.e. to offer a favourable microclimate) when the power consumed in that microhabitat was lower than in other microhabitats, for a given T_e measured in the stand. One thing we wanted to establish was whether ranking of microhabitats (from best to worst microhabitat) was the same at cold and warm T_e.

Third, we evaluated the behavioural response of porcupines to variations in T_e. We recorded time spent outside of the den, number of activity bouts, and a nocturnality index (equation 2 below) for each day (from 00:00 am to 24:00 pm) and compared them to the mean T_e of the day (recalculated from continuous measures of T_a, wind speed and net radiation made at our weather station, equation 3 below). We also compared the duration of activity bouts to the mean T_e during the activity bout. Finally, we determined which microhabitats were used when porcupines were outside of their den, according to T_e measured in the stand at the time of observation. Because porcupines are sexually dimorphic, we tested for sexual differences in behaviour.

Meteorological conditions

Our automated weather station measured air temperature in the shade (T_a) using a temperature sensor (8-bit Temperature Smart Sensor, Hobo, Onset) placed 1 m above ground, wind speed using a wind and direction sensor (Wind speed/Direction Smart Sensor, Hobo) placed 2 m above ground, and net radiation (0-100 μm) using a net radiometer sensor (model NR-Lite Net Radiometer, Kipp & Zonen) placed 1.5 m above ground. All sensors were connected to a datalogger (four channels Micro-station, Hobo) that collected data every minute.

We placed temperature loggers (SmartButton Temperature Loggers, ACR systems Inc.) inside nine dens that were regularly used by porcupines during our long-term study, but that were not occupied during the sampling period. Loggers were placed on the ground as far as possible from the entrance of the den (0.5 to 6.5 m deep, depending on den structure). Loggers recorded temperature every 15 minutes.

Thermal mapping

We worked during two winters to establish the thermal map: 29 January to 30 March 2004 and 13 December 2004 to 8 February 2005. Following Bakken et al.(1983), we built two heated taxidermic mounts in the form of North American porcupines. To cover the copper core we used pelts from animals that died naturally in our study area during winter 2003. We built the mounts in a standing posture with the head facing down. We lined the inside surface of the hollow copper mould with 24 gauge Teflon-coated iron wire that was connected to an external control circuit and to a Campbell CR-21X data logger (Campbell Scientific). Electrical power was provided by four 6 V deep discharge batteries in series.

Body temperature (T_b) of the mounts was regulated at 37.5 ± 0.3°C, which is the core body temperature of winter acclimatized free-ranging porcupines (D.W. Thomas, unpublished data). We monitored temperature inside the copper mounts using a copper-constantan thermocouple placed in the centre of the mount. We wrote a program for the Campbell CR-21X to regulate T_b. Power was applied automatically as 24V pulse to maintain body temperature. The datalogger measured voltage (V_m) every five seconds, calculated the power consumption (see below), and stored the mean power over five minute intervals. We calculated the power drawn by each mount (P_m) from V_m and the resistance of the heater wire circuit (R) following equation 1:

$$P_m = \frac{V_m^2}{R} \tag{1}$$

with P_m expressed in Watts, V_m in Volts and R in Ohms.

We recorded meteorological conditions in the stand while mounts were functioning by measuring T_e with a copper-constantan thermocouple placed inside an anodized aluminium sphere, T_a with a copper-constantan thermocouple placed in the shade, and wind speed with a portable hot-wire anemometer (Series 440 Portable Air Velocity Meters, Kurz Instruments). Measurements were made 0.3 m above ground, averaged over five minute intervals, and stored in the data logger. We obtained measures of net radiation from our automated weather station. We used synchronous measurements of T_e, T_a, wind speed and net radiation to establish an equation relating T_e to the other meteorological parameters (see below).

We placed mounts in six microhabitats: "*den*"**,** "*ground open*", "*ground covered,*" "*conifer open*", "*conifer covered*", and "*deciduous*"(see Appendix 1 for a detailed description of the microhabitats). We placed each mount for about 24 hours in one geographical site corresponding to one of the six microhabitats, and subsequently moved it to a new site. Since easily accessible sites were scarce in the study area, we used some sites on several occasions but took this into account in our analyses (see *data analyses*).

Activity patterns

We captured 26 adult porcupines (10 males, 16 females) in summer and fall 2003 and 2004. Individuals were immobilized following Morin & Berteaux (2003) and equipped with radio transmitters (Lotek SMRC-5RB VHF transmitter, Lotek Wireless Inc.) (see chap. 2 for details). In January 2004 and 2005, we recaptured radiocollared porcupines to measure their pattern of den use over one or two winter seasons (n = 14 individuals followed from 23 January to 14 April 2004; n = 6 individuals followed from 05 January to 19 March 2005; among which three individuals were followed both years). For that, we attached temperature loggers (SmartButton Temperature Loggers, ACR systems Inc.) to their radio collar (total weight of collar with temperature recorders = 74 g). We used abrupt changes in temperature readings to estimate the timing of movements in and out of the dens. To complement data from temperature loggers, we placed movement detectors (Vigil 650X, Circuitronique Estrie Inc.) at the entrances of all dens used. Combining information from temperature loggers and movement detectors allowed us to determine when animals were inside or outside of a den and therefore to calculate the time spent outside of the den, the number and duration of activity bouts, and the nocturnality index. The nocturnality index I_n (after Zalewski 2000) reflects the relative distribution of activity between day and night, and is calculated as:

$$I_n = \frac{2Na/N}{(Na/N) + (Da/D)} \qquad (2)$$

where Na and Da are total duration of porcupine activity during night and day, respectively, and N and D are night and day lengths. Night started 30 min after sunset and ended 30 min before sunrise. I_n varies from 0 (diurnal activity) to 2 (nocturnal activity).

Microhabitats used outside of the den

We measured habitat use by porcupines from 12 January to 16 April 2004 and 11 January to 12 March 2005. Twice a week, we precisely located the 26 radiocollared porcupines. For that, we followed the telemetry signal to the animal (homing) instead of using triangulation. Each time we located an individual, we assigned its position to one of the six microhabitats (i.e. "*den*", "*ground open*", "*ground covered*", "*conifer open*", "*conifer covered*", or "*deciduous*"). If the animal was in a tree, we recorded its position according to one of three classes of height (lower third, middle, higher third of the canopy) and to one of two classes of distance to the trunk (base, tip of the branch). We also noted whether the porcupine was feeding or resting. We characterized thermal conditions in the stand by measuring T_e using a hand held thermocouple (HH11 with type K thermocouple input, Omega Engineering Inc., Stamford, Connecticut) inserted in a black bowl and placed 0.3 m above ground.

Data analyses

Thermal mapping

We measured power consumption 46 times in 38 sites (4 "*den*", 6 "*ground open*", 12 "*ground covered*", 3 "*deciduous*", 5 "*conifer open*", 8 "*conifer covered*"), and collected 1012 hours of data with both mounts. We averaged power consumed by the mounts over one-hour periods to match measures of T_e that were averaged over the same period. To insure that the mean power consumed referred to relatively stable meteorological conditions, we excluded one-hour periods during which T_e variation was > 3°C. This 3°C threshold allowed us to remove most directional changes in T_e. Following this sampling strategy, we calculated mean power consumption during 886 one-hour periods (mount 1: 494 h, mount 2: 392 h). We tested during calibration periods whether mounts had similar power consumption when exposed to similar thermal conditions. We placed the two mounts 2 m apart (similar position) in a "*ground open*" microhabitat and continuously recorded power consumed by the mounts. We ran four calibration trials and calculated power consumption during 46 one-hour periods covering a wide range of T_e (from –18.2°C to +4.2°C). We tested for differences between the two mounts using a paired t-test.

Our sampling design included repeated measurements of power consumption made on the same site on different occasions and for a given site and occasion, repeated measurements made at different hours. Therefore, we used general linear mixed models with normal distributions (proc MIXED, SAS software version 9.1, SAS 2002), including occasion of measurement as a random effect for a given site (because we used some sites on several occasions), and hour of measurement as a repeated effect for a given site and occasion (because measurements closer in time are more correlated than measurements further apart). We fitted T_e, microhabitat as fixed effects to test whether the power consumed by mounts was different between microhabitats (our variable of interest) when adjusting for T_e. We also fitted T_e×microhabitat as a fixed effect to test whether the relationship between power consumed and microhabitat differed according to T_e (e.g. to test whether the microhabitat offering the best microclimate was the same at cold and warm T_e). When testing the effect of microhabitat (as a main effect or in interaction with T_e), we first considered all microhabitats sampled (i.e. microhabitat had six modalities, Table 4.1, model 1) and then considered groups of microhabitats that we expected to offer similar thermal conditions (i.e. microhabitat had two modalities, Table 4.1, models 2 to 4). We first compared "*den*" to other microhabitats merged into a single category (Table 4.1, model 2). Among the non-den microhabitats, we then compared arboreal ("*deciduous*", "*conifer open*", "*conifer covered*") to terrestrial ("*ground open*", "*ground covered*") microhabitats (Table 4.1, model 3); and finally open ("*ground open*", "*deciduous*", "*conifer open*") to covered ("*ground covered*", "*conifer covered*") microhabitats (Table 4.1, model 4).

Calculating T_e from other meteorological variables

Because we did not measure T_e continuously during the study period, we used synchronous measurements of T_e, T_a, wind speed and net radiation to relate T_e to other meteorological variables. We considered only measures made during daytime (i.e. 30 min before sunrise to 30 min after sunset) because T_e measured with a black bowl integrates the effects of wind only when solar radiation occurs. We averaged measurements over one-hour periods and considered only periods when T_e varied by $\leq 3°C$. We obtained 160 one-hour periods from 37 occasions of measurements. We used general linear mixed models with normal distributions (proc MIXED) and included hour of measurement as a repeated effect in our analyses. We fitted air temperature, the square root of wind speed (Kreith & Black 1980), net radiation and their first order interactions as fixed effects to test how these variables influenced T_e.

Activity patterns

We wanted to test for an effect of T_e on activity patterns. Our data set included repeated measurements made on the same individual at different dates so we fitted general linear mixed models with porcupine identity as a repeated factor. We used mixed models with normal distributions (SAS software, proc MIXED, SAS 2002) to analyse the effects of T_e on time spent outside of the den, duration of activity bouts, and nocturnality index (i.e. continuous variables) and mixed models with binomial distributions (proc GLIMMIX) to analyse the effects of T_e on the number of activity bouts per day. This last variable had two categories (1 activity bout; >1 activity bout, range: 2 to 4) in order to test if changes in T_e influenced porcupines to shift from unimodal to plurimodal patterns of activity. Because sampling periods were different between 2004 and 2005, we tested the effect of year (fixed factor) before fitting other variables. We removed the effects of confounding variables on activity pattern by including as fixed factors Julian date, snow penetrability (daily measure in cm, made in the study area using a specially adapted Verme sinking-depth gauge, which was calibrated at the start of the study using fresh porcupine tracks) and their first-order interactions with sex. We chose Julian date because it can influence activity (Santee & Bakken 1987, Vispo & Bakken 1993) and was not independent from T_e (Pearson correlation: $r = 0.65$, $p<0.001$). We chose snow penetrability because predation rates appear to be linked to snow condition in our system (chap. 3) so we hypothesized snow penetrability could influence activity patterns. We finally included T_e, T_e^2, and their first order interaction with sex to test for thermal effects on activity and possible differences between sexes in the response to T_e.

Microhabitats used outside of the den

When outside of their den, porcupines were observed quasi-exclusively in coniferous trees (257 times over 268). We thus restricted our analyses of microhabitat use to microhabitats in coniferous trees. We tested whether microhabitat use, height in the tree, distance to the trunk, and feeding behaviour were influenced by T_e and sex. Microhabitat choice was either "*conifer open*" or "*conifer covered*". Because porcupines were never seen in the lower part of the canopy, height in the tree had two modalities: middle or upper canopy. Distance to the trunk was either base or tip of the branch, and behaviour was either feeding or resting. We therefore used mixed models with binomial distributions (proc GLIMMIX) with microhabitat choice, height in the tree, distance to the trunk, and behaviour as dependent variables. We included porcupine identity as a repeated factor, and tested T_e, T_e^2, sex, and the interactions with sex as fixed factors. Since sampling periods were different between 2004 and 2005, we also tested year as a fixed effect in all models.

Because T_e only had an effect on behaviour (see Results), we further investigated the factors explaining feeding behaviour (dependant variable). For that, we fitted mixed models with binomial distributions (proc GLIMMIX) with porcupine identity as a repeated factor and year, T_e, T_e^2, microhabitat choice, height in the tree, distance to the trunk, sex, and all the interactions with sex as fixed factors.

Time spent feeding

We used data on time spent outside of the den and occurrence of feeding when outside, to estimate the time spent feeding in a day according to the mean T_e of the day. We calculated the mean time spent outside for each individual and multiplied it by the mean occurrence of feeding behaviour for the population (obtained from Fig. 4.3). Means were computed over six classes of Te (<-19.9°C, -19.9 to –15°C, -14.9 to –10°C, -9.9 to –5°C, -4.9 to 0°C and >0°C). We therefore obtained a time spent feeding for each individual and for each class of T_e. We tested whether time spent feeding differed between sexes and between classes of T_e using ANOVAs. We performed multiple comparisons between classes of T_e using *post hoc* tests.

4.4. Results

Meteorological conditions

The mean T_a (± SE) measured outside dens between 15 December and 15 April was –7.1 ± 0.7°C in 2004 and –7.3 ± 0.6°C in 2005. The mean wind speed (± SE) was 2.35 ± 0.09 m/s and 2.42 ± 0.09 m/s respectively in 2004 and 2005. We did not calculate the mean net radiation between 15 December and 15 April because of sampling interruptions both in 2004 and 2005. The mean T_a (± SE) inside the nine dens sampled was –4.6 ± 0.3°C in 2005 (not measured in 2004). Air temperature remained higher inside than outside dens as long as the outside T_a was below –2.4°C (Fig. 4.1), a condition encountered during most of the winter.

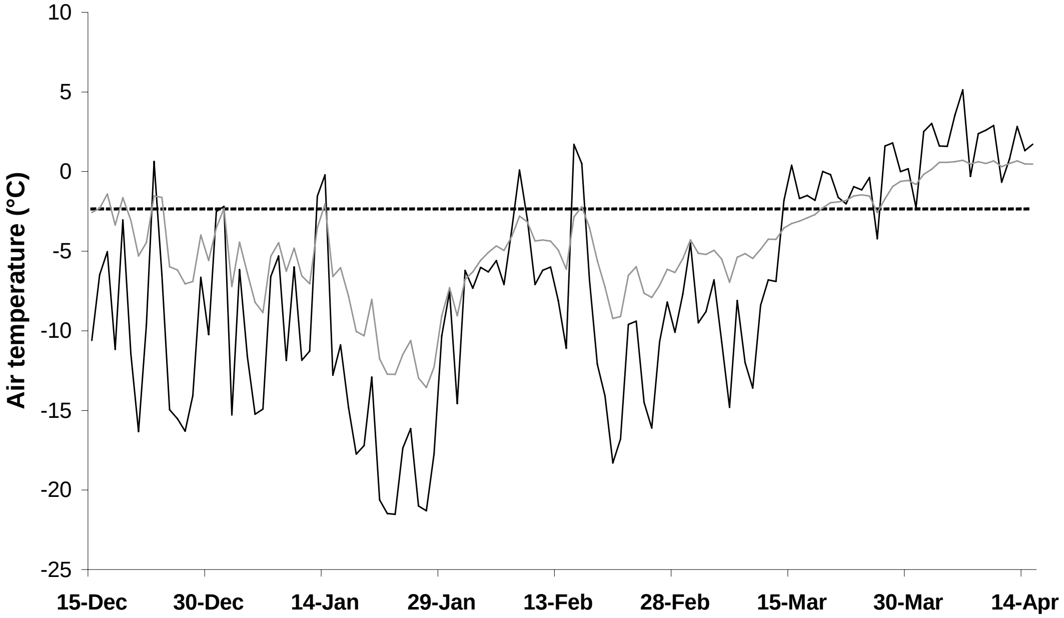

Figure 4.1 : Mean daily air temperature (°C) measured outside (black solid line) and inside (grey solid line) nine porcupine dens, Parc National du Bic, Québec, 15 December 2004-14 April 2005. Black dashed line indicates the mean outside temperature (-2.4°C) above which temperature inside the den became lower than outside temperature.

Thermal mapping

We found no difference in the power necessary to maintain the inner temperature of the two taxidermic mounts exposed to similar thermal environments (Appendix 2, paired t-test, t = -0.80, df = 45, p = 0.426) so data from both mounts were pooled in analyses. Operative temperature had a general negative effect on the power consumed by mounts (Appendix 3, Table 4.1). In the full model including the six initial microhabitats, we found that T_e interacted with the microhabitat to influence the power consumed by the mounts (Table 4.1 model 1). This means that ranking of microhabitats (from microhabitat of best "thermal quality" to microhabitat of worst "thermal quality") was not the same at cold and warm T_e.

Table 4.1 : Linear mixed effect models for the power consumed by porcupine mounts exposed to available conditions of operative temperature (T_e), Parc National du Bic, Québec, December to March 2004-2005. We first tested for an effect of T_e, microhabitat, and T_e×microhabitat. We removed non-significant (NS) interactions between T_e×microhabitat from final models. When testing the effect of microhabitat, we first considered all microhabitats sampled (i.e. "*den*", "*ground open*", "*ground covered*", "*deciduous*", "*conifer open*", "*conifer covered*": model 1). Then we grouped certain microhabitats and compared effects of groups of microhabitats ("den" vs non-den microhabitats: model 2; arboreal vs terrestrial: model 3; open vs covered: model 4). The type and number (n) of measures considered for analysis are specified

Model	Categories of microhabitat	Measures considered	T_e	Microhabitat	T_e×microhabitat
1	6 : initial categories	All n = 883	$F_{(1,808)} = 48.75$ $p<0.001$	$F_{(5,808)} = 1.75$ $p = 0.120$	$F_{(5,808)} = 4.29$ $p<0.001$
2	2 : "*den*" vs non-den	All n = 883	$F_{(1,813)} = 73.36$ $p<0.001$	$F_{(1,813)} = 3.90$ $p = 0.049$	NS
3	2 : arboreal vs terrestrial	Non-den n = 791	$F_{(1,725)} = 77.07$ $p<0.001$	$F_{(1,725)} = 0.11$ $p = 0.742$	$F_{(1,725)} = 12.71$ $p<0.001$
4	2: open vs covered	Non-den n = 791	$F_{(1,725)} = 62.75$ $p<0.001$	$F_{(1,725)} = 8.18$ $p = 0.004$	$F_{(1,725)} = 10.93$ $p = 0.001$

When comparing "*den*" to the non-den microhabitats, power consumption was generally lower inside than outside dens (Table 4.1 model 2, Table 4.2), and this did not change with T_e. This means that the den was the microhabitat offering the best microclimate for the range of T_e we considered. However, we did not measure power consumption inside dens when T_e>0°C (Table 4.2). When comparing arboreal to terrestrial microhabitats, power consumed by mounts was generally lower in terrestrial than in arboreal microhabitats (Fig. 4.2a) although the difference was non significant (Table 4.1 model 3). Also, T_e interacted with the microhabitat to influence the power consumed by the mounts, with the result that the power consumption increased more slowly in terrestrial than in arboreal microhabitats (Table 4.1 model 3) when T_e decreased. Finally, when comparing open and covered microhabitats, the power consumed by mounts was generally lower in covered than in open microhabitats (Table 4.1 model 4, Fig. 4.2b). However, T_e interacted with the microhabitat to influence the power consumed by the mounts so that the power consumption increased more slowly in open than in covered microhabitats (Table 4.1 model 4) when T_e decreased. At cold temperatures (T_e<-19.9°C), the power consumed in arboreal or open microhabitats was about 25% higher than the power consumed inside dens (Fig. 4.2).

Table 4.2 : Power consumed (in Watts, mean ± SE) by porcupine mounts exposed to available conditions of operative temperature and placed in "*den*" and non-den microhabitats, Parc National du Bic, Québec, December to March, 2004-2005. Means were calculated by first averaging the measurements obtained for a given microhabitat and day, and then between days for each group of microhabitats. Samples sizes are specified as (number of days, number of measurements). Power consumed in non-den microhabitats is also given as a percentage of power consumed in "*den*"

T_e (°C)	Den (W)	Non-den (W)	Non-den (% den)
<-19.9	42.1 ± 0.0 (1, 1)	49.1 ± 2.7 (5, 20)	116.6
-19.9 to –15.0	42.0 ± 0.0 (1, 3)	49.6 ± 1.4 (18, 76)	118.1
-14.9 to –10.0	38.1 ± 2.1 (3, 38)	46.2 ± 0.7 (39, 219)	121.3
-9.9 to –5.0	35.7 ± 1.4 (3, 28)	42.7 ± 1.0 (30, 261)	119.6
-4.9 to 0.0	37.1 ± 1.1 (3, 22)	37.9 ± 0.8 (27, 152)	102.2
>0.0	37*	37.5 ± 1.9 (9, 63)	101.4

*As we had no measure of power consumed in den for Te>0°C, we used this value as an approximation for calculating power consumed in non-den microhabitats as a percentage of power consumed in "*den*"

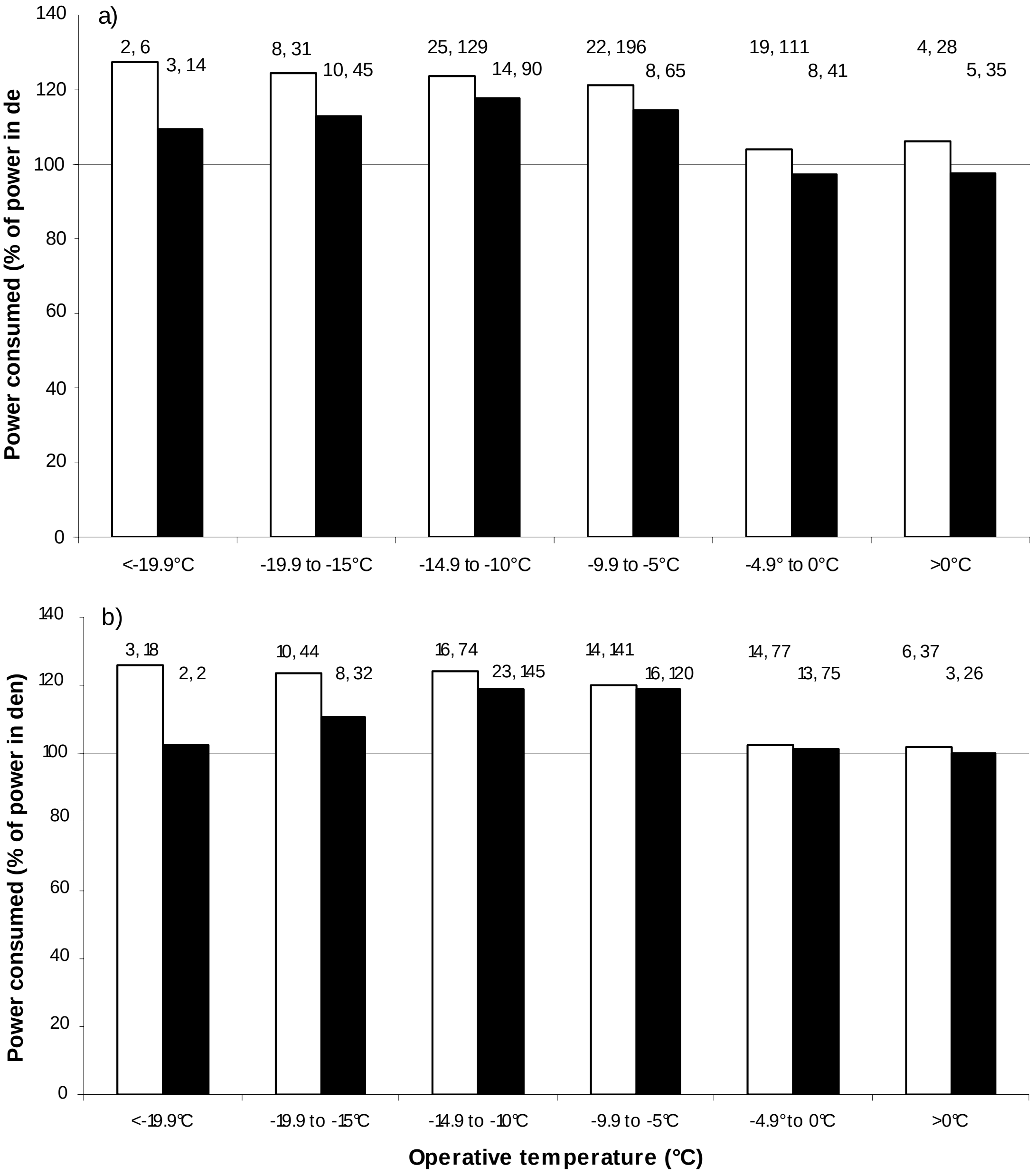

Figure 4.2 : Power consumed by porcupine mounts exposed to available conditions of operative temperature and placed in non-den microhabitats, Parc National du Bic, Québec, December to March, 2004-2005. Means for non-den microhabitats are shown as a percentage of power consumed in "*den*" (from Table 4.2). Sample sizes are specified above the bars as: number of days for which data was obtained, total number of measurements on those days. **a)** In arboreal ("*conifer open*", "*conifer covered*" and "*deciduous*" pooled, white bars) and terrestrial microhabitats ("*ground open*" and "*ground covered*" pooled, black bars). **b)** In open ("*conifer open*", "*deciduous*" and "*ground open*" pooled, white bars) and covered microhabitats ("*ground covered*" and "*coniferous covered*" pooled, black bars).

Calculating T_e from T_a, wind speed and net radiation

The final model explaining variations in T_e included effects of T_a ($F_{(1,120)} = 700.4$, $p<0.001$), wind speed (as a square root, $F_{(1,120)} = 18.5$, $p<0.001$), and net radiation ($F_{(1,120)} = 14.5$, $p<0.001$). The equation used to recalculate T_e was:

$$T_e = -3.637 + 1.050 * T_a + 1.576 * \sqrt{Wind} + 0.007 * NetRadiation \qquad (3)$$

with T_e and T_a in °C, wind speed in m/s, and net radiation in Watts. We calculated the percent of variance in T_e explained by this equation (Pseudo R^2) as:

$$PseudoR^2 = 1 - \frac{\sum_i (y_i - \hat{y}_i)^2}{\sum_i (y_i - \bar{Y})^2} = 0.89 \qquad (4)$$

with y_i the observed value for observation *i*, $\hat{y}_i$ the predicted value for observation *i*, and $\bar{Y}$ the mean of all observed values.

Activity patterns

Time spent outside of the den

Mean time spent outside of the den was 6.7 ± 0.5 h (range: 3.3 to 10.2 h, n = 14 individuals and 690 observations). The final model explaining time spent outside included a quadratic effect of T_e, effects of several non thermal variables (year, sex, Julian date, and snow penetrability) and two first-order interactions with sex (T_e×sex and snow penetrability×sex). Time spent outside increased with T_e ($F_{(1,669)} = 29.15$, $p<0.001$), increased more with T_e at higher T_e ($F_{(1,669)} = 12.23$, $p<0.001$) and increased more with T_e for male than for female porcupines ($F_{(1,669)} = 29.22$, $p<0.001$, Fig. 4.3).

Overall, females spent 25% less time outside dens than males ($F_{(1,12)} = 17.49$, $p = 0.001$, Fig. 4.3). Time spent by porcupines outside dens increased with Julian date ($F_{(1,669)} = 29.16$, $p<0.001$), but decreased with snow penetrability ($F_{(1,669)} = 32.89$, $p<0.001$). The interaction between snow penetrability and sex arose because females were less sensitive to changes in snow penetrability: an increase in snow penetrability had a more negative effect on time spent outside by males than by females ($F_{(1,669)} = 6.47$, $p = 0.011$).

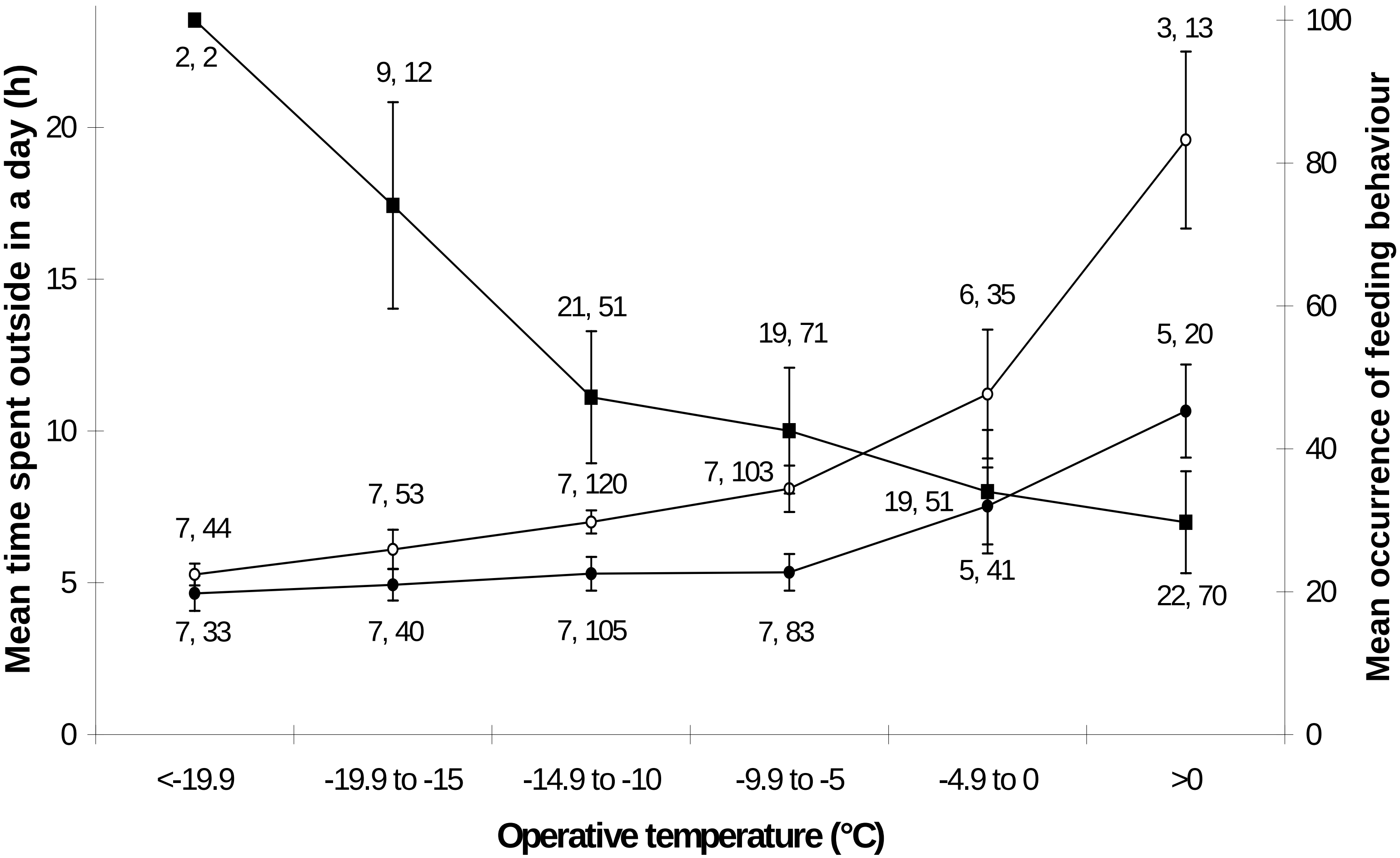

Figure 4.3 : Time spent outside of a den (mean ± SE) in a day for male (open circles) and female (filled circles) North American porcupines and occurrence of feeding behaviour (mean ± SE) when in a coniferous tree (filled squares: males and females pooled since difference between sexes was not significant) as a function of operative temperature, Parc National du Bic, Québec, January to April, 2004-2005. Sample sizes are specified near each symbol as: number of individuals, number of observations on those individuals.

Number and duration of activity bouts

Mean number of activity bouts was 1.40 ± 0.07 (range: 1.07 to 1.91, n = 14 individuals and 679 observations) and the mean duration of activity bouts was 5.0 ± 0.4 h (range: 2.8 to 7.3 h, n = 14 individuals and 966 observations). Number of activity bouts increased when T_e decreased ($F_{(1,664)} = 20.59$, $p<0.001$, Table 4.3) but was not affected by other variables.

The duration of activity bouts was dependent on year, Julian date, snow penetrability, T_e, and T_e×sex. The duration of activity bouts increased with increasing T_e ($F_{(1,946)} = 55.91$, $p<0.001$) and increased more with T_e for male than for female porcupines ($F_{(1,946)} = 17.95$, $p<0.001$, Table 4.3). Activity bouts also lengthened with Julian date ($F_{(1,946)} = 12.89$, $p<0.001$), but shortened when snow penetrability ($F_{(1,946)} = 20.54$, $p<0.001$) increased.

Nocturnality

The mean index of nocturnality was 0.93 ± 0.14 (range: 0.15 to 1.94, n = 14 individuals and 676 observations). This corresponds to 47% of porcupines' active time that was during the night. The nocturnality index was dependent on T_e, Julian date, and snow penetrability. Porcupines were increasingly diurnal when T_e decreased ($F_{(1,659)} = 33.18$, $p<0.001$, Table 4.3) and when Julian date ($F_{(1,659)} = 70.72$, $p<0.001$) and snow penetrability ($F_{(1,659)} = 16.94$, $p<0.001$) increased.

Table 4.3 : Number of activity bouts in a day (mean ± SE), duration of activity bouts (in hour, mean ± SE), and relative distribution of activity between day and night (nocturnality index: between 0: totally diurnal and 2: totally nocturnal, mean ± SE) as a function of operative temperature for North American porcupines, Parc National du Bic, Québec, January to April, 2004-2005. Samples sizes are specified as (number of individuals, number of observations)

T_e (°C)	Number of activity bouts	Duration of activity bouts (males, h)	Duration of activity bouts (females, h)	Nocturnality index
<-19.9	1.61±0.11 (14, 80)	3.4±0.5 (7, 78)	2.6±0.3 (7, 69)	0.94±0.13 (14, 76)
-19.9 to -15	1.43±0.09 (14, 94)	4.4±0.6 (7, 85)	3.5±0.3 (7, 64)	0.92±0.15 (14, 92)
-14.9 to -10	1.38±0.08 (14, 221)	5.0±0.5 (7, 146)	4.0±0.3 (7, 126)	0.88±0.16 (14, 223)
-9.9 to -5	1.37±0.08 (14, 184)	7.0±0.9 (7, 132)	4.3±0.3 (7, 101)	1.01±0.16 (14, 182)
-4.9 to 0	1.27±0.09 (11, 72)	6.8±1.0 (7, 44)	5.6±0.5 (7, 77)	0.92±0.17 (11, 70)
>0	1.29±0.13 (7, 28)	10.1±1.8 (6, 23)	6.9±1.8 (5, 21)	1.06±0.18 (8, 33)
All	1.40±0.07 (14, 679)	5.7±0.6 (7, 508)	4.2±0.2 (7, 458)	0.93±0.14 (14, 676)

Microhabitats used outside of the den

Effects of T_e

Within coniferous trees, T_e had no effect on the microhabitat used by porcupines ($F_{(1,230)} = 0.05$, $p = 0.818$), on their height in tree ($F_{(1,230)} = 0.10$, $p = 0.749$), or on their distance to the trunk ($F_{(1,230)} = 2.93$, $p = 0.088$). However, T_e had an effect on the foraging behaviour of porcupines ($F_{(1,230)} = 10.66$, $p = 0.001$), with occurrence of feeding increasing at low temperatures (Fig. 4.3).

Factors explaining feeding behaviour

Mean occurrence of feeding in coniferous trees was 39.3 ± 5.0% (range: 0.0 to 80.0%, n=26 individuals and 257 observations). Occurrence of feeding was best explained by a model including T_e, microhabitat used, and height of the porcupine in the tree. As described above, occurrence of feeding increased when T_e decreased ($F_{(1,228)} = 11.37$, $p<0.001$, Fig. 4.3). The occurrence of feeding also increased when porcupines were in a "*conifer open*" compared to a "*conifer covered*" microhabitat ($F_{(1,13)} = 5.13$, $p = 0.041$) and when they were in the higher part compared to the middle part of the tree ($F_{(1,21)} = 4.62$, $p = 0.043$). Occurrence of feeding was 38% higher when they were in open than in covered microhabitats (open: 51.0 ± 9.9%, n = 14 individuals and 50 observations; covered: 37.0 ± 4.7%, n = 26 individuals and 207 observations) and 39% higher when they were in upper than in middle canopy (upper: 48.1 ± 5.9%, n = 25 individuals and 138 observations; middle: 34.6 ± 6.3%, n = 23 individuals and 119 observations).

Time spent feeding

Males spent more time feeding than female porcupines ($F_{(1,73)} = 12.135$, $p = 0.001$, Fig. 4.4), both of which spent more time feeding at $T_e<–20°C$ than when T_e was between 0 and –14.9°C (Fig. 4.4, $p<0.001$, $p<0.001$ and $p = 0.003$ for time spent feeding at $T_e<–20°C$ compared to time spent feeding at $–14.9≤T_e<–10°C$, $–9.9≤T_e<–5°C$, $–4.9≤T_e<0°C$, respectively, *post hoc* tests using LS means).

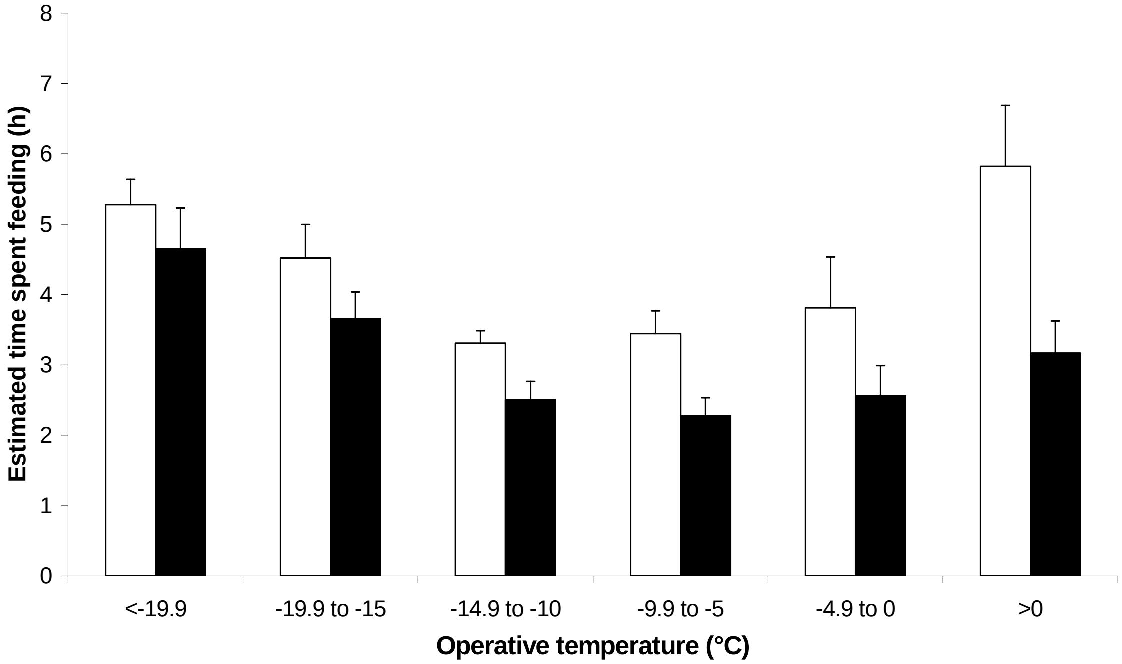

Figure 4.4 : Estimated time spent feeding (mean ± SE) in a day for male (white bars) and female (dark bars) North American porcupines, Parc National du Bic, Québec, January to April, 2004-2005. Time spent feeding was estimated for each individual and class of operative temperature (T_e) and then averaged for males and females for each class of T_e.

4.5. Discussion

Estimated energy expenditure differed across microhabitats for a given T_e and the relationship between energy expenditure and microhabitat varied with T_e. In other words, ranking of microhabitats from microhabitat offering the best, to microhabitat offering the worst thermal environment was not the same at cold and warm T_e. Dens offered the best protection against cold temperatures. Porcupines altered their patterns of den use and foraging behaviour according to T_e. When T_e decreased, they reduced the time spent outside of the den, increased the number of activity bouts per day, reduced the duration of activity bouts, became more diurnal, and increased feeding intensity. Activity patterns also varied with snow conditions. Outside of the den, porcupines did not modify their microhabitat use according to T_e. Rather, they used microhabitats according to their activities: they exploited open microhabitats and top of trees for feeding and covered microhabitats and bottom of trees for resting. Porcupines also showed sex differences in their patterns of habitat use.

Thermal mapping

When studying the physiological consequences of habitat selection, the first step is to establish a map of the microclimates available in a habitat (Huey 1991). Our thermal mapping showed that for a given T_e measured in the stand, different microhabitats resulted in different microclimates. Furthermore, the quality of one microhabitat relative to the others was not the same at cold and warm $T_{e,}$ so that the thermal map was variable both in space and time. In such an heterogeneous environment, porcupines should constantly adjust behaviour to minimize energy expenditure. The main contrast we observed was between den and non-den microhabitats. The difference was mainly due to the higher and less variable T_a observed inside than outside dens for most of the winter. According to our measures of power consumption, porcupines should reduce metabolic rate by about 25% when moving from a tree to their den at T_e=-20°C. Den use is known as an energy-saving strategy for species exposed to cold conditions (Prestrud 1991, Clark et al. 1997, Zimmerling 2005) but we are not aware of previous studies estimating energy saved when using a den in field conditions (but see Scantlebury et al. 2006). Reducing energy expenditure by using a den in cold conditions certainly helps porcupines to maintain their energy balance during the winter and this may be why pattern of den use is at the centre of their behavioural thermoregulation strategy (see below). Outside of the den, energy expenditure was overall higher in open compared to covered microhabitats and in arboreal compared to terrestrial microhabitats. Porcupines should therefore use terrestrial and covered microhabitats when feeding outside of their den if they were to minimize thermoregulatory costs.

Activity patterns

Thermal conditions influenced activity patterns of porcupines. The time spent outside of the den decreased as the operative temperature got colder, and porcupines tended to exit their den for several short rather than one long time period when the cold stress increased. Several species have been shown to use plurimodal activity patterns to avoid temperature extremes (Turk & Arnold 1988, Sharpe & Van Horne 1999, Jedrzejewski et al. 2000), with subsequent decreases in activity time. Thermal constraints appear to limit the time available for above ground activity and porcupines compensated this reduction in time spent outside by increasing feeding rate when T_e decreased. Another constraint that leads animals to reduce the time spent in activity is predator avoidance (Lima & Dill 1990, Kie 1999, Ripple &

Beschta 2004). Predation rates were high on porcupines during the two years of study and predation on adults was linked to the presence of snow covering the ground (chap. 3). We observed porcupines reducing the time spent outside of the den and the duration of activity bouts when snow penetrability increased. We suggest porcupines lowered exposure to predators by reducing the time spent outside of the den when snow penetrability, and therefore predation risk, was high.

Besides reducing the time spent outside of the den, porcupines also became more diurnal with decreasing T_e. North American porcupines and rodents from the Hystricidae family are known to be essentially nocturnal (Roze 1989, Roll et al. 2006). However, only 47% of porcupines' active time was during the night and porcupines were more diurnal at cold temperatures. Rodents living in cold environments are more likely to be diurnal, possibly because they exploit the warmer hours of the diel cycle (Roll et al. 2006). Still, diel activity patterns are phylogenetically constrained (Roll et al. 2006). Hence, being cathemeral (i.e. being active during both day and night, Tattersall 1987, Tattersall 2006) may represent the best compromise nocturnal animals like porcupines can make to avoid exposure to cold night temperatures. Porcupines also became more diurnal when snow penetrability increased and one hypothesis is that being active during the daytime reduced the likelihood of encountering predators (Bakker et al. 2005).

As we could expect from our thermal map, using a den was at the basis of porcupines' behavioural thermoregulatory strategy. Porcupines modified the time spent outside of the den and the timing of activity according to T_e, and this may allow huge energy savings (this study, Humphries et al. 2005).

Microhabitats used outside of the den

Outside their dens, porcupines mainly used coniferous trees. Operative temperature did not influence microhabitat use once porcupines were inside coniferous trees. Rather, the microhabitat choice varied with the behaviour of the animal: porcupines preferentially exploited open microhabitats and tops of trees for feeding and covered microhabitats and bottoms of trees for resting. According to our thermal map, energy expenditure was generally higher in open and arboreal than in other microhabitats. Feeding sites therefore did not appear to be chosen based on the protection they offered against the thermal environment. We generate the testable hypothesis that porcupines fed on tops of trees because they offered the most beneficial food. Leaf chemistry varies with light exposure in the tree canopy (Hirose et al. 1989, Close et al. 2005) and open habitats and tops of trees receive more light than other habitats. By feeding there, porcupines may access needles with higher nitrogen or energy content, and therefore make the best of a bad job to acquire profitable food even if this implies trading off nutrition against thermoregulation (Torres-Contreras & Bozinovic 1997). Alternatively, but not exclusively, porcupines may forage on tops of trees because it lowers probability of detection by predators.

Time spent feeding

Feeding time generally increased with decreasing T_e, probably because energy requirements increased with thermal stress (Systad & Bustnes 2001). A non exclusive hypothesis would be that porcupines' foraging abilities were lower at extreme temperatures (Bozinovic & Vasquez 1999) which increased the time spent searching or handling food. As discussed above, porcupines increased feeding time at low T_e by intensifying feeding rate rather than by spending more time outside. We therefore believe that cold temperatures did not limit foraging abilities of porcupines, contrary to what Bozinovic and Vasquez (1999) showed for degus (*Octodon degus*) exposed to hot temperatures.

Sex differences

At cold temperatures (T_e<-19.9°C) there was no difference between sexes in the mean time spent outside of the den. Both males and females spent about five hours outside and fed for most of their time. When T_e increased, males increased their time spent outside faster than females. In fact, females hardly increased time spent outside before T_e>-5°C (i.e. $T_e \approx$ estimated T_{lc} for porcupines in southern Québec). Why males started to increase time spent outside before females was unclear. Males, having a higher body size, may be better protected than females against cold temperatures (Scholander et al. 1950a, McNab 1970) and may therefore have lower T_{lc} than females. At T_e>-5°C, females started increasing time spent outside but males still spent 49 to 84% more time outside compared to females. This difference in time spent outside may create sex differences in predation risk. Indeed, if being outside increases probability of being detected and/or killed by a predator (Lima & Dill 1990, Blumstein 1998), then males were exposed to higher predation risk than females. We found that an increase in snow penetrability had a more negative effect on the time spent outside by males than by females. As said before, predation risk appears to be linked to snow conditions in our population (chap. 3). Males may then lower exposure to predation by reducing the time spent outside of the den when snow penetrability, and hence predation risk, is high.

Male and female porcupines showed differences in their patterns of activity and this may reflect the different constraints that they are faced with. Females being of smaller size appear to minimize the time spent outside because of thermal constraints while males seem more constrained by predation risk. Our study therefore illustrates that behaviour of generalist herbivores during winter may be constrained not only by thermal conditions, but also by constraints on food acquisition and predation risk. We also demonstrate that microclimates vary greatly from one microhabitat to another and that porcupines appear to use microhabitats to both reduce energy expenditure while resting and maximize energy intake while feeding.

4.6. Complément d'information

L'un des objectifs de ce doctorat était d'examiner si le patron d'activité des animaux et leur utilisation de l'habitat avaient un impact sur leur survie. Pour cela, nous avons calculé les valeurs moyennes d'utilisation de l'habitat pour chaque individu et avons utilisé ces valeurs individuelles pour tenter d'expliquer la survie des animaux au cours de l'hiver.

Indicateurs individuels d'utilisation de l'habitat

D'abord, nous avons calculé pour chaque individu le temps moyen passé dehors en 24 h, la durée moyenne des sorties, le nombre moyen de sorties en 24 h, l'indice de nocturnalité moyen (Tableau 4.4) au mois de février 2004 (n = 11 individus) et au mois de février 2005 (n = 6 individus). Ensuite, nous avons calculé les pourcentages moyens de fois où chaque individu était observé : en train de s'alimenter, en haut d'un arbre, en milieu ouvert (Tableau 4.5) au mois de février 2004 (n = 21 individus) et au mois de février 2005 (n = 5 individus). Nous avons calculé les moyennes pour le mois de février car c'est un mois où nous avions des données sur tout le mois pour la plupart des individus (deux individus sont morts au cours du mois, respectivement le 10 et le 27 février).

Ensuite, nous avons testé si les individus différaient dans leur patron d'activité et utilisation de l'habitat (Tableau 4.4, Tableau 4.5). Pour ça, nous avons utilisé des modèles linéaires généralisés dans SAS version 9.1. (SAS 2002) avec l'identité des animaux en variable explicative et les variables décrivant le patron d'activité et l'utilisation de l'habitat (e.g. temps dehors, occurrence d'un animal en milieu ouvert) comme variables dépendantes (dans des analyses séparées). Finalement, nous avons utilisé les variables où les animaux présentaient des différences individuelles significatives comme variables expliquant la survie, en se servant des moyennes individuelles dans les analyses de survie.

Tableau 4.4 : Temps moyen passé dehors en 24 h (h), durée moyenne des sorties (min), nombre moyen de sorties en 24 h et indice de nocturnalité moyen (0 : activité totalement diurne, 2 : activité totalement nocturne) pour les porcs-épics d'Amérique suivis en février 2004 et février 2005 au Parc National du Bic, Québec, Canada. Les seuils de signification pour les différences entre individus dans l'utilisation de l'habitat sont indiqués par * (p<0.05), ** (p<0.01), et *** (p<0.001)

	Temps dehors***	Durée sorties***	Nbre sorties***	Nocturnalité***
Février 2004				
A	7.6	358	1.30	1.58
B	9.9	475	1.25	1.94
C	11.7	647	1.25	0.58
D	6.6	285	1.39	0.21
E	5.7	213	1.58	1.92
F	8.6	340	1.57	0.79
G	6.7	365	1.10	0.56
H	5.0	233	1.26	1.23
I	3.7	189	1.18	0.81
J	6.4	192	1.97	1.47
K	5.4	300	1.07	0.04
Février 2005				
A	5.1	250	1.33	0.32
B	4.7	133	2.13	1.15
C	4.8	155	1.80	0.97
L	8.1	451	1.07	0.52
M	6.4	302	1.40	0.32
N	3.2	165	1.55	1.97

Tableau 4.5 : Pourcentage d'observations où l'animal est en train de s'alimenter (%), où l'animal est au sommet d'un arbre (%), où l'animal est en milieu ouvert (%) lorsqu'il se trouve à l'extérieur de sa tanière, et temps de survie (jours) à partir du 1er janvier pour les porcs-épics d'Amérique suivis en février 2004 et février 2005 au Parc National du Bic, Québec, Canada. Les différences entre individus dans l'utilisation de l'habitat n'étaient pas statistiquement significatives

	Alimentation	Sommet d'arbre	Milieu ouvert	Survie
Février 2004				
A	37.5	12.5	12.5	106†
B	44.4	66.7	0.0	106†
C	40.0	0.0	0.0	106†
D	33.3	66.7	0.0	106†
E	100.0	50.0	0.0	106†
F	0.0	0.0	0.0	83
G	0.0	100.0	0.0	82
H	66.7	50.0	0.0	106†
I	100.0	50.0	0.0	106†
J	75.0	37.5	12.5	103
K	0.0	100.0	0.0	106†
O	0.0	100.0	0.0	71
P	0.0	100.0	0.0	76
Q	50.0	50.0	0.0	69
R	50.0	75.0	0.0	106†
S	100.0	100.0	0.0	106†
T	0.0	100.0	0.0	40
U	0.0	66.7	0.0	106†
V	33.3	66.7	0.0	106†
W	100.0	100.0	0.0	106†
X	50.0	50.0	0.0	106†
Février 2005				
A	85.7	100.0	42.9	57
B	100.0	100.0	0.0	73
C	100.0	100.0	0.0	62
L	10.0	90.0	30.0	77†
M	40.0	80.0	60.0	68
N	ND	ND	ND	77†

† Temps de survie censuré (i.e. l'animal était encore vivant à la fin de la période de suivi)

Survie

Nous avons calculé le temps de survie des animaux comme le temps entre le 1er janvier et la mort (temps de survie exact) ou entre le 1er janvier et la fin de la période d'étude (15 avril en 2004, 18 mars en 2005, temps de survie censuré). En 2004, nous connaissions la date de mort pour sept des 21 individus suivis et en 2005 pour quatre des six individus suivis (i.e. les autres individus ont survécu). Quand nous trouvions un animal mort nous déterminions la cause de mortalité comme inanition (animal non blessé et maigre), mort par accident routier, mort d'une chute d'arbre (blessé et trouvé sous un arbre), mort par prédation (traces de sang, restes de peau, intestins ou estomac avec ou sans traces de prédateurs) ou mort non naturelle (mort à l'anesthésie ou pendu par son collier dans un arbre). Sur les 11 animaux morts pendant la période d'étude, trois sont morts par inanition, 0 par accident routier, un par chute d'arbre, six par prédation et un de mort non naturelle.

Nous avons analysé la survie en utilisant le modèle de régression à effet proportionnel de Cox (1972). Dans ce modèle la fonction de survie cumulative S(t), qui définit la probabilité de survivre plus longtemps que le temps t (ici en jours), est exprimée comme fonction du risque, qui est la dérivée de la fonction de survie au cours du temps (i.e. la probabilité de mort instantanée).

$$h(t) = dS(t)/dt \qquad (5)$$

Le modèle de régression à effet proportionnel est :

$$h(t) = h_0(t)e[\beta_1x_1+\beta_2x_2+\ldots+\beta_px_p] \qquad (6)$$

où $h_0(t)$ est la fonction de risque de base, β_i sont les coefficients de régression, et x_i sont les variables explicatives. Chaque coefficient de régression est interprété comme pour une régression logistique classique : une augmentation d'une unité dans la variable explicative entraîne une augmentation de $e^{\beta i}$ dans le rapport de risque (*hazard ratio*). Un rapport de risque >1 indique une augmentation de la probabilité de mort instantanée quand la valeur de la variable explicative augmente. Un rapport de risque <1 indique une diminution de la probabilité de mort instantanée quand la valeur de la variable explicative augmente. Les variables que nous avons utilisées pour expliquer la survie sont le temps dehors en 24 h, la durée des sorties, le nombre de sorties par 24 h et l'indice de nocturnalité. Nous avons utilisé SAS version 9.1. (SAS 2002) pour examiner comment ces différentes variables étaient associées avec le temps de survie (procédure PHREG). On ne trouve pas d'effet du temps passé dehors en 24 h ($\chi^2_1 = 0.59$, $p = 0.443$), de la durée des sorties ($\chi^2_1 = 1.52$, $p = 0.217$) ou de l'indice de nocturnalité ($\chi^2_1 = 0.90$, $p = 0.343$) sur la survie. Par contre, on trouve que le nombre de sorties par 24 h influence la survie de façon très marquée et que cet effet est presque significatif au seuil 0.05. En effet, l'examen du rapport de risque montre que sortir une fois de plus chaque jour multiplie par sept la probabilité de mort instantanée ($\chi^2_1 = 3.80$, $p = 0.051$, *hazard ratio* = 8.58).

La principale cause de mortalité des adultes au cours de l'hiver est la prédation et ce résultat suggère que la probabilité de prédation augmente quand les animaux augmentent le nombre de sorties par 24 h. Les porcs-épics passent plus de temps au sol lorsqu'ils font plusieurs sorties dans une journée au lieu d'une et sont probablement plus facilement détectables pour un prédateur lorsqu'ils marchent dans la neige que lorsqu'ils se trouvent au sommet d'un arbre (observations personnelles). Une augmentation du nombre de sorties moyen par 24 h a un effet négatif très important sur la probabilité de survie et c'est sans doute pourquoi les animaux augmentent le nombre de sorties par 24 h quand le stress thermique augmente (i.e. quand la température diminue) mais pas quand le risque de prédation augmente (i.e. quand l'enfoncement dans la neige augmente). On n'observe pas de diminution du nombre de sorties quand le risque de prédation augmente, sans doute parce que les animaux doivent sortir chaque jour au moins une fois pour s'alimenter.

Chapitre 5 Are juvenile porcupines maximizing survival by selecting their microhabitat?

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(à soumettre, *Écoscience*)

Les patrons d'activité des porcs-épics adultes pendant l'hiver semblent varier à la fois en fonction des conditions climatiques et du risque de prédation (chap. 4). Nous examinons ici l'utilisation de l'habitat par les porcs-épics juvéniles pendant l'été afin de déterminer si les animaux utilisent leur habitat de manière à minimiser l'exposition au froid et/ou à la prédation. Comme déjà discuté, le risque de prédation était élevé pendant notre étude (chap. 3) et les juvéniles sont particulièrment vulnérables à la prédation à cause de leur mobilité restreinte et de leur manque d'expérience. Par ailleurs, les juvéniles ont un système de thermorégulation immature et sont sensibles à l'hypothermie. Comme pour les porcs-épics adultes en hiver, les contraintes dues à l'environnement thermique et à la prédation sont donc substantielles pour les juvéniles au cours du premier été. L'utilisation de couvert végétal est réputée fournir une certaine protection contre la prédation. Cependant, la température ambiante est plus basse dans les habitats avec plus de couvert. On montre que les juvéniles utilisent des microhabitats offrant un fort couvert protecteur, et que les juvéniles utilisant les habitats les plus couverts survivent le mieux. Ici encore, on interprète ces différences dans la survie comme des différences dans l'exposition à la prédation, principale cause de mortalité des juvéniles. L'utilisation du couvert à l'extérieur des tanières n'est pas dépendante des conditions de température. Néanmoins, l'utilisation des tanières augmente quand il fait froid et quand il pleut. Comme en hiver, les tanières semblent donc offrir un refuge à la fois contre les prédateurs et contre les conditions thermiques défavorables. L'utilisation de l'habitat permet donc de moduler l'exposition au froid et à la prédation, avec des conséquences positives de l'évitement de la prédation pour la survie des individus.

5.1. Abstract

In many mammals, juveniles are highly vulnerable to predators because of their low mobility and small body size. Use of dense ground cover by juveniles has been assumed to lower predation risk. On the other hand, use of cover during sunny summer days decreases access to radiative heat gain and may be detrimental for juveniles that are sensitive to hypothermia. Studies relating use of cover to survival of juveniles remain infrequent and have been essentially performed on ungulates. We measured habitat selection and monitored survival of 14 North American juvenile porcupines. We tested 1) whether juveniles selected for cover at the microhabitat scale (within 1 m of the animal) and at the local scale (within 15 m), 2) whether use of cover depended on meteorological conditions, and 3) whether use of cover influenced survival. We also examined how sex, body mass, mobility of the juvenile, and distance between juvenile and mother affected survival. Our results indicate that juvenile porcupines selected microhabitats providing high protective cover (microhabitat scale) within areas showing low herb cover (local scale). Use of cover depended on weather, with juveniles using dens to avoid low air temperature and rain. Ten out of 14 juveniles died before the end of the summer and nine out of 10 deaths were due to predation. Habitat use (at both the microhabitat and local scales) influenced survival. At the microhabitat scale, use of protective cover and use of trees enhanced survival compared to use of ground locations. At the local scale, use of sites with high shrub cover enhanced survival. We found no effect of sex, body mass, mobility, and distance to the mother on survival. These results support the hypothesis that predation was the main factor limiting survival of juveniles in our population and that predation risk was modulated by habitat use of juveniles.

Key-words : climate, conditional logistic regression, *Erethizon dorsatum*, hider-follower behaviour, Québec, survival analysis

5.2. Introduction

In large herbivores, juvenile survival is more sensitive to environmental variation than is adult survival (Gaillard et al. 2000, Eberhardt 2002, Gaillard & Yoccoz 2003), and has been reported to play a fundamental role in driving the dynamics of several populations (Coulson et al. 1997, Gaillard et al. 2000). Therefore, identifying the causes of variation in early survival of large herbivores constitutes an important issue in evolutionary ecology, population management, and conservation (Linnell et al. 1995, Gaillard et al. 1998, Gaillard et al. 2000 for reviews). One reason why juvenile survival is highly variable may have to do with predation. Juveniles are highly vulnerable to predation because of their small size, low mobility, and lack of experience (Molinari-Jobin et al. 2004, Hoogland et al. 2006). Newborn mammals are often categorised as followers or hiders depending on their anti-predatory strategy (Lent 1974). In species where juveniles follow their mother, mothers minimize predation risk to their offspring by using habitats with fewer predators or greater opportunities to evade predation (Bleich et al. 1997, Rachlow & Bowyer 1998). For species relying on a hiding behaviour, characteristics of the hiding site may be important in determining protection from predators. For example, it is well documented that ungulate fawns select hiding sites providing large amounts of cover (see review in Mysterud & Ostbye 1999), and presence of cover is believed to lower the risk of predation, either through reduction of the detection probability, or through obstruction from attacks. However, even if it is generally assumed that such habitat selection has important survival consequences, studies relating use of cover to survival of juveniles are rare (but see Linnell et al. 1995, Aanes & Andersen 1996, Canon & Bryant 1997, Farmer et al. 2006).

On the other hand, presence of cover decreases exposure to solar radiation (Demarchi & Bunnell 1993) and some large mammals have been shown to use cover during summer to reduce heat stress (Demarchi & Bunnell 1995, Dussault et al. 2004). For neonates that are sensitive to hypothermia (Doolan & Macdonald 1997, Andersen & Linnell 1998, Gilbert & Raedeke 2004, Olson et al. 2005), use of cover during sunny summer days may be detrimental because it may decrease access to radiative heat gain (Bowyer et al. 1998). In particular, risk of hypothermia increases with decreasing body size because animals with a small body size have a high surface area to volume ratio, which means that they have a high rate of heat loss to the environment (Scholander et al. 1950b, Kreith & Black 1980). Although ungulate hiding fawns select for cover, with possible positive effects on survival, it is therefore unclear whether selection for cover should be beneficial to hiding neonates of smaller body size, that are relatively more susceptible to hypothermia.

In this study, we used North American porcupines (*Erethizon dorsatum*), a medium-sized mammal that relies on a hiding anti-predatory strategy (Roze 1989), to investigate how the use of cover influenced summer survival of juveniles. Juvenile porcupines weigh about 400g at birth and are potentially exposed to both predation and hypothermia. Potential predators of juvenile porcupines include the great horned owl (*Bubo virginianus*), the lynx (*Lynx canadensis*), the bobcat (*Lynx rufus*), the coyote (*Canis latrans*), the wolf (*Canis lupus*), the wolverine (*Gulo luscus*), the mountain lion (*Felis concolor*) and the fisher (*Martes pennanti*) (Roze 1989). Fishers, coyotes, and great horned owls were all regularly observed in our study area, therefore exposing juveniles to a significant predation risk. Yet, juvenile porcupines are born in mid-May when air temperature in our study site may still be as low as 0°C. We thus expected juvenile porcupines to face a clear trade-off between using cover to decrease predation risk and avoiding cover to increase solar heat gain. In such a situation, two scenarios can be proposed. First, if predation is the main factor limiting survival in our population we would expect juveniles to select for cover, and juveniles using the more protective cover to survive better. Second, if hypothermia is the main limiting factor, we would expect juveniles to select areas offering the best thermal environment (i.e. in the daytime, open areas), and juveniles using the more open areas to survive better. We expected predation to be the main factor limiting survival in our population because predation rates on porcupines of all age classes were substantial during the study period, leading to a large decline in the size of our population (chap. 3).

The main goal of our study was to determine whether juvenile porcupines selected for cover (considered at two spatial scales) to avoid predators, and whether use of cover at one or the other scale enhanced survival. We tested the following predictions:

1) selection for cover occurs at both spatial scales because juvenile porcupines are highly vulnerable to predation (Sweitzer & Berger 1992).

2) juveniles are more likely to use open areas under cold conditions. Even though we predicted avoidance of predators to be the main factor driving habitat selection by juveniles, we expected risk of hypothermia to be high on cold days and therefore to influence habitat use on those days. Juvenile porcupines are poorly insulated (Haim et al. 1992) and may be faced with relatively low temperatures during their first weeks of life. We therefore expected them to trade off protection from predators with access to radiative heat gain by using open habitats when sun was shining (i.e. during the daytime) but air temperature was low.

3) individual differences exist in the use of cover and translate into variations in survival probability. As we predicted that predation is the main factor limiting survival and driving habitat use by juvenile porcupines, we expected individuals using relatively covered habitats to survive better than those using more open habitats.

In addition, because factors other than habitat use are known to affect survival either directly or through an increased vulnerability to predation, we tested whether sex (Webb 1993, Aanes & Andersen 1996), body mass (Keech et al. 2000, Côté & Festa-Bianchet 2001), mobility (Daly et al. 1990, Norrdahl & Korpimaki 1998, Yoder et al. 2004) and distance between a juvenile and its mother (Mathisen et al. 2003) influenced summer survival of juveniles.

5.3. Material and methods

Study area and study population

We worked from 1 May to 15 August for two consecutive years (2003-2004) in the Parc National du Bic (48°20'N, 68°46'W, elevation 0-150m), Québec, Canada. The study area is characterized by a rugged topography, abundance of natural rock dens, and a mixed-boreal forest dominated (in order of importance) by quaking aspen (*Populus tremuloides*), eastern white cedar (*Thuja occidentalis*), white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*). The area is fragmented by abandoned and cultivated fields where porcupines feed in summer and where they are easily captured. We worked on a population of individually-marked porcupines monitored each summer since 2000. We fitted adult females with radio transmitters (Lotek SMRC-5RB VHF transmitter, Lotek Wireless Inc., Newmarket, Ontario) at the beginning of spring and searched for juveniles around lactating females (chap. 2). We performed searches in 2003 and 2004 and totalized >240 hours of search. We found 14 juveniles (2003: 10; 2004: 4), fitted them with Holohil VHF transmitters (model R1-2DM 7.5 g, Holohil Systems Ltd., Carp, Ontario) and subsequently followed their habitat use until 15 August. We located juveniles five days a week by following the signal to the animal (homing, see Morin et al. 2005 for details), and recorded their location using UTM coordinates (hand-held Global Positioning System). When approaching juveniles, we carefully listened for any changes in signal regularity and for noises in the woods to determine whether the approached juvenile was moving to escape from us. Juveniles usually didn't move when approached but we removed all observations of disturbed or moving juveniles from analyses (n = 8 observations). Our telemetry effort was concentrated in the daytime (90% of locations were obtained between 9 am and 5 pm). We paid special attention to distribute sampling along the diurnal cycle evenly across individuals.

Study design

Each time we located an animal, we characterized the habitat where the animal was hiding and at a paired random location. For both the animal and the random location, we made one set of measures at the microhabitat scale (within 1 m of the animal or random location) and one at the local scale (within 15 m of the animal or random location). We first determined whether selection for cover occurred at one or both scales to verify our prediction 1. Because the number of observations was low for some animals (mean ± SE: 21 ± 4 observations, range: 2- 47, Table 5.3), we could not determine habitat selection for each individual. Rather, we determined habitat selection for the population, taking into account the pseudo-replication in our analyses (following Fortin et al. 2005, see statistical analyses). To verify our prediction 2, we tested whether the use of cover depended on meteorological conditions using data for the population and again taking pseudo-replication into account (see statistical analyses). Finally, we used mean cover used by individual juveniles (at both scales), sex, body mass on 10 June, mean daily movements, and mean distance to the mother as covariates in survival analyses in order to verify our prediction 3 and test for the effects of sex, body mass, mobility, and distance to the mother on survival time. Below we detail how we implemented this study design.

Habitat selection

When we located a juvenile, we first noted whether it was in a den (usually rock dens), on the ground, or in a tree (at least 30 cm above ground). If the juvenile was in a tree, we recorded the species of the tree and measured its circumference at breast height. Then, we visually estimated (<5%, 5-25%, 25-50%, 50-75%, >75%) the protective cover (vegetation or rock, Mysterud & Ostbye 1999) present within 1 m of the porcupine. Finally, we measured air temperature and wind speed at the animal location using a handheld thermometer-windmeter (TFA 42.6000.06, TFA Dostmann Ltd Co., Germany). At the local scale (15 m-radius), we visually estimated (<5%, 5-25%, 25-50%, 50-75%, >75%) tree, shrub (any woody vegetation between 50 and 150 cm tall), and herb cover (any non-woody vegetation) as well as the species of the dominant tree.

Finally, we sampled in the same manner a random location, located 20 m away from the animal location, in a random direction. We determined the 20 m-distance according to preliminary observations indicating that juveniles made daily movements generally <20 m. Note that we were interested to detect selection of particular trees by juvenile porcupines. Indeed, adult porcupines select quaking aspens for feeding in summer in our study area (Morin et al. 2005) and we wanted to test if juveniles also did. Therefore, when the animal was in a tree, we used a tree as the random location. Conversely, when the animal was located on the ground or in a den, we used a terrestrial location as the random location. One drawback of this sampling strategy however, is that it precluded testing for a selective use of tree or ground locations.

Effects of meteorological conditions on the use of cover

Each time we located a porcupine, we recorded Julian date, air temperature (°C), wind intensity (no wind, leaves agitated, twigs move, branches move, branches bend, whole trees move), and intensity of precipitations in the last 12 hours (no fog, fog, light rain, heavy rain). We first tested if weather influenced the use of den and then, for non-den observations, if weather influenced the percentage of protective cover used at the microhabitat scale.

Individual indicators of habitat use

We first compiled individual indicators of habitat use for descriptive purposes. At the microhabitat scale, we determined the percentage of times a juvenile was in a den, on the ground and in a tree. In addition, we computed the mean protective cover, the mean air temperature and the mean wind speed experienced by each individual. For cover, we assigned values of 0, 25, 50, 75 and 100% of cover to observations that fell respectively in categories <5%, 5-25%, 25-50%, 50-75%, and >75% of cover during the visual evaluation. We also calculated for each juvenile the mean circumference of trees used and the percent use of the following tree species or group of species (Morin et al. 2005): quaking aspen (hereafter called aspen), fruit-bearing trees (serviceberry *Amelanchier sp.*, American mountain-ash *Sorbus Americana,* and pin cherry *Prunus pensylvanica*), other deciduous trees, eastern white cedar (hereafter called cedar), and other coniferous trees (white spruce, balsam fir). At the local scale, we computed the mean tree, shrub and herb cover present in sites used by each individual (using approximations described above) and the percentage of times the dominant tree within 15 m was an aspen, fruit-bearing, deciduous, cedar or coniferous tree.

Second, we tested whether juveniles differed in their use of cover (at both scales) as well as in their use of den, ground and tree locations. Finally, when juveniles showed significant individual differences in use for a given variable, we utilized this variable of habitat use in survival analyses.

Sex, body mass, mobility and distance to the mother

We sexed juveniles by palpating the genital area (Dodge 1982) and weighted them once a week from the date they were found to 15 August. We used body mass as a proxy for age of the individuals as we expected earlier born individuals to be heavier than later born individuals. We chose body mass on 10 June because all juveniles were born on or before that date (range of birth date: 6 May-10 June), and because we measured body mass for 10 of 14 juveniles on that date. For the remaining four individuals, we estimated body mass on 10 June by adding or removing 30 g/day (average daily weight gain in June calculated over all individuals) from the body mass measured on the day closest to 10 June (27 May, 01 June, 01 July, 06 July for these four juveniles). We characterized the mobility of juveniles using the mean distance they moved in a day. We calculated this distance by dividing the total distance (straight line) moved from one location to the next by the number of days elapsed between successive locations. Finally, when we knew the identity of the mother (n = 11), we located it twice a week, just before or after locating its juvenile, in order to calculate the distance between mother and juvenile (m).

Survival

We calculated survival time as the time from birth to death (exact time) or to the end of the study period (15 August, censored time). We estimated date of birth from weight on first capture considering a mean weight gain of 30 g /day. Over 14 juveniles, we knew the exact death time for 10 individuals and death time was censored for the remaining four individuals (i.e. these individuals were still alive at the end of the study period). When we found a dead juvenile, we determined cause of mortality as starvation (not injured, intact carcass), predator killed (traces of blood on radio collar or wounds on the carcass), or unknown.

Statistical analyses

Habitat selection

We built models of habitat selection by comparing used and random locations to obtain Resource Selection Functions (RSF, Manly et al. 2002). RSFs are equations that predict the relative probability of use, taking the form:

$$w(x) = e(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n), \qquad (1)$$

where w(x) is the RSF value, e is the base of the natural logarithm, β_i are the estimated coefficients, and x_i are habitat variables. We used matched case-control or conditional logistic regression (Hosmer & Lemeshow 1989) to estimate coefficients. Each pair of used-random points was defined as a stratum in analyses so that conditional logistic regression compared use with availability in a given pair, which is particularly adapted to studies of microhabitat and/or microclimate selection (Compton et al. 2002). Because we had repeated measurements of habitat use on the same individuals, measurements were not independent. Such correlation does not influence coefficient estimates (β values), but biases their standard errors (Nielson et al. 2002). We used a robust sandwich estimate of the covariance matrix (Lin & Wei 1989, Wei et al. 1989) to obtain robust standard errors of coefficients. For that we defined all observations coming from a given individual as a cluster, pairs of used-random points as a stratum, and analysed our data using SAS software, proc PHREG, version 9.1 (SAS 2002) following Fortin et al. (2005). Each estimated coefficient is interpreted as usual for logistic regression: a one unit increase in an explanatory variable results in a $e^{\beta i}$ increase in the odds ratio. For low-probability events (such as the presence of a juvenile porcupine), the odds ratio approximates the relative risk, i.e. the ratio of the probability of event x (e.g. a porcupine being present) given A to the probability of x given B (Hosmer & Lemeshow 1989, Compton et al. 2002). Because we used a Cox proportional hazards model for regression analyses (also used for survival analyses, see below), we show hazard ratios instead of typical odds ratios. However, interpretation of hazard ratios is similar to interpretation of odds ratio.

Effects of meteorological conditions on the use of cover

Our data set included repeated measurements made on the same individuals at different dates so we fitted mixed effect models with porcupine identity as a repeated factor. We used SAS software, version 9.1 (SAS 2002) to analyse the effects of meteorological covariates on den use (treated as a binary variable: inside-outside den; proc GLIMMIX) and on the percentage of protective cover used (treated as a continuous variable: 0 to 100% of cover; proc MIXED).

Individual indicators of habitat use

We tested for individual differences in habitat use using all observations ($n = 299$ for each variable) and general linear models in SAS software version 9.1. (SAS 2002). We used identity of juveniles as the explanatory variable in all analyses and amount of protective cover, amount of tree, shrub, and herb cover (continuous variables; proc GLM), or use of a den, ground, and tree location (binary variables; proc LOGISTIC) as dependent variables.

Sex, body mass, mobility, and distance to the mother

We calculated mean daily movements of juveniles and mean distance to the mother for May, June, July and August but used overall mean daily movements and overall mean distance to the mother as covariates in survival analyses.

Survival

We analysed juvenile survival using a Cox proportional hazards model (Cox 1972). In the proportional hazards model, the cumulative survival function $S(t)$, which defines the probability of surviving longer than time t (here expressed in days), is expressed as a hazard function, which is the derivative of the survivor function over time (i.e. instantaneous probability of death):

$$h(t) = dS(t)/dt \tag{2}$$

The proportional hazards model is:

$$h(t) = h_0(t)e[\beta_1x_1+\beta_2x_2+\ldots+\beta_px_p] \tag{3}$$

where $h_0(t)$ is the baseline hazard function, e is the base of the natural logarithm, β_i are regression coefficients, and x_i are model covariates. We wanted our covariates to describe the habitat use of each juvenile porcupine as well as its sex, mass on 10 June, mobility, and mean distance to the mother. We used proc PHREG in SAS software version 9.1 (SAS 2002) to examine how these different covariates were associated with survival time. We ran separate analyses for three combinations of response variables: 1) cover used at the microhabitat scale: percentage of protective cover, percent use of den, ground, and tree locations; 2) cover used at the local scale: percentage of tree, shrub and herb cover in sites used; 3) sex, body mass, mobility of the juvenile, and distance to the mother.

5.4. Results

Habitat selection

At the microhabitat scale, selection for dens was obvious because juveniles were using dens in 47% of observations while we never found dens in the random locations we sampled (Fig. 5.1a). Juveniles also selected sites characterized by a high protective cover, low air temperature, and low wind speed (Fig. 5.1a, Table 5.1). The hazard ratios allowed us to quantify this selection and indicate that a 10% increase in protective cover was associated with a 69% increase in selection, that a 1°C increase in temperature was associated with a 21% decrease in selection and that a 0.1 m/s increase in wind speed was associated with a 20% decrease in selection (Table 5.1). When using a tree, juveniles selected large trees but did not significantly use any tree species compared to aspens (Fig. 5.1b, Table 5.1). According to the hazard ratio, a 10 cm increase in the circumference of the tree was associated with a 72% increase in selection (Table 5.1).

At the local scale, juveniles selected areas with low herb cover and with cedar trees as dominant tree species (Fig. 5.2, Table 5.1). The hazard ratios indicate that a 10% increase in herb cover was associated with a 14% decrease in selection and that the presence of cedar as dominant tree species was associated with a 136% increase in selection compared to when aspen was dominant (Table 5.1).

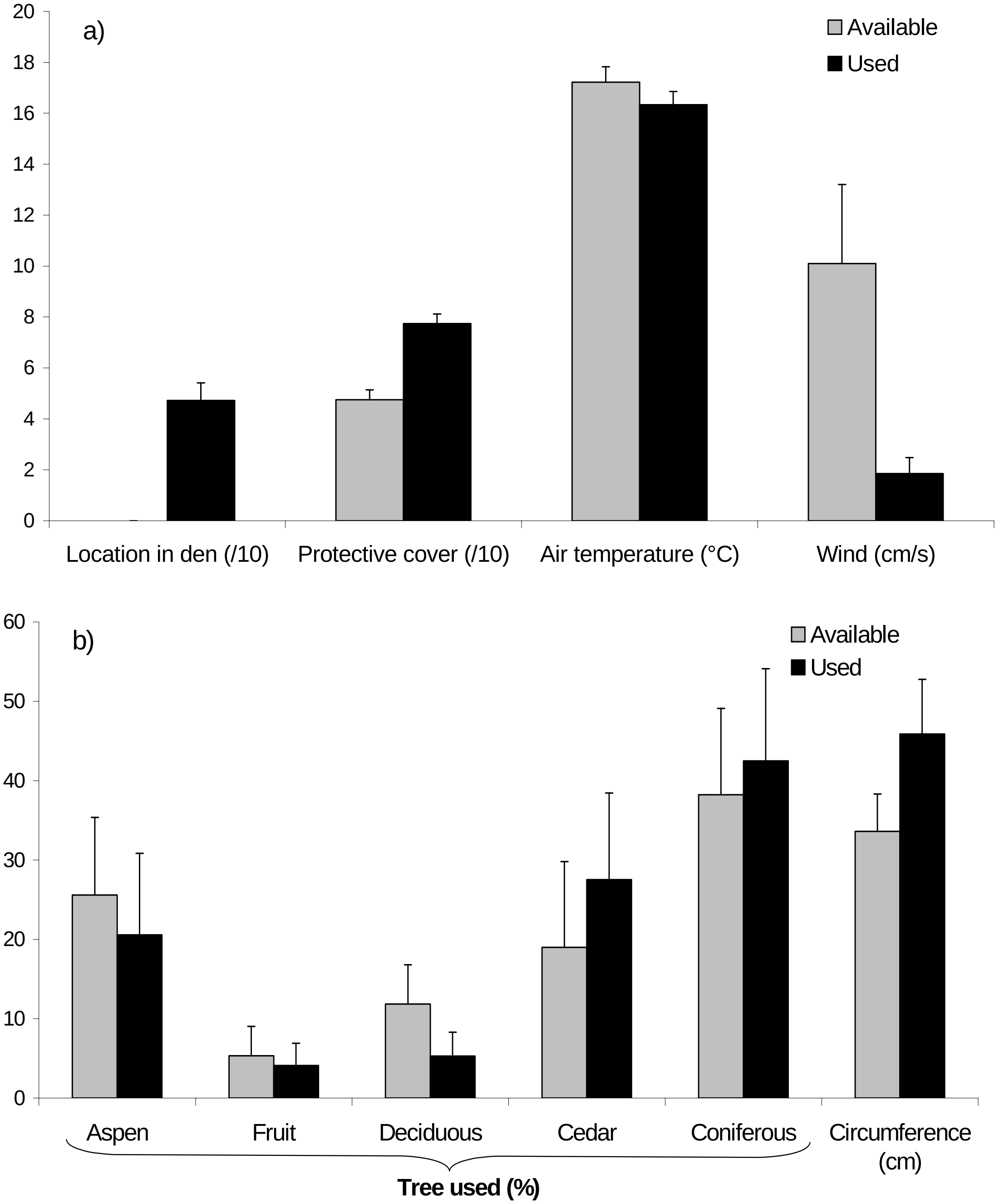


Figure 5.1 : Characteristics of microhabitats measured within 1 m of hiding sites used by 14 juvenile North American porcupines, and at random locations in Parc National du Bic, Québec, May to August, 2003-2004. Results shown are means (± SE) for the population (calculated from individual means). **a)** Proportion of hiding sites that were in a den (/10), proportion of protective cover (/10) around hiding sites, air temperature (°C), and wind speed (cm/s) in the microhabitat (n = 14 individuals and 299 observations for all variables). **b)** Percentage of times the tree used was an aspen, fruit-bearing, other deciduous, cedar, or other coniferous tree Bars to the right show mean circumference (cm) of the tree (n = 10 individuals and 73 observations for all variables).

Table 5.1 : Coefficients for the resource selection functions at the microhabitat (1 m) and local (15 m) scales for hiding sites used by 14 juvenile North American porcupines in Parc National du Bic, Québec, May to August, 2003-2004

Variable	β value	Robust SE	χ^2	P	Hazard ratio
Microhabitat scale					
Percentage cover	0.522	0.042	151.72	<0.001	1.69 (10%)
Air temperature	-0.240	0.064	13.91	<0.001	0.79 (1°C)
Wind speed	-0.228	0.089	6.57	0.010	0.80 (0.1 m/s)
Tree use					
Circumference	0.548	0.099	30.82	<0.001	1.73 (10 cm)
Tree species					
Aspen	0	ND	ND	ND	reference category
Fruit-bearing	0.603	1.085	0.31	0.578	1.83
Other deciduous	-0.978	1.137	0.74	0.390	0.38
Cedar	1.469	0.861	2.91	0.088	4.34
Other coniferous	0.202	0.781	0.07	0.796	1.22
Local scale					
Tree cover	-0.034	0.090	0.14	0.704	0.97 (10%)
Shrub cover	-0.044	0.043	1.04	0.308	0.96 (10%)
Herb cover	-0.150	0.068	4.81	0.028	0.86 (10%)
Dominant tree					
Aspen	0	ND	ND	ND	reference category
Fruit-bearing	-0.679	1.458	0.22	0.641	0.51
Other deciduous	0.237	0.466	0.26	0.611	1.27
Cedar	0.860	0.261	10.85	0.001	2.36
Other coniferous	0.397	0.260	2.32	0.127	1.49

Effects of meteorological conditions on the use of cover

Air temperature was positively correlated to Julian date during summer (Pearson correlation, r = 0.275, p = 0.009, n = 90) so we tested for effects of temperature while correcting for Julian date. Wind intensity and rain intensity in the last 12 hours were both independent of Julian date (Spearman rank correlation, r = -0.136 and 0.025, p = 0.201 and 0.818 respectively, n = 90) so we did not correct for Julian date when testing for effects of wind and rain.

The probability that juveniles were outside their den increased with Julian date ($F_{(1,284)}$ = 5.29, p = 0.022), and also with air temperature (Table 5.2), even after taking Julian date into account ($F_{(1,283)}$ = 16.99, p<0.001). The probability that juveniles were outside their

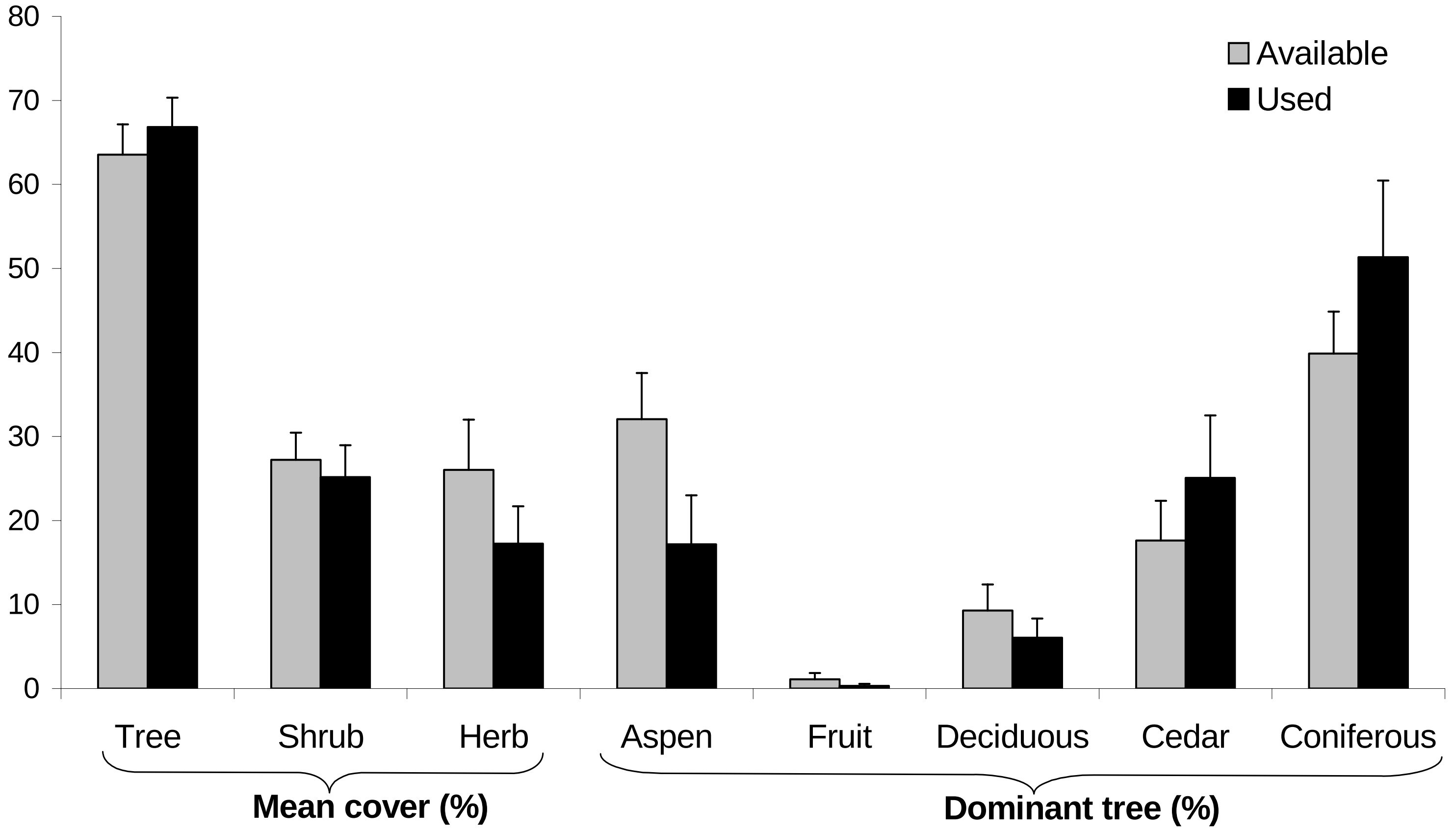


Figure 5.2 : Characteristics of vegetative cover within 15 m of hiding sites used by 14 juvenile North American porcupines compared to vegetative cover available at random locations, in Parc National du Bic, Québec, May to August, 2003-2004. From left to right: percentage of tree, shrub and herb cover present on the site, and mean percentage of times the dominant tree species was an aspen, fruit-bearing, other deciduous, cedar, or other coniferous tree (n = 14 individuals and 299 observations for all variables). Results shown are means (± SE) for the population (calculated from individual means).

den also increased with wind intensity (Table 5.2, $F_{(1,284)} = 5.11$, $p = 0.025$), and with decreasing rain intensity in the last 12 hours (Table 5.2, $F_{(1,284)} = 4.21$, $p = 0.041$).

Outside of the den, juveniles decreased the amount of cover used as Julian date increased ($F_{(1,135)} = 9.79$, $p = 0.002$) and with increasing rain intensity in the last 12 hours (Table 5.2, $F_{(1,135)} = 5.35$, $p = 0.022$). There was no effect of temperature ($F_{(1,134)} = 1.23$, $p = 0.270$) or of wind intensity ($F_{(1,135)} = 0.20$, $p = 0.653$) on the amount of cover used (Table 5.2).

Table 5.2 : Use of den (% of locations in den) and use of cover when outside of the den (mean % of protective cover) as a function of meteorological conditions for 14 juvenile North American porcupines in Parc National du Bic, Québec, May to August, 2003-2004. We considered wind to be present when tree leaves were agitated and rain to be present when at least a light rain was falling (see methods). Sample sizes (N) represent number of individuals and number of observations

	Use of den		Use of cover	
	Mean ± SE	N	Mean ± SE	N
Air temperature				
>15°C	61 ± 10	12, 65	68 ± 7	9, 21
15-19°C	54 ± 7	13, 106	55 ± 6	12, 50
20-24°C	42 ± 12	10, 105	63 ± 4	9, 63
≥25°C	27 ± 11	8, 23	70 ± 9	8, 16
Wind				
No wind	61 ± 8	13, 112	63 ± 4	11, 47
Wind	45 ± 6	13, 187	61 ± 5	13, 103
Rain in the last 12 h				
No rain	50 ± 8	13, 192	68 ± 5	12, 103
Rain	55 ± 9	14, 107	56 ± 6	12, 47

Individual indicators of habitat use

We found juveniles inside dens, on the ground, and in a tree 47%, 26% and 27% of the times we located them, respectively. Individuals significantly differed in their use of den, tree, and ground locations (Table 5.3). On average, juveniles used microhabitats providing 77% of protective cover but individuals significantly differed in the mean protective cover they used (Table 5.3). The amount of protective cover was negatively correlated to the air

Table 5.3 : Use of cover by juvenile North American porcupines at the microhabitat (1 m) and local (15 m) scales in Parc National du Bic, Québec, May to August, 2003-2004. Results are reported as the mean for each individual (A to N) and for the population (mean calculated from individual means). Levels of significance for between-individual differences in habitat use are indicated as * ($p<0.05$), ** ($p<0.01$), and *** ($p<0.001$)

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	Mean
Observations (n)	5	3	46	13	33	3	18	8	30	47	38	2	28	25	21
Survival time (days)	22	30	87†	31	67	27	37	29	66	101†	83	23	71†	73†	53
Microhabitat scale															
Protective cover** (%)	65	42	74	94	70	75	89	84	82	80	86	63	90	89	77
Use of den** (%)	40	0	28	46	40	67	67	75	53	43	45	0	82	76	47
Use of ground* (%)	20	33	13	54	33	33	17	13	27	13	39	50	4	8	26
Use of tree*** (%)	40	67	59	0	27	0	16	12	20	44	16	50	14	16	27
Local scale															
Tree Cover*** (%)	70	75	65	54	63	50	49	97	58	62	67	75	84	67	67
Shrub Cover*** (%)	0	25	32	10	28	33	56	6	27	31	34	13	31	27	25
Herb Cover*** (%)	0	33	14	0	2	58	32	13	27	24	16	0	17	5	17

†Survival time is censored (i.e. individual was still alive on 15 August)

temperature (Spearman rank correlation, $r = -0.258$, $p<0.001$, $n = 299$) and wind speed (Spearman rank correlation, $r = -0.168$, $p = 0.003$, $n = 299$) measured in the microhabitat.

At the local scale, juveniles used sites with an average of 67% of tree cover, 25% of shrub cover and 17% of herb cover but individuals significantly differed in the mean tree, shrub and herb cover they used (Table 5.3). The amount of tree cover was negatively correlated to the amount of shrub (Spearman rank correlation, $r=-0.176$, $p = 0.002$, $n = 299$) and herb cover (Spearman rank correlation, $r=-0.243$, $p<0.001$, $n = 299$) present in the site.

Sex, body mass, mobility and distance to the mother

Eight of the studied juveniles were females and six were males. Mean body mass on 10 June was 930 ± 96 g (range: 350-1380 g, $n = 14$), and was not different between sexes (ANOVA, $F_{(1,12)} = 0.05$, $p = 0.821$). Mean daily length of movement was not constant through time (ANOVA, $F_{(3,27)} = 7.470$, $p = 0.001$, Table 5.4) and was not different between sexes (ANOVA, $F_{(1,12)} = 0.52$, $p = 0.486$). Mean distance between juvenile and mother did not significantly change with time (ANOVA, $F_{(3,18)} = 1.505$, $p = 0.247$, Table 5.4) and was not different between sexes (ANOVA, $F_{(1,9)} = 0.11$, $p = 0.752$).

Table 5.4 : Length of daily movements (m) and distance from mother (m) for juvenile North American porcupines followed in Parc National du Bic, Québec, May to August, 2003-2004. Means (± SE) for the population (calculated from individual means) are given by month and for the study period. The range of individual means and the sample sizes (number of individuals, number of observations) are also given

	May	June	July	August	Overall
Daily movements					
Mean ± SE	9 ± 3	36 ± 5	61 ± 12	57 ± 14	42 ± 6
Range	3-24	8-63	31-113	30-97	7-86
N	7, 13	12, 146	8, 125	4, 35	14, 319
Distance to the mother					
Mean ± SE	15 ± 9	99 ± 19	171 ± 52	135 ± 125	96 ± 21
Range	5-33	24-201	48-380	7-384	24-236
N	3, 5	10, 60	6, 39	3, 14	11, 118

Survival

Nine of the 10 observed deaths were due to predation and one juvenile died of unknown cause. The youngest juvenile to die was 22 days-old but one juvenile was still alive after 101 days (Table 5.3). Habitat use at the microhabitat and local scales influenced survival of juveniles. At the microhabitat scale, the type of hiding site (den, ground, or tree) and the amount of protective cover significantly influenced survival (Table 5.5). For a given location, use of sites with high protective cover enhanced survival (a 10% increase in the mean protective cover used was associated with a 66% decrease in death probability, Table 5.5). Also, when taking into account the protective cover used, use of trees enhanced survival compared to use of ground locations (8% decrease in death probability, Table 5.5).

At the local scale, use of sites with higher shrub cover significantly increased survival (Table 5.5) when percentages of tree and herb cover were taken into account. According to the hazard ratio, a 10% increase in mean shrub cover used was associated with a 74% decrease in death probability. Also, when taking tree and shrub cover into account, use of sites with higher herb cover decreased survival (78% increase in death probability, Table 5.5) although this effect was not statistically significant. Finally we found no effect of sex (χ^2_1 = 0.30, p = 0.586), mass on 10 June (χ^2_1 = 0.01, p = 0.915), mobility (χ^2_1 = 1.94, p = 0.163), or distance to the mother (χ^2_1 = 0.32, p = 0.570) on survival.

Table 5.5 : Coefficients for the survival analyses for 14 juvenile North American porcupines studied in Parc National du Bic, Québec, May to August, 2003-2004

Variable	β value	SE	χ^2	P	Hazard ratio
Microhabitat scale					
Protective cover	-1.072	0.478	5.03	0.025	0.34 (10%)
Location					
Ground	0	ND	ND	ND	reference category
Den	-0.026	0.030	0.75	0.388	0.97
Tree	-0.089	0.037	5.89	0.015	0.92
Local scale					
Tree cover	-0.213	0.272	0.61	0.433	0.81 (10%)
Shrub cover	-1.338	0.534	6.29	0.012	0.26 (10%)
Herb cover	0.579	0.312	3.44	0.064	1.78 (10%)

5.5. Discussion

Juvenile porcupines showed selection for high protective cover at the microhabitat (1 m) scale only. At the local (15 m) scale, juveniles selected sites characterized by a low herb cover and with cedar as dominant tree species. The use of cover decreased as juveniles grew older and was dependent on meteorological conditions. Particularly, juveniles used dens to avoid low air temperature and rain. Outside of the den, juveniles used more open habitats after it had rained. The main cause of mortality was predation and habitat use, both at the microhabitat and at the local scales, influenced survival. At the microhabitat scale, use of protective cover and use of trees compared to use of the ground enhanced survival, whereas at the local scale, use of sites with high shrub cover enhanced survival. We did not detect any effect of sex, body mass, mobility, and distance to the mother on survival of juveniles. We now discuss these findings in order to evaluate our three original predictions.

Habitat selection

We predicted selection for cover to occur at both the microhabitat and local scales (prediction 1) because juvenile porcupines were found by Sweitzer and Berger (1992) to avoid open areas in presence of predators, and because predation risk was high in our system (chap. 3). Our study animals selected microhabitats with high protective cover within habitat patches showing low herb cover and dominated by cedar trees. We could not detect selection for high tree or shrub cover (at the local scale), even though stands with low herb cover were typically dense in our study area, as illustrated by the negative relationship we found between tree and herb cover. We suggest some selection for cover occurred at the scale of the stand (not investigated in this study) because we always located juveniles in forested environments, while our study area was fragmented by open fields that were used by adult porcupines for feeding (Morin et al. 2005). Open areas therefore constituted exploitable areas for adults but were not used by juveniles.

Our results support the hypothesis that predator avoidance was the main factor driving habitat selection at the two scales studied. Indeed, use of covered microhabitats is likely to decrease probability of detection by predators (Mysterud & Ostbye 1999) while use of areas with low herb cover should reduce likelihood of encountering predators since herb cover in forested environments is mainly associated with open or edge habitats, that are easily accessible to predators (Bider 1968, Andren & Angelstam 1988). We found no evidence that juveniles selected their microhabitat so as to increase access to radiative gain (i.e. they did not select open microhabitats). Covered microhabitats that were selected by juveniles were characterized by low air temperatures and low wind speeds. Besides providing protection from predators, covered microhabitats therefore provided protection against high winds.

However, we think protection from wind was not the main factor driving selection of covered microhabitats by juveniles because selection for cover did not vary according to wind conditions (see below).

Effects of meteorological conditions on the use of cover

In summer, use of cover by animals usually results in a lower access to incoming radiation and thus to exposure to lower temperatures (Cook et al. 1998). Our results confirmed this pattern since air temperature was negatively correlated with protective cover at a given site. As predation was expected to drive habitat selection by juvenile porcupines, we predicted juvenile porcupines would use open environments only under cold conditions (prediction 2). We found that animals increased their use of dens when temperature decreased and when rain intensity increased. It was not surprising that juveniles used their den when rain intensity increased because a wet coat provides a poor insulation against cold temperatures (Kreith & Black 1980) so porcupines used dens to avoid wetting their coat. However, the fact that juveniles used dens under cold temperature conditions does not support our prediction that juveniles should use open areas on cold days to maximize radiative heat gain. We trust juveniles were able to warm up their dens when using them so that dens constituted unique covered microhabitats that provided shelter against cold temperatures, rain, and predators. Juveniles therefore did not face a trade-off between use of cover and thermal exposure, but rather faced a trade-off between use of den and non-den microhabitats. Dens provided hiding cover and protection against harsh weather conditions but no foraging opportunities. As energy needs of juveniles increased (i.e. as their body mass increased with Julian date), porcupines decreased their use of dens, possibly to increase the time spent foraging. An alternate (non-exclusive) hypothesis would be that juveniles decreased use of their dens because the thermal environment became more favourable or because animals were able to thermoregulate better as the season advanced.

Wind also influenced the use of dens with juveniles being increasingly outside of their den as wind speed increased. Biting insects are less abundant inside than outside dens (Comtois & Berteaux 2005) so that juveniles may well use dens on calm (i.e. non windy) days to avoid biting flies when insect harassment is high (i.e. when there is no wind). Outside of the den, we found no effect of air temperature on the use of cover (at the microhabitat scale). However, juveniles used open microhabitats more often with increasing past rain intensity, potentially to avoid wetting their coat with raindrops left on vegetation by the rain. The fact that juveniles didn’t modify the use of cover outside of the den with changing temperature conditions suggests that cover outside of the den was rather used as a hiding cover, with juveniles retreating to dens when temperature decreased.

Habitat use and survival

Predation was the main cause of mortality in juvenile porcupines. Several predators hunt and kill porcupines more effectively in open habitats (coyotes: Keller 1935, mountain lions: Robinette et al. 1959, fishers: Powell & Brander 1977) and porcupines perceive open habitats as risky habitats (Sweitzer & Berger 1992). Consistent with the hypothesis that open habitats are more risky, we found that use of cover (both at the microhabitat and local scales) enhanced survival. There were individual differences in the use of cover and juveniles survived better when using habitat patches with high shrub cover and, within those patches, when using microhabitats with high protective cover. Numerous studies have reported that ungulate fawns bed down in dense ground cover (review in Mysterud & Ostbye 1999) but only a few studies have related habitat use to survival (Linnell et al. 1995, Aanes & Andersen 1996, Canon & Bryant 1997, Farmer et al. 2006). In addition, studies on rodents (Moreno et al. 1996, Schooley et al. 1996, Ebensperger & Hurtado 2005) suggested that cover may be obstructive rather than protective for small mammals. Here we exploited a multivariate and hierarchical analysis of habitat use by juvenile porcupines to show that use of cover at both scales studied enhanced survival of one small-bodied animal. Use of cover indeed has diverse ecological consequences depending probably partly on the size of the study animal, and on the limiting factors with which it is faced (Mysterud & Ostbye 1999).

Besides individual differences in the use of cover, we also found individual differences in the use of dens, ground and trees. Juveniles survived better when using trees than when using ground. We suggest that juveniles were more vulnerable to predators when they were on the ground than when they were in trees. Use of trees prevents attack by some predators (e.g. coyotes) but not from others (e.g. fishers, Powell & Brander 1977). According to the few signs of presence we found, fishers appeared to be the main predators of juvenile porcupines during the study period (results not shown) and the use of trees is therefore not expected to decrease risk of attack. However, use of trees may have decreased detectability by fishers, therefore leading to higher survival of juveniles. Our third prediction was supported because we found that most mortalities were due to predation and that use of cover enhanced survival. Predation was therefore the main factor limiting survival of juveniles in our population, as supported by the evidence that habitat selection headed towards predator avoidance, even at fine scales of selection.

Sex, body mass, mobility, distance to the mother, and survival

Juveniles were not sexually dimorphic and we found no effect of sex or body mass on survival. Because predation was the main limiting factor in our population, we would expect increased body mass to enhance survival if larger (i.e. older) animals were less vulnerable to predators as in several other mammal species (white-tailed deer: Nelson & Woolf 1987, pronghorns: Fairbanks 1993). Even though males were not heavier than females, sex could also have influenced survival because of sex-differences in behaviour (Webb 1993). We observed juvenile porcupines to stay still when approached, whatever their size and sex. Males and heavier (older) juveniles did not show higher escape speed or aggressiveness compared to other juveniles (G.M. personal observation). Therefore, it is not surprising they did not survive better.

We also found no effect of mobility on survival of juveniles. Juveniles are often argued to suffer high predation risk during dispersal because of greater activity rates, lower familiarity with new habitats, or use of lower-quality habitats (Gaines & McClenaghan 1980, Yoder et al. 2004). We expected more active individuals to show decreased survival because of higher exposure to predation risk. As stated before, juvenile porcupines performed mainly small movements (<20 m) on a daily basis. However, porcupines were sometimes observed to move longer distances (up to 500 m) that could have exposed them to the same risks as dispersing animals. However, in “hider” species, mothers initiate the changes in location and accompany their young during long moves (Lent 1974). They also certainly influenced the choice of the immigration area, even though the exact location of the new hiding site depends upon the infant (Lent 1974). One previous study (Stuart-Smith & Boutin 1995) investigated whether movements made by juvenile red squirrels (*Tamiasciurus hudsonicus*) before weaning (i.e. when they were still dependent on mother for food) influenced survival. This work found no effect of total movements on survival but found that individuals that spend relatively more time off their natal territory were more likely to be depredated. We suggest that the presence of the mother in the vicinity of the juvenile and, for porcupines, the possibility that mothers were choosing the stand to leave their young, largely reduced most of the risks usually associated with movements in dispersing juveniles.

Finally, we found no effect of the distance between juvenile and mother on survival of the juvenile. Females from several hiding species have been shown to reduce their home range during rearing of their young (Fisher & Goldizen 2001, Ciuti et al. 2006). This may allow females to feed their young more regularly and, in some species, to alert the young of approaching danger (gazelles: Fitzgibbon 1993, roe deer: Aanes & Andersen 1996). We never observed mothers to warn their young or to protect them in any manner when we approached or captured juvenile porcupines. Still, females remained fairly close to their young, especially in their first weeks of life and we trust this could have enhanced juveniles survival if predation pressure had not been so high (chap. 3).

The fact that we found no effect of sex, body mass, mobility, or distance to the mother on survival of juveniles may alternatively be due to a lack of statistical power in our analyses. Because hiding juveniles are hard to find, we collected data on 14 juveniles only. However, we found clear effects of individual differences in habitat use on survival. This suggests that fitness consequences of habitat use were strong in our population and demonstrates the importance of comparing habitat use with measures of fitness to evaluate habitat suitability for a given species.

Chapitre 6 Conclusion

Dans le cadre de ma thèse, j'ai abordé différents aspects associés aux effets du climat et de la prédation sur le comportement et la survie des individus (Fig. 6.1), dans le but de comprendre les mécanismes par lesquels le climat et les prédateurs influencent la taille des populations. Je me suis d'abord intéressée aux variations de survie observées au cours du temps, et ai tenté de mettre en évidence les facteurs à l'origine de ces variations (chap. 3, Fig. 6.1). Ensuite, l'étude détaillée du comportement des individus m'a permis de démontrer l'effet de certaines variables environnementales (i.e. conditions météorologiques, risque de prédation) sur l'utilisation de l'habitat et les patrons d'activité des animaux (chap. 4 et 5, Fig. 6.1). J'ai finalement examiné les effets de l'utilisation de l'habitat sur la survie afin d'évaluer comment les différences individuelles d'utilisation de l'habitat peuvent moduler les effets des facteurs climatiques et des prédateurs sur la survie (chap. 4 et 5, Fig. 6.1). Ce travail repose sur un suivi fin de la survie et du comportement des individus, et j'ai également détaillé les méthodes nécessaires à un tel suivi (chap. 2).

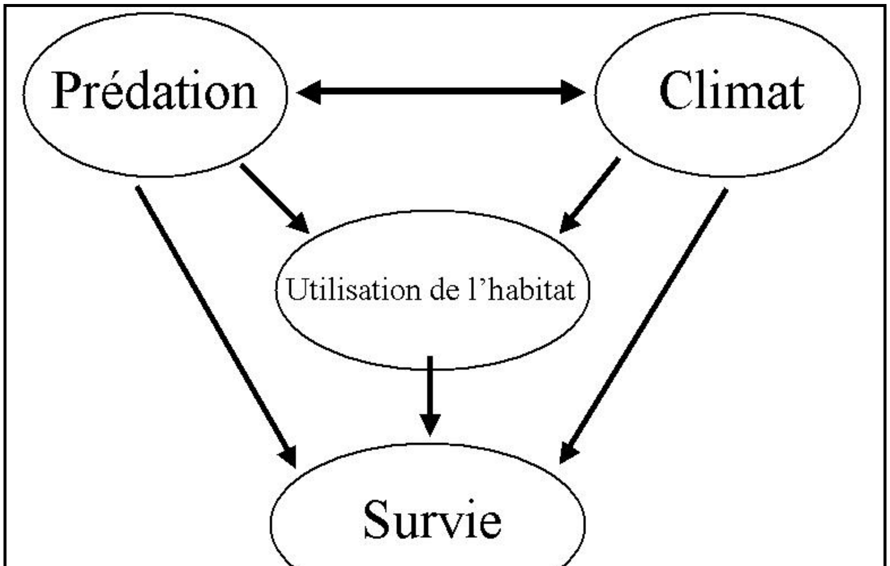


Figure 6.1 : Schéma récapitulatif des principaux sujets traités dans la thèse. On s'est intéressé aux effets du climat et de la prédation sur la survie, aux effets du climat et de la prédation sur l'utilisation de l'habitat, et aux conséquences des différences individuelles d'utilisation de l'habitat sur la survie.

Méthodes mises en place pour le suivi individuel

Le porc-épic d'Amérique est un animal essentiellement arboricole, qui est difficile à localiser dans la canopée dense des forêts mixtes ou conifèriennes (Hale & Fuller 1999). Une fois localisé, le porc-épic est également difficile à capturer, notamment lorsqu'il utilise des arbres ou des tanières rocheuses profondes. Sans doute à cause de ces difficultés, peu d'études se sont intéressées aux facteurs influençant la démographie de cet herbivore, qui peut pourtant atteindre de fortes abondances, et jouer un rôle important dans certains écosystèmes (Curtis 1941, Curtis 1944). Le centre de notre aire d'étude est occupé par des champs que les porcs-épics utilisent pour se nourrir au cours de l'été, et où ils sont facilement capturables. Cette particularité a permis de mettre en place un suivi détaillé de la population basé sur la recherche systématique de porcs-épics autour des champs pendant l'été.

Au cours des sept années de suivi, nous avons amélioré les méthodes de capture existantes pour les rendre plus efficaces (e.g. capture par épuisette), et développé de nouvelles méthodes de capture qui s'adaptent à toutes les situations (e.g. pose de trappes sur le tronc des arbres). Nous avons d'autre part raffiné le système de marquage des individus par boucles d'oreilles afin de le rendre plus durable, et donc de limiter les pertes d'identité (Griesemer et al. 1999). Aucune méthode n'ayant été décrite pour chercher les jeunes porcs-épics et les équiper de colliers émetteurs, nous avons mis au point des techniques pour trouver les jeunes et déterminer leur taux de survie, élément nécessaire à toute étude démographique. Finalement, nous avons développé une méthode pour poser des colliers émetteurs en minimisant les blessures au cou des individus, blessures qui peuvent être particulièrement sévères si les colliers sont posés sur le long terme, ou en hiver (à cause du froid qui rend le plastique du collier très rigide et donc blessant).

Grâce aux techniques développées, nous avons pu récolter des données individuelles précises que je mets à contribution dans le reste de mon doctorat. Notamment, nous décrivons le déclin d'abondance de la population d'étude au cours du temps. Le suivi mis en place étant assez intensif (en moyenne, chaque animal était recapturé une fois tous les deux mois) on peut se demander si le déclin d'abondance observé pourrait être dû à un dérangement des animaux. La plupart des captures avaient lieu au cours de l'été (entre Mai et Août) lorsque les porcs-épics fréquentent les champs pour s'y alimenter. Or, nous montrons au chapitre 3 que l'hiver constitue la période la plus critique pour la survie des pors-épics et que la diminution de la survie en hiver paraît liée à une augmentation de la prédation les années de fortes précipitations hivernales. Le déclin d'abondance observé ne semble donc pas dû à un dérangement occasionné par les captures estivales. Le fait que la densité de porcs-épics ait également grandement diminué dans les autres secteurs du Parc National du Bic (où aucun suivi n'était effectué), confirme que le suivi mis en place n'avait pas d'effet important sur la dynamique de la population d'étude. Nous espérons que les méthodes que nous décrivons pourront être mises à profit par d'autres chercheurs qui étudient les porcs-épics ou d'autres animaux à piquants.

Abondance, survie, et facteurs influençant la survie

Le climat influence la dynamique des populations de mammifères (Krebs & Berteaux 2006). Il peut avoir des effets directs sur les espèces mais aussi modifier la nature des interactions entre espèces (Davis et al. 1998, Post et al. 1999b, Wilmers & Post 2006). Klvana et al. (2004) génèrent l'hypothèse que l'abondance des populations de porcs-épics dans la région du Bas-St-Laurent est influencée par les variations d'activité solaire, *via* un impact sur certaines variables météorologiques locales.

Dans le cadre de mon doctorat, j'ai utilisé une population de porcs-épics de la région du Bas-St-Laurent pour mettre à l'épreuve l'hypothèse générée par l'étude de Klvana et al. (2004) et identifier le(s) mécanisme(s) par lesquel(s) l'activité solaire influence l'abondance de porcs-épics. Notre étude confirme l'existence d'un lien entre les variations d'activité solaire et le taux d'accroissement de la population. D'après nos résultats, la radiation solaire pourrait affecter l'abondance de porcs-épics par des effets en cascades sur les précipitations hivernales, les taux de survie des porcs-épics en hiver, et le niveau de prédation par le pékan. On identifie en effet une corrélation négative entre la radiation solaire et le niveau de précipitations hivernales, qui sont elles-mêmes reliées aux variations de la survie hivernale. Chez les espèces longévives, le taux de survie des adultes est en général le paramètre démographique qui influence le plus fortement le taux d'accroissement de la population (Gaillard et al. 2000, Saether & Bakke 2000, Eberhardt 2002). Dans notre population, la survie des adultes est variable d'un hiver à l'autre, et la diminution du taux de survie des adultes est certainement responsable, au moins en partie, du déclin d'abondance observé (de 117 individus en 2000 à 1 individu en 2006). On observe également une variation de la survie des juvéniles d'un hiver à l'autre. Les taux de survie en hiver sont plus bas et plus variables que les taux de survie en été, pour les deux classes d'âge considérées. On identifie donc l'hiver comme la période de l'année étant la plus critique pour le porc-épic, et la réduction marquée de la taille de notre population illustre les conséquences sévères que peuvent engendrer des variations de la survie adulte chez les espèces longévives.

Concernant les mécanismes par lesquels les précipitations hivernales influencent les taux de survie, on constate que la diminution de survie en hiver est concomitante avec une augmentation du pourcentage de mortalités dues à la prédation. Face à ce constat, on peut envisager deux possibilités : d'une part, l'augmentation des taux de prédation les années de fortes précipitations hivernales pourrait être un simple hasard. Le pékan est en augmentation dans l'est du Québec depuis le milieu des années 1990 (Poulin et al. 2006) et son retour dans le parc du Bic semble dater du début de l'année 1999 (A. Pelletier, Ministère des Ressources Naturelles et de la Faune, communication personnelle). On pourrait donc supposer que l'augmentation des taux de prédation que l'on observe en 2003 et 2004 soit due à une simple augmentation du nombre des prédateurs qui, par hasard, aurait eu lieu pendant les années de fortes précipitations hivernales (hypothèse 1). D'autre part, la probabilité de prédation pourrait effectivement être liée au niveau de précipitations hivernales (hypothèse 2). La prédation sur les porcs-épics adultes semble liée à la présence de neige au sol puisque 95% des adultes qui meurent par prédation, meurent pendant la période de l'hiver où de la neige recouvre le sol. D'après nos connaissances de la biologie du porc-épic et du pékan, les prédateurs pourraient changer leur comportement de chasse et/ou les porcs-épics pourraient devenir plus vulnérables à la prédation en fonction des conditions de neige. Puisque nous n'avons pas effectué de dénombrements du nombre de prédateurs, et puisque notre nombre d'années d'étude est assez réduit, nous ne pouvons pas complètement écarter la première hypothèse. Cependant, Klvana et al. (2004) montrent l'existence d'un lien persistant entre le niveau de précipitations hivernales et l'abondance des populations de porcs-épics dans la région. Les résultats de notre étude, en conjonction avec les résultats de Klvana et al. (2004), viennent donc confirmer la possibilité d'un effet du climat hivernal sur l'abondance de porcs-épics, *via* un impact des conditions de neige sur les probabilités de prédation, et donc sur la survie au cours de l'hiver (hypothèse 2).

Si cette deuxième hypothèse est vraie, les fluctuations d'abondance de porcs-épics seraient donc liées à la présence de prédateurs dans le système. Hors, nous avons déjà dit que l'abondance de pékans était actuellement en augmentation dans le Bas-St-Laurent après plusieurs années de faible abondance (Poulin et al. 2006). Dans ce contexte, l'hypothèse d'un effet des prédateurs sur la survie hivernale des porcs-épics semble contradictoire avec le cycle régulier et continu trouvé par Klvana et al. (2004) dans l'abondance des porcs-épics entre 1868 et 2000. En fait, je pense qu'il n'y a pas de contradiction entre ces deux résultats. Mon interprétation est que la survie hivernale des porcs-épics est de toutes manières liée aux conditions météorologiques hivernales, mais que les causes de mortalité changent selon que les prédateurs soient présents en quantité importante ou non. En absence de prédateurs, les animaux meurent par inanition les années de fort enneigement (à cause du coût élevé des déplacements et d'une accessibilité réduite à la nourriture) alors que lorsque les prédateurs sont présents, les animaux meurent par inanition ou par prédation, avec des taux de prédation plus élevés les années de fort enneigement.

Ce travail de doctorat identifie un mécanisme possible (i.e. variation des probabilités de prédation en fonction des conditions de neige) par lequel les conditions météorologiques influencent la taille des populations. On va donc une étape plus loin que la plupart des études s'intéressant aux effets du climat sur la dynamique des populations (Krebs & Berteaux 2006). Dans un contexte plus global, notre étude vient également ajouter aux quelques travaux montrant un effet possible du climat sur les relations prédateurs-proies. À ma connaissance, plusieurs études se sont intéressées aux effets des conditions de neige sur le succès de prédation du loup (*Canis lupus*) sur des herbivores de grande taille (e.g. orignal (Post et al. 1999b, Wilmers et al. 2006), cerf (Hebblewhite et al. 2002)) et une étude récente montre que l'impact des araignées sur les taux de décomposition de la litière feuillue est dépendant du niveau de précipitations (Lensing & Wise 2006). Notre étude suggère un effet des conditions de neige sur les interactions entre pékans et porcs-épics. C'est donc encore une fois un effet des précipitations qui est mis en avant, mais sur des mammifères de taille moyenne. Notre étude appuie donc l'hypothèse d'un effet du climat sur les relations prédateurs-proies, en l'étendant à de nouvelles espèces de mammifère. Ainsi, elle souligne l'importance de comprendre comment les interactions entre espèces varient en fonction des conditions météorologiques pour modéliser et comprendre le plus rigoureusement possible la réponse des communautés aux changements climatiques (Schmitz 2003).

Pour confirmer que les probabilités de prédation sont bien liées aux conditions de neige, une perspective de recherche serait de comparer nos résultats avec des résultats obtenus dans d'autres populations soumises à des conditions climatiques différentes. Par exemple, la population de porcs-épics suivie par Uldis Roze, et située au Nord-Ouest de la ville de New York, a connu une réintroduction du pékan au début des années 1990s après plusieurs années d'absence. Suite au retour du pékan, la population a subi un déclin marqué d'abondance avec une perte d'environ 90% des individus en 17 ans (Uldis Roze, New York Queens College, communication personnelle). Il serait intéressant d'évaluer si le déclin plus marqué et plus rapide que l'on observe dans notre population pourrait être dû à des différences de conditions de neige entre les deux sites d'études qui rendraient les porcs-épics du Bas-St-Laurent plus vulnérables à la prédation que les porcs-épics plus au sud.

Effets des variations environnementales sur l'utilisation de l'habitat

Les variations spatiales et temporelles des conditions météorologiques (Wiersma & Piersma 1994, Brotons et al. 2000, Humphries et al. 2005) et du risque de prédation (Lima & Dill 1990, Brown 1999, Beaudoin et al. 2004, Creel et al. 2005) peuvent influencer l'utilisation de l'habitat et le patron d'activité des animaux. Les taux de prédation étaient relativement élevés pendant notre étude et apparemment liés aux conditions de neige pendant l'hiver (chap. 3). D'autre part, les conditions thermiques constituent une contrainte potentielle pour les porcs-épics pendant l'hiver (quand les températures sont beaucoup plus basses que la température critique inférieure des porcs-épics), ainsi qu'en début d'été pour les jeunes dont le système de thermorégulation est encore immature (Hull 1973, Leon 1986). Les contraintes dues à l'environnement thermique et à la prédation étaient donc substantielles pendant notre étude, et nous avons examiné l'influence de ces contraintes sur l'utilisation de l'habitat par les animaux. En particulier, nous nous sommes intéressés à l'utilisation de l'habitat des adultes au cours de l'hiver et des jeunes au cours du premier été de vie.

Hiver

En hiver, on montre que la tanière est le microhabitat offrant la meilleure protection contre les températures froides et que les animaux modifient leur patron d'utilisation de la tanière en fonction de la température. L'enfoncement dans la neige, qui est possiblement relié au risque de prédation, influence également le patron d'activité des animaux. Les animaux réduisent le temps passé dehors et augmentent leur activité diurne quand la température baisse et quand l'enfoncement dans la neige augmente. Les animaux semblent donc utiliser leur tanière à la fois comme un refuge contre le froid mais aussi comme un refuge contre les prédateurs. Mon travail de doctorat démontre que les tanières offrent effectivement un abri contre les températures basses, et il a été plusieurs fois suggéré que les porcs-épics peuvent également les utiliser pour se soustraire aux prédateurs (Roze 1989, Griesemer et al. 1996, Comtois & Berteaux 2005). Les porcs-épics ne semblent donc pas avoir de compromis à faire entre protection contre le froid et protection contre les prédateurs au cours de l'hiver. Par contre, les animaux devant sortir pour s'alimenter, ils font face à un compromis entre recherche de nourriture et protection contre le froid et les prédateurs. On montre qu'ils y répondent en réduisant le temps passé dehors et en augmentant l'intensité de l'alimentation quand il fait froid. On montre également que les animaux ne choisissent pas leurs sites d'alimentation en fonction de la température (i.e. ils n'utilisent pas les microhabitats offrant la meilleure protection thermique pour manger et ne modifient pas leur utilisation des microhabitats extérieurs en fonction de la température). L'hypothèse la plus probable est qu'ils choisissent les sites offrant la nourriture la plus digestible possible, quelque soient les conditions de température. Aussi, les animaux pourraient s'alimenter dans les sites où le risque de prédation est le plus faible (par exemple si les porcs-épics sont moins facilement détectables par les prédateurs si ils sont au sommet d'un arbre). Le comportement des animaux pendant l'hiver semble donc être influencé à la fois par les contraintes thermiques, le risque de prédation, et l'acquisition de nourriture.

Nous avons montré que la tanière semble être utilisée comme protection contre les prédateurs. Cependant, il n'a jamais été prouvé que les tanières offrent effectivement une telle protection. Afin d'établir si les tanières sont utilisées pour se soustraire aux prédateurs, une perspective de recherche serait de déterminer comment les animaux utilisent leur tanière en réponse à une augmentation expérimentale du risque de prédation en dehors de la période hivernale. Les tanières pouvant également constituer un refuge contre les insectes piqueurs (Comtois & Berteaux 2005), on pourrait utiliser des urines de prédateurs pour manipuler le risque de prédation perçu (Sweitzer & Berger 1992) au cours du printemps ou de l'automne quand ni l'environnement thermique ni les insectes ne constituent une contrainte pour les porcs-épics. D'autre part, comme la tanière semble être le meilleur habitat pour se protéger à la fois du froid et des prédateurs il nous est difficile de discerner les effets de l'un et l'autre facteur sur le comportement des animaux (i.e. les hypothèses permettant d'expliquer le patron d'utilisation des tanières ne sont pas mutuellement exclusives). Une perspective dans ce domaine serait de réchauffer expériementalement certaines tanières afin d'évaluer si ces tanières sont plus utilisées (nombre de porcs-épics présents dans la tanière) ou plus longtemps utilisées (temps passé dans la tanière) que les tanières contrôles. Finalement, pour préciser l'importance des contraintes liées à l'acquisition de nourriture, une perspective serait de déterminer si la digestibilité des ramilles d'épinette est liée à leur position dans l'arbre (e.g. les ramilles situées en haut des arbres, c'est à dire où s'alimentent les porcs-épics, sont-elles plus digestibles que celles situées en bas des arbres ?). Ces recherches permettraient de préciser l'importance relative des contraintes liées au climat, à la prédation, et à la recherche de nourriture, sur le comportement des animaux pendant l'hiver.

Été

En été, on montre que les jeunes porcs-épics utilisent des microhabitats offrant un fort couvert protecteur, même si la température ambiante y est plus basse. Les animaux augmentent leur utilisation des tanières quand les températures sont basses et quand il pleut mais l'utilisation du couvert à l'extérieur des tanières n'est pas influencée par les conditions thermiques. Même en été où le gain d'énergie par radiation solaire est potentiellement important (Demarchi & Bunnell 1993), et où l'utilisation d'habitats ouverts peut donc être bénéfique pour des jeunes sensibles à l'hypothermie, la tanière semble constituer un habitat couvert particulier que les animaux utilisent comme refuge contre les conditions climatiques les plus sévères. Quand les conditions sont plus clémentes, les jeunes sortent des tanières mais utilisent un couvert végétatif dense, probablement pour se protéger des prédateurs. Comme en hiver, et en désaccord avec nos prédictions basées sur l'importance du gain d'énergie par radiation solaire pendant l'été, les tanières représentent donc un refuge à la fois contre les prédateurs et contre les conditions climatiques défavorables. Là encore, le compromis auquel les animaux font face est de devoir quitter la tanière pour chercher de la nourriture. On constate que les jeunes diminuent leur utilisation des tanières et du couvert à l'extérieur de la tanière au cours de la saison. Une hypothèse (pour les tanières) est qu'ils quittent davantage les tanières quand leurs besoins énergétiques augmentent et que leur capacité de thermorégulation s'améliore. Pour le couvert à l'extérieur de la tanière, on pourrait supposer que les jeunes diminuent son utilisation lorsqu'ils deviennent, en grandissant, moins vulnérables aux prédateurs. Cependant, l'analyse de la survie des individus n'indique pas que les animaux plus âgés soient moins vulnérables à la prédation. Une hypothèse serait que les jeunes lorsqu'ils grandissent deviennent plus autonomes dans le choix des sites utilisés, et qu'ils choisissent des sites moins couverts que ceux où leurs mères les cachaient au début de leur vie.

Au cours de mon doctorat, j'ai évalué l'utilisation de l'habitat à des échelles temporelles et spatiales très fines. Ceci a permis de mettre en évidence des changements subtils dans le comportement des animaux en réponse aux variations environnementales auxquelles ils sont exposés. Pour des animaux qui se déplacent peu, comme les jeunes porcs-épics pendant leur premier été (chap. 5) ou les adultes au cours de l'hiver (Roze 1984), la sélection de l'habitat se fait à une échelle très fine. Une étude faite à l'échelle du domaine vital par exemple (3ème ordre de sélection, Johnson 1980) de l'utilisation de l'habitat n'aurait sans doute pas permis de déceler de telles variations comportementales chez les animaux. On montre que, à la fois les conditions météorologiques et le risque de prédation, semblent influencer le comportement des animaux. Étant donné que certains habitats offrent une protection à la fois contre le froid et les prédateurs, il nous est difficile d'interpréter de manière sûre le comportement des animaux. En fait, le climat et la prédation pouvant tous deux exercer de fortes contraintes sur le comportement des animaux, avec des conséquences sur la survie et le succès reproducteur des individus (e.g. Sealander 1952, Hik 1995, Dawson et al. 2005), il est fort probable que les deux facteurs interagissent pour influencer l'utilisation de l'habitat et le patron d'activité des animaux.

Différences individuelles d'utilisation de l'habitat et conséquences sur la survie

La qualité de l'habitat qu'un animal utilise peut potentiellement influencer sa survie et son succès reproducteur (McLoughlin et al. 2005, Pettorelli et al. 2005, McLoughlin et al. 2006). En conséquence, des différences individuelles dans l'utilisation de l'habitat peuvent se traduire par des différences de survie entre individus. En identifiant les principales causes de mortalité dans notre population, et en examinant quels patrons d'utilisation de l'habitat amélioraient la survie individuelle, on a mis en évidence les caractéristiques de l'habitat qui pouvaient servir à moduler les effets négatifs des différentes variables environnementales (prédation et exposition au froid).

En hiver, la prédation et l'inanition sont les deux principales causes de mortalité dans notre population. On identifie des différences individuelles dans le patron d'activité des animaux, avec certaines conséquences sur la survie. En effet, les animaux faisant le plus de sorties par jour sont ceux qui survivent le moins bien, sans doute car ils passent plus de temps au sol (lorsqu'ils voyagent entre la tanière et les arbres d'alimentation) où ils sont facilement détectables et vulnérables aux prédateurs. Réduire le nombre de sorties par jour semble donc un moyen efficace de limiter la probabilité de prédation. Cependant, étant donné que les porcs-épics épuisent leurs réserves de graisse tôt dans l'hiver (Sweitzer & Berger 1993), et qu'ils n'accumulent pas de réserves de nourriture dans leur tanière, ils sortent au moins une fois chaque jour pour s'alimenter (chap. 4). On ne trouve pas d'effet des autres différences individuelles dans les patrons d'activité sur la survie. Par exemple, un animal qui passe plus de temps dehors ne survit pas nécessairement mieux qu'un autre. Il est possible que les différences individuelles dans le temps passé dehors, par exemple, aient des effets plus subtils que des effets directs sur la survie. Ainsi, une femelle passant plus de temps dehors qu'une autre va peut être maintenir une meilleure condition corporelle au cours de l'hiver, ce qui pourra influencer son succès reproducteur l'été suivant. Notre protocole de suivi ne permet pas de mettre en évidence ces possibles différences, notamment car il est difficile de connaître le statut reproducteur d'une femelle de manière sûre et de trouver les jeunes pour déterminer le succès reproducteur (chap. 2). On arrive cependant à mettre en évidence les effets des différences individuelles de patron d'activité sur la survie, et on interprète ces différences de survie comme des différences dans le risque de détection par les prédateurs.

En été, la mortalité des jeunes est élevée et la prédation est la cause de presque toutes les mortalités. Là encore, les individus diffèrent dans leur utilisation de l'habitat avec des conséquences pour la survie. Les animaux utilisant le plus de couvert protecteur et utilisant le moins de localisations au sol survivent le mieux, ainsi que ceux utilisant des zones avec le plus d'arbustes. Ici encore, on interprète ces différences de survie comme des différences d'exposition aux prédateurs. Été comme hiver, la modification des patrons d'activité et de l'utilisation de l'habitat semblent permettre, dans une certaine mesure, de moduler les risques de prédation.

Un suivi détaillé du comportement des animaux nous a permis de mettre en évidence quelles caractéristiques de l'habitat ou quels patrons d'activité affectaient la survie des porcs-épics en présence de prédateurs. Un tel suivi demande un investissement en temps considérable et le nombre d'individus suivis est par conséquent relativement petit. Malgré notre petite taille d'échantillon, nous montrons des effets importants de l'utilisation de l'habitat sur la survie, particulièrement pour les jeunes qui sont les plus susceptibles à la prédation. Notre étude met en évidence l'importance de comparer l'utilisation de l'habitat avec des mesures de survie ou de succès reproducteur des individus afin de définir l'importance d'un habitat ou d'une caractéristique d'habitat pour une espèce donnée (Garshelis 2000).

Prédation, climat, et réchauffement climatique

Mon travail de doctorat a permis de mettre en évidence certains effets du climat et de la prédation sur la survie des individus, avec des conséquences sur la taille des populations. Dans un contexte de réchauffement climatique, j'étais particulièrement intéressée à comprendre l'importance relative du climat et de la prédation sur les changements d'abondance des populations. Bien que le but général de mon doctorat n'était pas de prédire l'effet du réchauffement climatique sur les populations de porcs-épics, nous pouvons émettre certaines suppositions à partir des résultats obtenus.

Mon étude montre que la présence de prédateurs a un effet marqué sur la survie des individus et que les conditions de neige peuvent influencer les probabilités de prédation. Les modélisations climatiques prévoient une augmentation du niveau de précipitation dans la plupart des régions du globe pour le $21^{\text{ème}}$ siècle (Houghton et al. 2001). Dans les régions tempérées, les précipitations sous forme de neige devraient par ailleurs diminuer au profit de précipitations sous forme de pluie. Ces changements dans la quantité et la forme des précipitations hivernales ont donc le potentiel pour affecter les interactions prédateurs-proies, *via* des effets sur les conditions de neige au sol.

D'autre part, mon travail montre un effet de l'environnement thermique et des conditions de neige sur les patrons d'activité des animaux au cours de l'hiver. D'après nos résultats, un réchauffement des températures hivernales devrait favoriser les porcs-épics qui pourraient passer plus de temps dehors à s'alimenter s'il fait plus doux. Cependant, puisque les animaux diminuent le temps passé dehors lorsque l'enfoncement dans la neige est élevé, les effets bénéfiques d'une hausse des températures pourraient être minimisés ou annulés si l'enfoncement dans la neige augmente suite aux changements prévus dans le régime des précipitations. En été, le principal facteur influençant le comportement et la survie des jeunes est la prédation. Le risque de prédation ne semblant pas varier en fonction des conditions météorologiques au cours de l'été, le réchauffement climatique ne devrait pas avoir d'impact direct marqué sur la survie des jeunes. Par contre, des effets indirects peuvent être envisagés par exemple si l'augmentation des précipitations modifie la disponibilité en nourriture pendant la croissance des jeunes (Albon et al. 1987, Langvatn et al. 1996, Post & Stenseth 1999).

Une des étapes essentielles pour prédire les conséquences du réchauffement climatique sur les écosystèmes est de mettre en évidence des relations de cause à effet entre processus biologiques et fluctuations climatiques (Berteaux et al. 2006). Notre étude est essentiellement basée sur la mise en évidence de corrélations entre certaines variables environnementales (i.e. conditions climatiques, risque de prédation) et le comportement ou la survie des porcs-épics. Nous ne pouvons donc pas effectuer de prédictions quant à l'effet des variations climatiques sur les populations de porcs-épics. Néanmoins, en identifiant certains mécanismes possibles par lesquels le climat pourrait agir sur les populations, notre étude permet de générer des hypothèses qui pourraient être testées dans des conditions similaires ou légérement différentes de celles rencontrées pendant notre étude.

J'ai effectué mes recherches dans un contexte particulier où la pression de prédation sur les porcs-épics était très importante, suite à une augmentation récente de l'abondance du pékan dans la région. On montre un effet marqué de la présence de prédateurs sur la survie et le comportement des animaux. On montre aussi les effets de certains facteurs climatiques, mais les effets de la prédation semblent beaucoup plus drastiques que les effets du climat. Une perspective de recherche intéressante serait de comparer l'effet du climat mis en évidence dans notre population à l'effet du climat dans d'autres populations où les prédateurs seraient soit absents, soit en faible abondance. Alternativement, on pourrait effectuer des comparaisons entre populations soumises à des niveaux de prédation similaires d'une population à l'autre, mais à des conditions climatiques différentes (le long d'un gradient nord-sud par exemple). Ceci devrait permettre de mettre en perspective les résultats apportés par notre étude quant à l'importance relative des effets du climat et de la prédation sur le comportement et la survie des individus, et ainsi d'améliorer les connaissances des effets du climat sur la dynamique des populations chez des herbivores de taille moyenne. L'importance relative des facteurs densité-dépendants et densité-indépendants dans la détermination de l'abondance des populations reste en effet un débat d'actualité, et qui reprend toute son ampleur dans le contexte actuel de réchauffement climatique.

"*… the climate change research agenda, when studied at the population level, ties back to the old debate on the relative merits of density-independent and density-dependent processes being responsible for population fluctuations.*" (Kaitala & Ranta 2001).

Annexe 1 Description des microhabitats - chapitre 4

Categories used when describing microhabitats where we placed North American porcupine mounts in Parc National du Bic, Québec, December to March, 2004-2005. We visually estimated the vegetative cover present within 1 m of the mount to classify microhabitats as open or covered.

"*Den*": mount placed in a rock den usually frequented by porcupines: 1 to 3 m from the entrance, depending on den structure,

"*Ground open*": mount placed on the ground, <25% of vegetative cover,

"*Ground covered*": mount placed on the ground, >25% of vegetative cover,

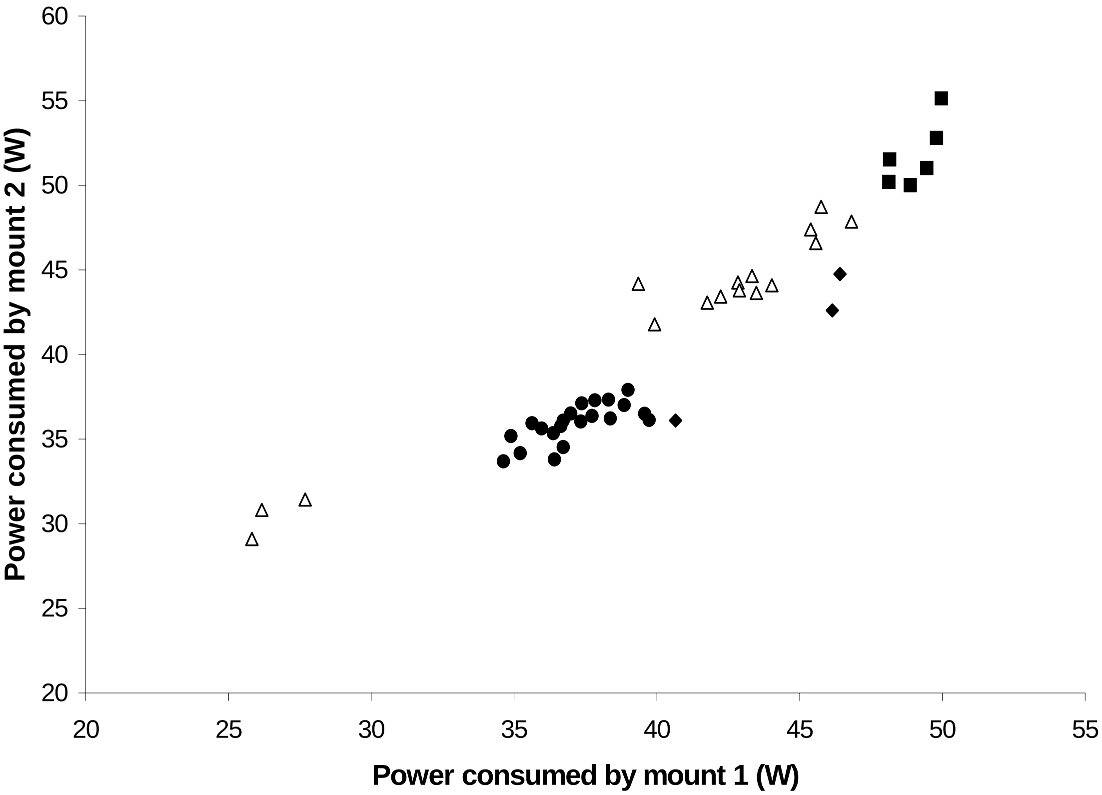
"*Conifer open*": mount placed 2 m above ground in a coniferous tree, <25% of vegetative cover,

"*Conifer covered*": mount placed 2 m above ground in a coniferous tree, >25% of vegetative cover,

"*Deciduous*": mount placed 2 m above ground in a deciduous tree, vegetative cover always <25%

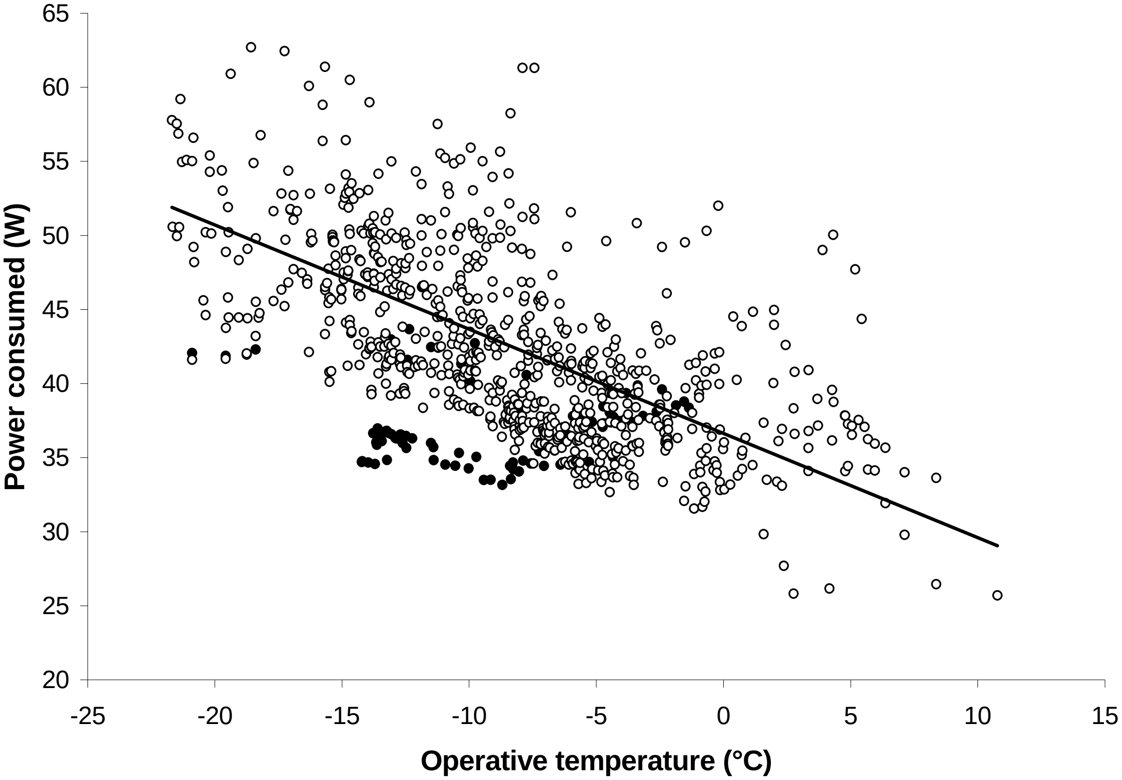
Annexe 2 Étalonnage des modèles en cuivre - chapitre 4

Correlation between power consumed by mounts 1 and 2 (hourly means) when exposed to available conditions of operative temperature during four events of calibration (specified by four different symbols) in Parc National du Bic, Québec, December to March, 2004-2005 (Pearson correlation coefficient: r = 0.94, p<0.001).



Annexe 3 Puissance consommée par les modèles taxidermiques en fonction de la température opérante - chapitre 4

General relationship between power consumed (W) by North American porcupine mounts and operative temperature (°C) measured in the stand (0.3 m above ground) when mounts were placed in "*den*" (filled circles) and non-den (open circles) microhabitats in Parc National du Bic, Québec, December to March, 2004-2005. We observed a negative relationship for non-den microhabitats (y=-0.704*x+36.64, $F_{(1, 789)} = 620.24$, p<0.001, $r^2 = 0.44$).



Références

Aanes, R., & R. Andersen. 1996. The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. *Canadian Journal of Zoology* **74**:1857-1865.

Aars, J., & R. A. Ims. 2002. Intrinsic and climatic determinants of population demography: The winter dynamics of tundra voles. *Ecology* **83**:3449-3456.

Albon, S. D., & T. Clutton-Brock. 1988. Climate and the population dynamics of red deer in Scotland. Pages 93-107 *in* M. B. Usher & D. B. A. Thompson, editors. *Ecological change in the Uplands*. Blackwell Scientific, Oxford, UK.

Albon, S. D., T. H. Clutton-Brock, & F. E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. *Journal of Animal Ecology* **56**:69-81.

Andersen, R., & J. D. C. Linnell. 1998. Ecological correlates of mortality of roe deer fawns in a predator-free environment. *Canadian Journal of Zoology* **76**:1217-1225.

Andren, H., & P. Angelstam. 1988. Elevated predation rates as an edge effect in habitat islands - Experimental evidence. *Ecology* **69**:544-547.

Arakaki, S., & M. Tokeshi. 2005. Microhabitat selection in intertidal gobiid fishes: species- and size-associated variation. *Marine Biology Research* **1**:39-47.

Baker, J. D., & P. M. Thompson. 2007. Temporal and spatial variation in age-specific survival rates of a long-lived mammal, the Hawaiian monk seal. *Proceedings of the Royal Society B-Biological Sciences* **274**:407-415.

Bakken, G. S. 1991. Wind-speed dependence of the overall thermal conductance of fur and feather insulation. *Journal of Thermal Biology* **16**:121-126.

Bakken, G. S., D. J. Erskine, & W. R. Santee. 1983. Construction and operation of heated taxidermic mounts used to measure standard operative temperature. *Ecology* **64**:1658-1662.

Bakken, G. S., & D. M. Gates. 1975. Heat-transfer analysis of animals: some implications for field ecology, physiology, and evolution. Pages 255-290 *in* D. M. Gates & R. B. Schmerl, editors. *Perspectives of biophysical ecology*. Springer-Verlag, New York, USA.

Bakker, E. S., R. C. Reiffers, H. Olff, & J. M. Gleichman. 2005. Experimental manipulation of predation risk and food quality: effect on grazing behaviour in a central-place foraging herbivore. *Oecologia* **146**:157-167.

Barbraud, C., & H. Weimerskirch. 2003. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society of London - Series B: Biological Sciences* **270**:2111-2116.

Beaudoin, C., M. Crete, J. Huot, P. Etcheverry, & S. D. Côté. 2004. Does predation risk affect habitat use in snowshoe hares? *Ecoscience* **11**:370-378.

Begon, M., J. L. Harper, & C. R. Townsend. 1996. Ecology: individuals, populations and communities, 3rd edition. Blackwell Science, Oxford, UK.

Beier, P. 2005. Being ethical as conservation biologists and as a society. *Conservation Biology* **19**:1-2.

Bennett, A. F., R. B. Huey, H. Johnalder, & K. A. Nagy. 1984. The parasol tail and thermoregulatory behavior of the Cape ground-squirrel, *Xerus inauris*. *Physiological Zoology* **57**:57-62.

Berryman, A., & M. Lima. 2006. Deciphering the effects of climate on animal populations: diagnostic analysis provides new interpretation of Soay sheep dynamics. *American Naturalist* **168**:784-795.

Berteaux, D., I. Klvana, & C. Trudeau. 2005. Spring-to-fall mass gain in a northern population of North American porcupines. *Journal of Mammalogy* **86**:514-519.

Berteaux, D., M. M. Humphries, C. J. Krebs, M. Lima, A. G. McAdam, N. Pettorelli, D. Réale, T. Saitoh, E. Tkadlec, R. B. Weladji, & N. Chr. Stenseth. 2006. Constraints to projecting the effects of climate change on mammals. *Climate Research* **32**:151-158.

Bider, J. R. 1968. Animal activity in uncontrolled terrestrial communities as determined by a sand transect technique. *Ecological Monographs* **38**:269-308.

Bleich, V. C., R. T. Bowyer, & J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* **134**:1-50.

Blumstein, D. T. 1998. Quantifying predation risk for refuging animals: a case study with golden marmots. *Ethology* **104**:501-516.

Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, & M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**:1-28.

Bonenfant, C., J. M. Gaillard, F. Klein, & A. Loison. 2002. Sex- and age-dependent effects of population density on life history traits of red deer *Cervus elaphus* in a temperate forest. *Ecography* **25**:446-458.

Bowers, M. A. 1995. Use of space and habitats by the eastern chipmunk, *Tamias striatus*. *Journal of Mammalogy* **76**:12-21.

Bowyer, R. T., J. G. Kie, & V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *Journal of Mammalogy* **79**:415-425.

Bozinovic, E., & R. A. Vasquez. 1999. Patch use in a diurnal rodent: handling and searching under thermoregulatory costs. *Functional Ecology* **13**:602-610.

Brotons, L., M. Orell, K. Lahti, & K. Koivula. 2000. Age-related microhabitat segregation in willow tit *Parus montanus* winter flocks. *Ethology* **106**:993-1005.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research* **1**:49-71.

Bult, A., & C. B. Lynch. 1997. Nesting and fitness: lifetime reproductive success in house mice bidirectionally selected for thermoregulatory nest-building behavior. *Behavior Genetics* **27**:231-240.

Burnham, K. P., & D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York, USA.

Buskirk, S. W., S. C. Forrest, M. G. Raphael, & H. J. Harlow. 1989. Winter resting site ecology of marten in the central Rocky Mountains. *Journal of Wildlife Management* **53**:191-196.

Bustamante, D. M., R. F. Nespolo, E. L. Rezende, & F. Bozinovic. 2002. Dynamic thermal balance in the leaf-eared mouse: The interplay among ambient temperature, body size, and behavior. *Physiological and Biochemical Zoology* **75**:396-404.

Byman, D., D. B. Hay, & G. S. Bakken. 1988. Energetic costs of the winter arboreal microclimate: the gray squirrel in a tree. *International Journal of Biometeorology* **32**:112-122.

Campbell, J. L., M. J. Mitchell, P. M. Groffman, L. M. Christenson, & J. P. Hardy. 2005. Winter in northeastern North America: a critical period for ecological processes. *Frontiers in Ecology and the Environment* **3**:314-322.

Canon, S. K., & F. C. Bryant. 1997. Bed-site characteristics of pronghorn fawns. *Journal of Wildlife Management* **61**:1134-1141.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation, 2nd edition. Sinauer Associates, Sunderland, USA.

Chappell, M. A. 1981. Standard operative temperatures and cost of thermoregulation in the Arctic ground-squirrel, *Spermophilus undulatus*. *Oecologia* **49**:397-403.

Chappell, M. A., & G. A. Bartholomew. 1981. Activity and thermoregulation of the antelope ground-squirrel *Ammospermophilus leucurus* in winter and summer. *Physiological Zoology* **54**:215-223.

Chappell, M. A., A. V. Calvo, & H. C. Heller. 1978. Hypothalamic thermosensitivity and adaptations for heat-storage behavior in three species of chipmunks (*Eutamias*) from different thermal environments. *Journal of Comparative Physiology B* **125**:175-183.

Charlesworth, B. 1994. Evolution in age-structured populations., 2nd edition. Cambridge University Press, Cambridge, UK.

Choquet, R., A.-M. Reboulet, R. Pradel, O. Gimenez, & J.-D. Lebreton. 2003. User's manual for U-CARE. Mimeographed document, CEFE/CNRS, Montpellier, France. (http://ftp.cefe.cnrs.fr/biom/Soft-CR/).

Choquet, R., A.-M. Reboulet, R. Pradel, O. Gimenez, & J. D. Lebreton. 2004. M-SURGE: new software specifically designed for multistate capture recapture models. *Animal Biodiversity and Conservation* **27**:207-215.

Choquet, R., A.-M. Reboulet, R. Pradel, O. Gimenez, & J. D. Lebreton. 2005. M-SURGE 1.7 user’s manual. CEFE/CNRS, Montpellier, France. (http://ftp.cefe.cnrs.fr/biom/Soft-CR/).

Christian, K., C. R. Tracy, & W. P. Porter. 1983. Seasonal shifts in body-temperature and use of microhabitats by Galapagos land iguanas (*Conolophus*, Pallidus). *Ecology* **64**:463-468.

Ciuti, S., P. Bongi, S. Vassale, & M. Apollonio. 2006. Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. *Journal of Zoology* **268**:97-107.

Clark, D. A., I. Stirling, & W. Calvert. 1997. Distribution, characteristics, and use of earth dens and related excavations by polar bears on the Western Hudson Bay lowlands. *Arctic* **50**:158-166.

Close, D. C., C. McArthur, A. E. Hagerman, & H. Fitzgerald. 2005. Differential distribution of leaf chemistry in eucalypt seedlings due to variation in whole-plant nutrient availability. *Phytochemistry* **66**:215-221.

Clutton-Brock, T. H., M. Major, S. D. Albon, & F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology* **56**:53-67.

Compton, B. W., J. M. Rhymer, & M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. *Ecology* **83**:833-843.

Comtois, A., & D. Berteaux. 2005. Impacts of mosquitoes and black flies on defensive behaviour and microhabitat use of the North American porcupine (*Erethizon dorsatum*) in southern Quebec. *Canadian Journal of Zoology* **83**:754-764.

Cook, J. G., L. L. Irwin, L. D. Bryant, R. A. Riggs, & J. W. Thomas. 1998. Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. *Wildlife Monographs*:5-61.

Côté, S. D., & M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**:230-238.

Coulson, T., S. Albon, F. Guinness, J. Pemberton, & T. CluttonBrock. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). *Ecology* **78**:852-863.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, & B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. *Science* **292**:1528-1531.

Cox, D. R. 1972. Regression models and life-tables. *Journal of the Royal Statistical Society Series B-Statistical Methodology* **34**:187-220.

Craig, E. H., & B. L. Keller. 1986. Movements and home range of porcupines, *Erethizon dorsatum*, in Idaho shrub desert. *Canadian Field Naturalist* **100**:167-173.

Crampe, J.-P., J.-M. Gaillard, & A. Loison. 2002. L'enneigement hivernal: un facteur de variation du recrutement chez l'isard (*Rupicapra pyrenaica pyrenaica*). *Canadian Journal of Zoology* **80**:1306-1312.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, & M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* **86**:3387-3397.

Crespin, L., R. Verhagen, N. C. Stenseth, N. G. Yoccoz, A. C. Prevot-Julliard, & J. D. Lebreton. 2002. Survival in fluctuating bank vole populations: seasonal and yearly variations. *Oikos* **98**:467-479.

Currie, R. G. 1993. Luni-solar 18.6 and 10-11 year solar cycle signals in USA air temperature records. *International Journal of Climatology* **13**:31-50.

Curtis, J. D. 1941. The silvicultural significance of the porcupine. *Journal of Forestry* **39**:583-594.

Curtis, J. D. 1944. Appraisal of porcupine damage. *Journal of Wildlife Management* **8**:88-91.

Daly, M., M. Wilson, P. R. Behrends, & L. F. Jacobs. 1990. Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. *Animal Behaviour* **40**:380-389.

Danchin, É., L.-A. Giraldeau, & F. Cézilly. 2005. Écologie comportementale. Dunod, Paris, France.

Davidson, J., & H. G. Andrewartha. 1948. The influence of rainfall, evaporation and atmospheric temperature on fluctuations in the size of a natural population of *Thrips imaginis* (Thysanoptera). *Journal of Animal Ecology* **17**:200-222.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, & S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**:783-786.

Dawson, R. D., C. C. Lawrie, & E. L. O'Brien. 2005. The importance of microclimate variation in determining size, growth and survival of avian offspring: experimental evidence from a cavity nesting passerine. *Oecologia* **144**:499-507.

Demarchi, M. W., & F. L. Bunnell. 1993. Estimating forest canopy effects on summer thermal cover for Cervidae (deer family). *Canadian Journal of Forest Research* **23**:2419-2426.

Demarchi, M. W., & F. L. Bunnell. 1995. Forest cover selection and activity of cow moose in summer. *Acta Theriologica* **40**:23-36.

DeMatteo, K. E., & H. J. Harlow. 1997. Thermoregulatory responses of the North American porcupine (*Erethizon dorsatum*) to decreasing ambient temperature and increasing wind speed. *Comparative Biochemistry and Physiology- Part B: Biochemistry & Molecular Biology* **116B**:339-346.

Dodge, W. E. 1982. Porcupine. Pages 355-366 *in* J. A. Chapman & G. A. Feldhamer, editors. *Wild mammals of North America: biology, management, and economics*. Johns Hopkins University Press, Baltimore, USA.

Doolan, S. P., & D. W. Macdonald. 1997. Breeding and juvenile survival among slender-tailed meerkats (*Suricata suricatta*) in the south-western Kalahari: ecological and social influences. *Journal of Zoology* **242**:309-327.

Douglas, C. L., & D. M. Leslie, Jr. 1986. Influence of weather and density of lamb survival of desert mountain sheep. *Journal of Wildlife Management* **50**:153-156.

Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, & J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience* **11**:321-328.

Dzialowski, E. M. 2005. Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology* **30**:317-334.

Earle, R. D., & K. R. Kramm. 1982. Correlation between fisher and porcupine abundance in upper Michigan. *American Midland Naturalist* **107**:244-249.

Ebensperger, L. A., & M. J. Hurtado. 2005. On the relationship between herbaceous cover and vigilance activity of degus (*Octodon degus*). *Ethology* **111**:593-608.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. *Ecology* **83**:2841-2854.

Fairbanks, W. S. 1993. Birth-date, birth-weight, and survival in pronghorn fawns. *Journal of Mammalogy* **74**:129-135.

Farmer, C. J., D. K. Person, & R. T. Bowyer. 2006. Risk factors and mortality of black-tailed deer in a managed forest landscape. *Journal of Wildlife Management* **70**:1403-1415.

Farnsworth, E. J., & J. Rosovsky. 1993. The ethics of ecological field experimentation. *Conservation Biology* **7**:463-472.

Fisher, D. O., & A. W. Goldizen. 2001. Maternal care and infant behaviour of the bridled nailtail wallaby (*Onychogalea fraenata*). *Journal of Zoology* **255**:321-330.

Fitzgibbon, C. D. 1993. Antipredator strategies of female Thomson gazelles with hidden fawns. *Journal of Mammalogy* **74**:758-762.

Forchhammer, M. C., T. H. Clutton-Brock, J. Lindström, & S. D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. *Journal of Animal Ecology* **70**:721-729.

Forchhammer, M. C., N. C. Stenseth, E. Post, & R. Langvatn. 1998. Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**:341-350.

Forman, D. W., & K. Williamson. 2005. From the field: an alternative method for handling and marking small carnivores without the need for sedation. *Wildlife Society Bulletin* **33**:313-316.

Fortin, D. 2001. The use of heated taxidermic mounts in studies of ecological energetics. *Mammalia* **65**:195-204.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, & J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**:1320-1330.

Fortin, D., & G. Gauthier. 2000. The effect of postural adjustment on the thermal environment of greater snow goose goslings. *Canadian Journal of Zoology* **78**:817-821.

Fournier, F., & D. W. Thomas. 1999. Thermoregulation and repeatability of oxygen-consumption measurements in winter-acclimatized North American porcupines (*Erethizon dorsatum*). *Canadian Journal of Zoology* **77**:194-202.

Frohlich, C. 2000. Observations of irradiance variations. *Space Science Reviews* **94**:15-24.

Gaillard, J. M., M. Festa-Bianchet, & N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution* **13**:58-63.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, & C. Toiego. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics* **31**:367-393.

Gaillard, J. M., A. Loison, & C. Toiego. 2003. Variation in life history traits and realistic population models for wildlife management: the case of ungulates. Pages 115-132 *in* M. Festa-Bianchet & M. Apollonio, editors. *Animal behavior and wildlife conservation*. Island Press, Washington, USA.

Gaillard, J. M., D. Pontier, D. Allaine, J. D. Lebreton, J. Trouvilliez, & J. Clobert. 1989. An analysis of demographic tactics in birds and mammals. *Oikos* **56**:59-76.

Gaillard, J. M., & N. G. Yoccoz. 2003. Temporal variation in survival of mammals: A case of environmental canalization? *Ecology* **84**:3294-3306.

Gaillard, J. M., N. G. Yoccoz, J. D. Lebreton, C. Bonenfant, S. Devillard, A. Loison, D. Pontier, & D. Allaine. 2005. Generation time: a reliable metric to measure life-history variation among mammalian populations. *American Naturalist* **166**:119-123.

Gaines, M. S., & L. R. McClenaghan. 1980. Dispersal in small mammals. *Annual Review of Ecology and Systematics* **11**:163-196.

Garshelis, D. L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. Pages 111-164 *in* L. Boitani & T. K. Fuller, editors. *Research techniques in animal ecology- Controversies and consequences*. Columbia University Press, New York, USA.

Gauthier, G., R. Pradel, S. Menu, & J. D. Lebreton. 2001. Seasonal survival of greater snow geese and effect of hunting under dependence in sighting probability. *Ecology* **82**:3105-3119.

Gese, E. M., R. L. Ruff, & R. L. Crabtree. 1996a. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. *Canadian Journal of Zoology* **74**:769-783.

Gese, E. M., R. L. Ruff, & R. L. Crabtree. 1996b. Intrinsic and extrinsic factors influencing coyote predation of small mammals in Yellowstone National Park. *Canadian Journal of Zoology* **74**:784-797.

Gilbert, B. A., & K. J. Raedeke. 2004. Recruitment dynamics of black-tailed deer in the western Cascades. *Journal of Wildlife Management* **68**:120-128.

Gillett, N. P., H. F. Graf, & T. J. Osborn. 2003. Climate change and the North Atlantic Oscillation. *in* J. W. Hurrell, Y. Kushnir, G. Ottersen, & M. Visbeck, editors. *The North Atlantic Oscillation: climatic significance and environmental impact*. American Geophysical Union, Washington, USA.

Grant, B. W., & A. E. Dunham. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* **69**:167-176.

Griesemer, S. J., T. K. Fuller, & R. M. Degraaf. 1996. Denning patterns of porcupines, *Erethizon dorsatum*. *Canadian Field Naturalist* **110**:634-637.

Griesemer, S. J., M. O. Hale, U. Roze, & T. K. Fuller. 1999. Capturing and marking adult North American porcupines. *Wildlife Society Bulletin* **27**:310-313.

Grondin, P., J. Blouin, & P. Racine. 1999. Rapport de classification écologique de sous-domaine bioclimatique de la sapinière à bouleau jaune de l'Est. Ministère des Ressources Naturelles du Québec, Direction des inventaires forestiers, Quebec, Canada.

Guthery, F. S., A. R. Rybak, S. D. Fuhlendorf, T. L. Hiller, S. G. Smith, W. H. Puckett, & R. A. Baker. 2005. Aspects of the thermal ecology of bobwhites in North Texas. *Wildlife Monographs* **159**:1-36.

Haim, A., R. J. van Aarde, & J. D. Skinner. 1992. Burrowing and huddling in newborn porcupine: the effect on thermoregulation. *Physiology & Behavior* **52**:247-250.

Hairston, N. G., F. E. Smith, & L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421-425.

Hale, M. B., & T. K. Fuller. 1996. Porcupine (*Erethizon dorsatum*) demography in central Massachusetts. *Canadian Journal of Zoology* **74**:480-484.

Hale, M. O., & T. K. Fuller. 1999. Estimating porcupine (*Erethizon dorsatum* Linnaeus, 1758) density using radiotelemetry and replicated mark-resight techniques. *International Journal of Mammalian Biology* **64**:85-90.

Halfpenny, J. C., & R. D. Ozanne. 1989. Winter, an ecological handbook. Johnson Books, Boulder, USA.

Harrington, R., I. Woiwod, & T. Sparks. 1999. Climate change and trophic interactions. *Trends in Ecology & Evolution* **14**:146-150.

Hayes, J. P., J. R. Speakman, & P. A. Racey. 1992. The contributions of local heating and reducing exposed surface-area to the energetic benefits of huddling by short-tailed field voles (*Microtus agrestis*). *Physiological Zoology* **65**:742-762.

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. *Journal of Animal Ecology* **74**:226-233.

Hebblewhite, M., D. H. Pletscher, & P. C. Paquet. 2002. Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology* **80**:789-799.

Hik, D. S. 1995. Does risk of predation influence population-dynamics - Evidence from the cyclic decline of snowshoe hares. *Wildlife Research* **22**:115-129.

Hirose, T., M. J. A. Werger, & J. W. A. Vanrheenen. 1989. Canopy development and leaf nitrogen distribution in a stand of *Carex acutiformis*. *Ecology* **70**:1610-1618.

Hodell, D. A., M. Brenner, J. H. Curtis, & T. Guilderson. 2001. Solar forcing of drought frequency in the Maya lowlands. *Science* **292**:1367-1370.

Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutierrez, & G. M. J. Mohren. 2001. El Nino effects on the dynamics of terrestrial ecosystems. *Trends in Ecology & Evolution* **16**:89-94.

Hoogland, J. L., K. E. Cannon, L. M. DeBarbieri, & T. G. Manno. 2006. Selective predation on Utah prairie dogs. *American Naturalist* **168**:546-552.

Hosmer, D. W., & S. Lemeshow. 1989. Applied logistic regression. Wiley, New York, USA.

Houghton, J. T., Y. Ding, D. J. Griggs, M. Noguer, P. J. Van der Linden, X. Dai, K. Maskell, & C. A. Johnson. 2001. Climate change 2001: The scientific basis. Cambridge University Press, Cambridge, UK.

Huey, R. B. 1991. Physiological consequences of habitat selection. *American Naturalist* **137**:S91-S115.

Huggard, D. J. 1993. Effect of snow depth on predation and scavenging by grey wolves. *Journal of Wildlife Management* **57**:382-388.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology & Evolution* **15**:56-61.

Hull, D. 1973. Thermoregulation in young mammals. Pages 167-200 *in* G. C. Whittow, editor. *Comparative physiology of temperature regulation: vol.3. Special aspects of thermoregulation*. Academic Press, New York, USA.

Humphries, M. M., S. Boutin, D. W. Thomas, J. D. Ryan, C. Selman, A. G. McAdam, D. Berteaux, & J. R. Speakman. 2005. Expenditure freeze: the metabolic response of small mammals to cold environments. *Ecology Letters* **8**:1326-1333.

Hurrell, J. W. 1995. Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* **269**:676-679.

Ilse, L. M., & E. C. Hellgren. 2001. Demographic and behavioral characteristics of North American porcupines (*Erethizon dorsatum*) in pinyon-juniper woodlands of Texas. *American Midland Naturalist* **146**:329-338.

Irving, L., H. Krog, & M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. *Physiological Zoology* **28**:173-185.

Jedrzejewski, W., B. Jedrzejewska, K. Zub, & W. K. Nowakowski. 2000. Activity patterns of radio-tracked weasels *Mustela nivalis* in Bialowieza National Park (E Poland). *Annales Zoologici Fennici* **37**:161-168.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, N. Selva, K. Zub, & L. Szymura. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza primeval forest (Poland). *Ecology* **83**:1341-1356.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**:65-71.

Jorgenson, J. T., M. FestaBianchet, J. M. Gaillard, & W. D. Wishart. 1997. Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* **78**:1019-1032.

Kaitala, V., & E. Ranta. 2001. Is the impact of environmental noise visible in the dynamics of age-structured populations? *Proceedings of the Royal Society of London- Series B: Biological Sciences* **268**:1769-1774.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, & T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. *Journal of Wildlife Management* **64**:450-462.

Keller, F. L. 1935. Porcupines killed and eaten by a coyote. *Journal of Mammalogy* **16**:232.

Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* **80**:1114-1129.

Klvana, I., D. Berteaux, & B. Cazelles. 2004. Porcupine feeding scars and climatic data show ecosystem effects of the solar cycle. *American Naturalist* **164**:283-297.

Korslund, L., & H. Steen. 2006. Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology* **75**:156-166.

Kortner, G., & F. Geiser. 2000. Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* **123**:350-357.

Krebs, C. J. 1994. Ecology. Harper Collins College Publishers, New York, USA.

Krebs, C. J., & D. Berteaux. 2006. Problems and pitfalls in relating climate variability to population dynamics. *Climate Research* **32**:143-149.

Kreith, F., & W. Z. Black. 1980. Basic heat transfer. Harper & Row, New York, USA.

Langvatn, R., S. D. Albon, T. Burkey, & T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. *Journal of Animal Ecology* **65**:653-670.

Larochelle, J. 1998. Comments on a negative appraisal of taxidermic mounts as tools for studies of ecological energetics. *Physiological Zoology* **71**:596-598.

Lean, J., J. Beer, & R. Bradley. 1995. Reconstruction of solar irradiance since 1610-Implications for climate-change. *Geophysical Research Letters* **22**:3195-3198.

Lebreton, J.-D., K. P. Burnham, J. Clobert, & D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**:67-118.

Lenart, E. A., R. T. Bowyer, J. Ver Hoef, & R. W. Ruess. 2002. Climate change and caribou: effects of summer weather on forage. *Canadian Journal of Zoology* **80**:664-678.

Lensing, J. R., & D. H. Wise. 2006. Predicted climate change alters the indirect effect of predators on an ecosystem process. *Proceedings of the National Academy of Sciences of the United States of America* **103**:15502-15505.

Lent, P. C. 1974. Mother-infant relationships in ungulates. Pages 14-54 *in* V. Geist & F. Walther, editors. *The behaviour of ungulates and its relation to management*. International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Leon, M. 1986. Development of thermoregulation. Pages 297-322 *in* E. M. Blass, editor. *Handbook of behavioral neurobiology: vol.8. Developmental psychobiology and developmental neurobiology*. Plenum Press, New York, USA.

Levins, R. 1968. Evolution in changing environnements. Princeton University Press, Princeton, USA.

Lima, M., J. E. Keymer, & F. M. Jaksic. 1999. El nino-Southern oscillation-driven rainfall variability and delayed density dependence cause rodent outbreaks in Western South America: linking demography and population dynamics. *American Naturalist* **5**:476-491.

Lima, M., N. Stenseth, & F. M. Jaksic. 2002a. Population dynamics of a South American rodent: seasonal structure interacting with climate, density dependence and predator effects. *Proceedings of Royal Society of London - Series B: Biological Sciences* **269**:2579-2586.

Lima, M., N. C. Stenseth, & F. M. Jaksic. 2002b. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. *Ecology Letters* **5**:273-284.

Lima, M., N. C. Stenseth, N. G. Yoccoz, & F. M. Jaksic. 2001. Demography and population dynamics of the mouse opossum (*Thylamys elegans*) in semi-arid Chile: seasonality, feedback structure and climate. *Proceedings of Royal Society of London - Series B: Biological Sciences* **268**:2053-2064.

Lima, S. L., & L. M. Dill. 1990. Behavioral decisions made under the risk of predation - A review and prospectus. *Canadian Journal of Zoology* **68**:619-640.

Lin, D. Y., & L. J. Wei. 1989. The robust inference for the Cox proportional hazards model. *Journal of the American Statistical Association* **84**:1074-1078.

Lindstrom, E. R., & B. Hornfeldt. 1994. Vole cycles, snow depth and fox predation. *Oikos* **70**:156-160.

Linnell, J. D. C., R. Aanes, & R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. *Wildlife Biology* **1**:209-223.

Loison, A., J. M. Gaillard, & H. Houssin. 1994. New insight on survivorship of female chamois (*Rupicapra rupicapra*) from observation of marked animals. *Canadian Journal of Zoology* **72**:591-597.

Loison, A., & R. Langvatn. 1998. Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. *Oecologia* **116**:489-500.

Lustick, S., B. Battersby, & M. Kelty. 1978. Behavioral thermoregulation - Orientation toward sun in herring gulls. *Science* **200**:81-83.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, & W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies, Second edition. Kluwer Academic Publishers, Norwell, USA.

Martin, S. K. 1994. Feeding ecology of American martens and fishers. *in* S. W. Buskirk, A. Harestad, M. Raphael, & R. A. Powell, editors. *Martens, sables, and fishers: biology and conservation*. Cornell University Press, Ithaca, USA.

Mathisen, J. H., A. Landa, R. Andersen, & J. L. Fox. 2003. Sex-specific differences in reindeer calf behavior and predation vulnerability. *Behavioral Ecology* **14**:10-15.

McLoughlin, P. D., M. S. Boyce, T. Coulson, & T. Clutton-Brock. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society - Series B: Biological Sciences* **273**:1449-1454.

McLoughlin, P. D., J. S. Dunford, & S. Boutin. 2005. Relating predation mortality to broad-scale habitat selection. *Journal of Animal Ecology* **74**:701-707.

McNab, B. K. 1970. Body weight and energetics of temperature regulation. *Journal of Experimental Biology* **53**:329-&.

Merritt, J. F., M. Lima, & F. Bozinovic. 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. *Oikos* **94**:505-514.

Merritt, J. F., & D. A. Zegers. 2002. Maximizing survivorship in cold: thermogenic profiles of non-hibernating mammals. *Acta Theriologica* **47**:221-234.

Michard, D., A. Ancel, J. P. Gender, J. Lage, Y. Le Maho, T. Zorn, L. Gangloff, A. Schierer, K. Stuyf, & G. Wey. 1995. Non-invasive bird tagging. *Nature* **376**:649.

Milner, J. M., D. A. Elston, & S. D. Albon. 1999. Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *Journal of Animal Ecology* **68**:1235-1247.

Minteer, B. A., & J. P. Collins. 2005. Why we need an "ecological ethics". *Frontiers in Ecology and the Environment* **3**:332-337.

Molinari-Jobin, A., P. Molinari, A. Loison, J. M. Gaillard, & U. Breitenmoser. 2004. Life cycle period and activity of prey influence their susceptibility to predators. *Ecography* **27**:323-329.

Moreno, S., R. Villafuerte, & M. Delibes. 1996. Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. *Canadian Journal of Zoology* **74**:1656-1660.

Morin, P., & D. Berteaux. 2003. Immobilization of North American porcupines (*Erethizon dorsatum*) using ketamine and xylazine. *Journal of Wildlife Diseases* **39**:675-682.

Morin, P., D. Berteaux, & I. Klvana. 2005. Hierarchical habitat selection by North American porcupines in southern boreal forest. *Canadian Journal of Zoology* **83**:1333-1342.

Murray, D. L., & S. Boutin. 1991. The influence of snow on lynx and coyote movements- Does morphology affect behavior? *Oecologia* **88**:463-469.

Mysterud, A., & E. Ostbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildlife Society Bulletin* **27**:385-394.

Mysterud, A., N. G. Yoccoz, N. C. Stenseth, & R. Langvatn. 2000. Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *Journal of Animal Ecology* **69**:959-974.

Nelson, T. A., & A. Woolf. 1987. Mortality of white-tailed deer fawns in southern Illinois. *Journal of Wildlife Management* **51**:326-329.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. *Australian Journal of Zoology* **2**:9-65.

Nielson, S. E., M. S. Boyce, G. B. Stenhouse, & R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus* **13**:45-56.

Niewiarowski, P. H. 2001. Energy budgets, growth rates, and thermal constraints: toward an integrative approach to the study of life-history variation. *American Naturalist* **157**:421-433.

Norrdahl, K., & E. Korpimaki. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology* **79**:226-232.

Olson, K. A., T. K. Fuller, G. B. Schaller, B. Lhagvasuren, & D. Odonkhuu. 2005. Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*). *Journal of Zoology* **265**:227-233.

Ottersen, G., B. Planque, A. Belgrano, E. Post, P. C. Reid, & N. C. Stenseth. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia* **128**:1-14.

Owen-Smith, N., & M. G. L. Mills. 2006. Manifold interactive influences on the population dynamics of a multispecies ungulate assemblage. *Ecological Monographs* **76**:73-92.

Ozgul, A., K. B. Armitage, D. T. Blumstein, & M. K. Oli. 2006. Spatiotemporal variation in survival rates: implications for population dynamics of yellow-bellied marmots. *Ecology* **87**:1027-1037.

Parmesan, C., & G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37-42.

Patten, M. A., D. H. Wolfe, E. Shochat, & S. K. Sherrod. 2005. Effects of microhabitat and microclimate selection on adult survivorship of the lesser prairie-chicken. *Journal of Wildlife Management* **69**:1270-1278.

Patterson, B. R., L. K. Benjamin, & F. Messier. 1998. Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. *Canadian Journal of Zoology* **76**:1885-1897.

Patterson, B. R., & F. Messier. 2000. Factors influencing killing rates of white-tailed deer by coyotes in eastern Canada. *Journal of Wildlife Management* **64**:721-732.

Perry, C. A. 1994. Solar-irradiance variations and regional precipitation fluctuations in the Western USA. *International Journal of Climatology* **14**:969-983.

Perry, C. A. 2006. Midwestern streamflow, precipitation, and atmospheric vorticity influenced by Pacific sea-surface temperatures and total solar-irradiance variations. *International Journal of Climatology* **26**:207-218.

Peters, D. P. C., & J. E. Herrick. 2004. Strategies for ecological extrapolation. *Oikos* **106**:627-636.

Petersen, J. E., & A. Hastings. 2001. Dimensional approaches to scaling experimental ecosystems: Designing mousetraps to catch elephants. *American Naturalist* **157**:324-333.

Petit, J. R., J. Jouzel, D. Raynaud, N. I. Barkov, J. M. Barnola, I. Basile, M. Bender, J. Chappellaz, M. Davis, G. Delaygue, M. Delmotte, V. M. Kotlyakov, M. Legrand, V. Y. Lipenkov, C. Lorius, L. Pepin, C. Ritz, E. Saltzman, & M. Stievenard. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**:429-436.

Pettorelli, N., J. M. Gaillard, N. G. Yoccoz, P. Duncan, D. Maillard, D. Delorme, G. Van Laere, & C. Toigo. 2005. The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. *Journal of Animal Ecology* **74**:972-981.

Philander, S. G. H. 1990. El Nino, la Nina and the Southern oscillation. Academic Press, San Diego, USA.

Portier, C., M. Festa-Bianchet, J. M. Gaillard, J. T. Jorgenson, & N. G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). *Journal of Zoology* **245**:271-278.

Post, E. 2005. Large-scale spatial gradients in herbivore population dynamics. *Ecology* **86**:2320-2328.

Post, E., & M. C. Forchhammer. 2001. Pervasive influence of large-scale climate in the dynamics of a terrestrial vertebrate community. *Biomedcentral Ecology* **1**:5.

Post, E., & M. C. Forchhammer. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature* **420**:168-171.

Post, E., M. C. Forchhammer, N. C. Stenseth, & R. Langvatn. 1999a. Extrinsic Modification of Vertebrate Sex Ratios by Climatic Variation. *American Naturalist [Am. Nat.]*. **154**:194-204.

Post, E., R. O. Peterson, N. C. Stenseth, & B. E. McLaren. 1999b. Ecosystem consequences of wolf behavioural response to climate. *Nature* **401**:905-907.

Post, E., & N. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. *Journal of Animal Ecology* **67**:537-543.

Post, E., & N. C. Stenseth. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology* **80**:1322-1339.

Poulin, J. F., H. Jolicoeur, P. Canac-Marquis, & S. Larivière. 2006. Investigation sur les facteurs à l'origine de la hausse de la récolte de pékans (*Martes pennanti*) au Québec depuis 1984. Ministère des Ressources Naturelles et de la Faune, Direction du développement de la faune et Université du Québec à Rimouski, Département de biologie et des sciences de la santé, Quebec, Canada.

Pounds, J. A., M. P. L. Fogden, & J. H. Campbell. 1999. Biological response to climate change on a tropical mountain. *Nature* **398**:611-615.

Powell, R. A. 1993. The fisher. University of Minnesota Press, Minneapolis, USA.

Powell, R. A., & R. B. Brander. 1977. Adaptations of fishers and porcupines to their predator prey system. *in* R. L. Phillips & C. Jonkel, editors. *Proceedings for 1975 predator symposium*. Montana Forest Conservation Experimental Station, University of Montana, Missoula, USA.

Powell, R. A., & G. Proulx. 2003. Trapping and marking terrestrial mammals for research: integrating ethics, performance criteria, techniques, and common sense. *Ilar Journal* **44**:259-276.

Pradel, R., C. M. A. Wintrebert, & O. Gimenez. 2003. A proposal for goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics* **59**:43-53.

Prestrud, P. 1991. Adaptations by the Arctic fox (*Alopex lagopus*) to the polar winter. *Arctic* **44**:132-138.

Putman, R. J., J. Langbein, A. J. M. Hewison, & S. K. Sharma. 1996. Relative roles of density-dependent and density-independent factors in population dynamics of British deer. *Mammal Review* **26**:81-101.

Rachlow, J. L., & R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *Journal of Zoology* **245**:457-465.

Ripple, W. J., & R. L. Beschta. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *Bioscience* **54**:755-766.

Robbins, C. T. 1993. Wildlife feeding and nutrition. Academic Press, San Diego, USA.

Robinette, W. L., J. S. Gashwiler, & O. W. Morris. 1959. Food habits of the cougar in Utah and Nevada. *Journal of Wildlife Management* **23**:261-273.

Roll, U., T. Dayan, & N. Kronfeld-Schor. 2006. On the role of phylogeny in determining activity patterns of rodents. *Evolutionary Ecology* **20**:479-490.

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

Root, T. L., & S. H. Schneider. 1995. Ecology and climate- Research strategies and implications. *Science* **269**:334-341.

Rosenberg, N. J. 1974. Microclimate: the biological environment. Wiley, New York, USA.

Rosenzweig, M. L. 1981. A theory of habitat selection. *Ecology* **62**:327-335.

Rosenzweig, M. L. 1991. Habitat selection and population interactions - The search for mechanism. *American Naturalist* **137**:S5-S28.

Roze, U. 1984. Winter foraging by individual porcupines. *Canadian Journal of Zoology* **62**:2425-2428.

Roze, U. 1987. Denning and winter range of the porcupine. *Canadian Journal of Zoology* **65**:981-986.

Roze, U. 1989. The North American porcupine. Smithsonian Institution Press, Washington, USA.

Saether, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: A search for mechanisms. *Trends in Ecology & Evolution* **12**:143-149.

Saether, B. E., & O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* **81**:642-653.

Saitoh, T., B. Cazelles, J. O. Vik, H. Viljugrein, & N. C. Stenseth. 2006. Effects of regime shifts on the population dynamics of the grey-sided vole in Hokkaido, Japan. *Climate Research* **32**:109-118.

Sala, E. 2006. Top predators provide insurance against climate change. *Trends in Ecology & Evolution* **21**:479-480.

Santee, W. R., & G. S. Bakken. 1987. Social displays in red-winged blackbirds (*Agelaius phoeniceus*): sensitivity to thermoregulatory costs. *Auk* **104**:413-420.

SAS. 2002. SAS statistical software. SAS Institute, Cary, USA.

Scantlebury, M., N. C. Bennett, J. R. Speakman, N. Pillay, & C. Schradin. 2006. Huddling in groups leads to daily energy savings in free-living African four-striped grass mice, *Rhabdomys pumilio*. *Functional Ecology* **20**:166-173.

Schemper, M. 1990. The explained variation in proportional hazards regression. *Biometrika* **77**:216-218.

Schmitz, O. 2003. Ecosystem responses to global climate change: moving beyond color mapping. *Bioscience* **53**:1199-1205.

Scholander, P. F., R. Hock, V. Walters, & L. Irving. 1950a. Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biological Bulletin* **99**:259-271.

Scholander, P. F., R. Hock, V. Walters, F. Johnson, & L. Irving. 1950b. Heat regulation in some arctic and tropical mammals and birds. *Biological Bulletin* **99**:237-258.

Schooley, R. L., P. B. Sharpe, & B. VanHorne. 1996. Can shrub cover increase predation risk for a desert rodent? *Canadian Journal of Zoology* **74**:157-163.

Schooley, R. L., B. Vanhorne, & K. P. Burnham. 1993. Passive integrated transponders for marking free-ranging Townsend ground-squirrels. *Journal of Mammalogy* **74**:480-484.

Sealander, J. A. 1952. The relationship of nest protection and huddling to survival of *Peromyscus* at low temperature. *Ecology* **33**:63-71.

Sears, M. W., J. P. Hayes, C. S. O'Connor, K. Geluso, & J. S. Sedinger. 2006. Individual variation in thermogenic capacity affects above-ground activity of high-altitude deer mice. *Functional Ecology* **20**:97-104.

Selas, V., A. Hogstad, S. Kobro, & T. Rafoss. 2004. Can sunspot activity and ultraviolet-B radiation explain cyclic outbreaks of forest moth pest species?

Proceedings of the Royal Society - Series B: Biological Sciences **271**:1897-1901.

Selas, V., & J. O. Vik. 2006. Possible impact of snow depth and ungulate carcasses on red fox (*Vulpes vulpes*) populations in Norway, 1897-1976. *Journal of Zoology* **269**:299-308.

Sendor, T., & M. Simon. 2003. Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. *Journal of Animal Ecology* **72**:308-320.

Sharpe, P. B., & B. Van Horne. 1999. Relationships between the thermal environment and activity of Piute ground squirrels (*Spermophilus mollis*). *Journal of Thermal Biology* **24**:265-278.

Sinclair, A. R. E., & J. M. Gosline. 1997. Solar activity and mammal cycles in the Northern hemisphere. *American Naturalist* **149**:776-784.

Sinclair, A. R. E., J. M. Gosline, G. Holdsworth, C. J. Krebs, S. Boutin, J. N. M. Smith, R. Boonstra, & M. Dale. 1993. Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. *American Naturalist* **141**:173-198.

Sokal, R. R., & F. J. Rohlf. 1981. Biometry, 2nd edition. Freeman, W.H., New York, USA.

Soto-Gamboa, M., M. Rosenmann, & F. Bozinovic. 1999. Thermal ecology of the Humboldt penguin (*Spheniscus humboldti*): effects of nest-site selection on adults and chicks survival. *Revista Chilena De Historia Natural* **72**:447-455.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.

Stefan, C. I., & C. J. Krebs. 2001. Reproductive changes in a cyclic population of snowshoe hares. *Canadian Journal of Zoology* **79**:2101-2108.

Stenseth, N. C., K.-S. Chan, H. Tong, R. Boonstra, S. Boutin, C. J. Krebs, E. Post, M. O'Donoghue, N. G. Yoccoz, M. C. Forchhammer, & J. W. Hurrell. 1999. Common dynamic structure of Canada lynx populations within three climatic regions. *Science* **285**:1071-1073.

Stenseth, N. C., H. Viljugrein, W. Jedrzejewski, A. Mysterud, & Z. Pucek. 2002. Population dynamics of *Clethrionomys glareolus* and *Apodemus flavicollis*: seasonal components of density dependence and density independence. *Acta Theriologica* **47**:39-67.

Stenseth, N. C., G. Ottersen, J. W. Hurrell, A. Mysterud, M. Lima, K.-S. Chan, N. G. Yoccoz, & B. Adlandsvik. 2003a. Studying climate effects on ecology through the use of climate indices: the North Atlantic oscillation, el Nino Southern oscillation and beyond. *Proceedings of Royal Society of London - Series B: Biological Sciences* **270**:2087-2096.

Stenseth, N. C., H. Viljugrein, T. Saitoh, T. F. Hansen, M. O. Kittilsen, E. Bolviken, & F. Glockner. 2003b. Seasonality, density dependence, and population cycles in Hokkaido voles. *Proceedings of the National Academy of Sciences of the United States of America* **100**:11478-11483.

Stenseth, N. C., A. Shabbar, K. S. Chan, S. Boutin, E. K. Rueness, D. Ehrich, J. W. Hurrell, O. C. Lingjaerde, K. S. Jakobsen. 2004. Snow conditions may create an invisible barrier for lynx. *Proceedings of the National Academy of Sciences of the United States of America* **101**:10632-10634.

Stricklan, D., J. T. Flinders, & R. G. Cates. 1995. Factors affecting selection of winter food and roosting resources by porcupines in Utah. *Great Basin Naturalist* **55**:29-36.

Struthers, P. H. 1928. Breeding habits of the Canadian porcupine (*Erethizon dorsatum*). *Journal of Mammalogy* **9**:300-309.

Stuart-Smith, A. K., & S. Boutin. 1995. Behavioral-differences between surviving and depredated juvenile red squirrels. *Ecoscience* **2**:34-40.

Suttle, K. B., M. A. Thomsen, & M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. *Science* **315**:640-642.

Sweitzer, R. A. 1996. Predation or starvation: consequences of foraging decisions by porcupines (*Erethizon dorsatum*). *Journal of Mammalogy* **77**:1068-1077.

Sweitzer, R. A., & J. Berger. 1992. Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). *Ecology* **73**:867-875.

Sweitzer, R. A., & J. Berger. 1993. Seasonal dynamics of mass and body condition in Great Basin porcupines (*Erethizon dorsatum*). *Journal of Mammalogy* **74**:198-203.

Sweitzer, R. A., S. H. Jenkins, & J. Berger. 1997. Near-extinction of porcupines by mountain lions and consequences of ecosystem change in Great Basin desert. *Conservation Biology* **11**:1407-1417.

Systad, G. H., & J. O. Bustnes. 2001. Coping with darkness and low temperatures: foraging strategies in Steller's eiders, *Polysticta stelleri*, wintering at high latitudes. *Canadian Journal of Zoology* **79**:402-406.

Tattersall, I. 1987. Cathemeral activity in primates - A definition. *Folia Primatologica* **49**:200-202.

Tattersall, I. 2006. The concept of cathemerality: history and definition. *Folia Primatologica* **77**:7-14.

Taylor, S. L., & S. W. Buskirk. 1994. Forest microenvironments and resting energetics of the American marten *Martes americana*. *Ecography* **17**:249-256.

Telfer, E. S., & J. P. Kelsall. 1984. Adaptation of some large North American mammals for survival in snow. *Ecology* **65**:1828-1834.

Thibault, I., & J. P. Ouellet. 2005. Hunting behaviour of eastern coyotes in relation to vegetation cover, snow conditions, and hare distribution. *Ecoscience* **12**:466-475.

Timmermann, A., J. Oberhuber, A. Bacher, M. Esch, M. Latif, & E. Roeckner. 1999. Increased El Nino frequency in a climate model forced by future greenhouse warming. *Nature* **398**:694-697.

Torres-Contreras, H., & F. Bozinovic. 1997. Food selection in an herbivorous rodent: balancing nutrition with thermoregulation. *Ecology* **78**:2230-2237.

Tsiropoula, G. 2003. Signatures of solar activity variability in meteorological parameters. *Journal of Atmospheric and Solar-Terrestrial Physics* **65**:469-482.

Turk, A., & W. Arnold. 1988. Thermoregulation as a limit to habitat use in alpine marmots (*Marmota marmota*). *Oecologia* **76**:544-548.

Turner, M. G., Y. A. Wu, L. L. Wallace, W. H. Romme, & A. Brenkert. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications* **4**:472-486.

Verschuren, D., K. R. Laird, & B. F. Cumming. 2000. Rainfall and drought in equatorial east Africa during the past 1,100 years. *Nature* **403**:410-414.

Versteegh, G. J. M. 2005. Solar forcing of climate. 2: evidence from the past. *Space Science Reviews* **120**:243-286.

Visbeck, M., J. W. Hurrell, L. Polvani, & H. M. Cullen. 2001. The North Atlantic oscillation: past, present and future. *Proceedings of the National Academy of Sciences, USA* **98**:12876-12877.

Vispo, C. R., & G. S. Bakken. 1993. The influence of thermal conditions on the surface activity of thirteen-lined ground squirrels. *Ecology* **74**:377-389.

Walsberg, G. E., & B. O. Wolf. 1996. An appraisal of operative temperature mounts as tools for studies of ecological energetics. *Physiological Zoology* **69**:658-681.

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

Wang, G., N. T. Hobbs, F. J. Singer, D. S. Ojima, & B. C. Lubow. 2002. Impacts of climate change on elk population dynamics in rocky mountain national park, Colorado, U.S.A. *Climatic change* **54**:205-223.

Webb, N. J. 1993. Growth and mortality in juvenile European wild rabbits (*Oryctolagus cuniculus*). *Journal of Zoology* **230**:665-677.

Wei, L. J., D. Y. Lin, & L. Weissfeld. 1989. Regression-analysis of multivariate incomplete failure time data by modeling marginal distributions. *Journal of the American Statistical Association* **84**:1065-1073.

Wiersma, P., & T. Piersma. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy-expenditure in the annual cycle of red knots. *Condor* **96**:257-279.

Wilmers, C. C., & W. M. Getz. 2005. Gray wolves as climate change buffers in Yellowstone. *PLOS Biology* **3**:0571-0576.

Wilmers, C. C., & E. Post. 2006. Predicting the influence of wolf-provided carrion on scavenger community dynamics under climate change scenarios. *Global Change Biology* **12**:403-409.

Wilmers, C. C., E. Post, R. O. Peterson, & J. A. Vucetich. 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters* **9**:383-389.

Winslow, C. E. A., L. P. Herrington, & A. P. Gagge. 1937. Physiological reactions of the human body to varying environmental temperatures. *American Journal of Physiology* **120**:1-22.

Yoder, J. M., E. A. Marschall, & D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* **15**:469-476.

Zalewski, A. 2000. Factors affecting the duration of activity by pine martens (*Martes martes*) in the Bialowieza national park, Poland. *Journal of Zoology* **251**:439-447.

Zimmerling, T. N. 2005. The influence of thermal protection on winter den selection by porcupines, *Erethizon dorsatum*, in second-growth conifer forests. *Canadian Field Naturalist* **119**:159-163.

Zimmerling, T. N., & C. D. Croft. 2001. Resource selection by porcupines: winter den sites and forage tree choices. *Western Journal of Applied Forestry* **16**:53-57.