

**University of Alberta**

Predicting conservation status of North American avian and mammalian scavengers: Implications of geography, life history, behaviour and human disturbance

by

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## **Dedication**

I would like to dedicate this thesis to those who were with me when I started this journey and were more than willing to provide support and encouragement, but who are no longer here to celebrate its conclusion. Grandpa Ives, Grandma King, Dallas Gendall and Suzanne Abele – missed always, never forgotten.

## **Abstract**

Conservation risk is spatially and taxonomically variable, affected by both biological (intrinsic) and environmental (extrinsic) factors. To better understand this variability, I examined how intrinsic and extrinsic factors influenced sub-national patterns of conservation risk in North America for 43 avian and 37 mammalian scavengers. Conservation risk for avian species was most influenced by life history and behavioral traits, while conservation risk for mammalian species was determined more by range size, body mass and human disturbance. Correlations between conservation statuses of scavengers suggested that co-extirpations might be due to losses of behavioral interactions among highly interactive scavengers. These losses may contribute to observed patterns in conservation risk. The most interactive species were ravens, black and grizzly bears, gray wolves and river otters. These findings emphasize the importance of behavioural interactions among species on conservation status. I suggest that dependencies be examined prior to reintroduction efforts, with multi-species reintroductions considered.

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# 1 Introduction

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In the context of a scientific field, conservation biology is still a relative newcomer. It is often referred to as a “crisis discipline” (Soulé 1985) or a “discipline with a deadline” (Wilson 2000), due to recent dramatic declines in biodiversity across the globe (Pimm *et al.* 1995; Regan *et al.* 2001). The question remains, how should conservation actions be prioritized to maximize their impact. Given that time and resources are limited, it is imperative that we make informed and effective management choices. Which species are most threatened? Are there patterns and/or generalizations of threatened species? In this thesis I will examine how intrinsic and extrinsic factors affect the conservation status of avian and mammalian species in the scavenging guild throughout North America, north of Mexico. In the following sections, I will describe each of the major factors affecting the conservation status of these vertebrate species, my hypotheses regarding patterns in the conservation status of scavengers, the significance of this work in the conservation field and my specific study objectives.

## 1.1 STUDY SCOPE AND SYSTEM

### 1.1.1 *Geographic Scale*

To date, several studies have examined factors influencing the extinction risk of species, most commonly on a global scale (Bennett and Owens 1997; Purvis *et al.* 2000; Long *et al.* 2007; Cardillo *et al.* 2008; Davidson *et al.* 2009; Lee & Jetz 2010). Most often these studies have focused on a single taxonomic group, or

charismatic, well described family such as mammals, with a particular focus on carnivores and primates (Purvis *et al.* 2000; Cardillo *et al.* 2008; Fritz *et al.* 2009). Although global analyses often provide the largest datasets and sample sizes, such approaches can mask regional variation in threats and species traits as a result of heterogeneity among both taxonomic groups and geographical regions (Fisher & Owens 2004; Collen *et al.* 2006; Cardillo *et al.* 2008). It is common for species risk and vulnerability to vary on a local scale from population to population. Accounting for this natural heterogeneity by limiting the study to a smaller area provides greater insight into the patterns and causes of species risk at the scale of which policy and management is directed. I therefore apply a North American focus to narrow the scope of the analysis of sub-national (state and province) patterns in species risk. Doing so provides a connection between large, multi-species global studies and targeted local studies (Collen *et al.* 2006), facilitating generalized results while accounting for regional variation in conservation status. By analyzing conservation status patterns at more intermediate spatial scales, more insight is gained on how local, extrinsic factors interact with intrinsic factors such as species traits to affect variations in conservation status. Such scales are therefore more practical and useful than global based studies for prioritization of conservation actions.

### **1.1.2 Taxonomic Focus**

Previous studies on extinction risk have typically focused on taxonomic groups, rather than functional groups. In many cases, the species within these taxonomic

groups perform unrelated ecological roles within a community, and as a result the specific functional relationships in the species assemblages remain unaccounted for when examining patterns in their risk. In this thesis, I instead examine patterns in conservation status in a guild of diverse, but ecologically connected species. A guild is defined as a group of species that are characterized by a similar exploitation of the same class of environmental resources (Root 1967). Species guilds are the “building blocks” of communities (Hawkins and MacMahon 1989) and recognizing this structure can be particularly useful in comparative studies of species assemblages. In North America, species that are known to scavenge carrion represent a highly important, but critically under-examined guild with high diversity in ecological strategies, life history and behaviour traits and responses to anthropogenic threats.

### **1.1.3 Scavenger Behaviour**

There is a continuing negative perception associated with scavenging behaviour, with few studies examining the assemblages of terrestrial vertebrate scavengers and their behavioural interactions (DeVault *et al.* 2003). A major reason for this gap in knowledge is our natural aversion to decomposing matter. Decomposing substances generally repulse humans – this material, however, is often the centerpiece of scavenging. Even today, species field guides and ecology texts will often omit any reference to scavenging behaviour in animals that we typically view as “noble”, despite evidence that the species may, at times, use carrion (Tømmeraas 1989). Scavenging behaviour is also often viewed as a behavioural



“curiosity” rather than a critical ecological process (Wilton 1986). This is especially true in regions such as North America where we do not see specialized scavenging guilds and very few obligate scavengers – species that rely on carrion for survival. Although the term scavenger is often applied to only those species that are obligate scavengers (e.g. vultures), the distinction between predatory and scavenging animals is not very useful. Most predatory carnivores will scavenge food whenever they have the opportunity (opportunistic, facultative scavenging) - there is little advantage in passing up a free meal, should the opportunity arise (DeVault *et al.* 2003) and at times there can be little advantage in killing prey if high quality meat can be obtained through scavenging (Houston 1979). Of literature on scavenging assemblages, most has been focused on the avian group, as birds are best designed for scavenging, with soaring abilities and keen eyesight, and in some cases an excellent sense of smell. In particular, African ecosystems have received the most attention, as both highly specialized scavenging guilds and obligate scavengers are common (Houston 1979; Braack 1987; Gasaway *et al.* 1991; Dudley 1996; Cooper *et al.* 1999).

Although scavenger assemblages are typically characterized by “weak links” between trophic levels, it is becoming clear that these linkages are essential for maintaining the stability and persistence of ecosystems – missing or critically declining species may have severe repercussions across trophic levels (McCann 1998; Neutel 2002). As carrion resources are spatially and temporally dynamic in their availability to scavengers, the intensity and nature of species interactions

among different trophic levels varies in space and time (DeVault 2003). For example, common ravens (*Corvus corax*) are known to commonly associate with gray wolf (*Canis lupus*) packs as a strategy to locate fresh carrion (Harrington 1978; Stahler *et al.* 2002). These strong linkages or interactions may be important for the maintenance of certain species in the community, with the loss of one species potentially affecting the other, in what has been referred to as co-extirpation (Ebenman & Jonsson 2005). In some American states, common ravens and wolves have both been considered extirpated – a connection between the loss of one species and subsequent extirpation of another may become evident once other factors are accounted for.

The scavenging guild in North America includes a large array of mammalian and avian species with considerable diversity in ecology, life history and tolerance of anthropogenic impacts. As a result, this group presents a unique opportunity to investigate the influence of biological (intrinsic) and landscape (extrinsic) factors on the conservation status of a guild of species at scales that acknowledge landscape heterogeneity within the range of a species. Specifically, I will examine sub-national patterns in conservation status for 13 taxonomic families representing 42 mammal and 46 bird species in North America. For the purpose of this study, I defined a scavenger as a vertebrate species that is known to be at least partially carnivorous in its feeding habits and is part of ecologically relevant behavioural interactions with other scavenger species in relation to carrion resources. As many of these species are considered charismatic, they are

relatively well known and well described in the literature, allowing for extensive querying of information on natural history, ecology, behavioural interactions and potential responses to anthropogenic threats.

## **1.2 PREDICTORS AND COMPETING HYPOTHESES OF CONSERVATION STATUS**

Intrinsic factors such as life history traits (e.g. body size, gestation period and age of sexual maturity), ecological traits (e.g. range size and distribution) and behaviour traits (e.g. sociality, circadian and annual activity patterns and seasonal migrations) may predispose a species to decline (Pimm 1988, Gaston & Blackburn 1995). It is unlikely, however, that these factors affect species conservation status independently, potentially interacting with each other in an additive manner. These intrinsic interactions are further affected by extrinsic environmental factors in the form of anthropogenic threats (Gaston & Blackburn 1995). Environmental factors are considered as levels of exposure to human impacts (threats) faced by species within their range. I will use these four broad explanatory factors (1. Life history traits; 2. Ecological traits; 3. Behavioural traits; and 4. Anthropogenic effects) as representatives of competing, but not necessarily mutually exclusive hypotheses for predicting the conservation status of species within the vertebrate scavenging guild of North America. I will subsequently examine whether behavioural interactions between species (a fifth co-extirpation hypothesis) help explain current patterns in conservation statuses of scavenger species.

The conservation status for each species in this thesis is recorded at a sub-national scale (provinces and states) using the online NatureServe database, an international network of biological (natural heritage) inventories operating in the United States and Canada (Stein 2002). NatureServe is internationally recognized and widely used for prioritizing species conservation (O'Grady *et al.* 2004).

### **1.3 SIGNIFICANCE**

Globally, the human population continues to increase, and with it, so too does the level of threat faced by many species. As a result, now more than ever, it is critical that we identify the underlying mechanisms behind species' current conservation statuses and associated risk, and make use of both intrinsic and extrinsic factors to predict which species may decline in the future in the face of escalating human pressure (Cardillo *et al.* 2004, 2008). Understanding the biological and anthropogenic mechanisms that result in different conservation statuses and utilizing this knowledge to reliably predict which species may be become threatened in the future allows biologists and managers to be proactive in their conservation decisions and the allocation of limited resources.

### **1.4 STUDY OBJECTIVES**

The first objective of this thesis is to determine the strength of relationships (correlations) between the conservation statuses of different species within the same scavenging guild for five major biomes of North America, north of Mexico. I examine whether behavioral interactions help explain significant positive

relationships between scavengers, suggesting the possible presence of co-risk and co-extirpation processes, where the loss of one species leads to increased risk for the other species. This objective is addressed in Chapter 2.

My second objective is to examine how ecological, life history and behavioral traits as well as anthropogenic impacts individually and interactively influence the sub-national (state and province) conservation status of species across North America, north of Mexico for the scavenging guild. This objective is addressed in Chapter 3.

By examining the relationships between species, different life history traits and the environment, I hope to better understand the degree to which variation in species' conservation status is related to extrinsic threats versus differences in intrinsic traits and behavioral interactions. This will help determine whether it is possible to predict which species are most at risk of decline in the future in the face of increasing anthropogenic threats associated with human population growth and land use changes.

## 1.5 REFERENCES

- Bennett, P. M. & Owens, I. P. F. 1997 Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proc. R. Soc. Lond. B.* **264**, 401–408.
- Braack, L. E. O. 1987 Community dynamics of carrion-attendant arthropods in tropical African woodland. *Oecologia* **72**, 402–409.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J. & Mace, G. M. 2004 Human population density and extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914.
- Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. & Purvis, A. 2008 The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. Lond. B.* **275**, 1441–1448.
- Collen, B., Bykova, E., Ling, S., Milner-Gulland, E. J. & Purvis, A. 2006 Extinction risk: a comparative analysis of Central Asian vertebrates. *Biodivers. Conserv.* **15**, 1859–1871.
- Cooper, S. M., Holekamp, K. E. & Smale, L. 1999 A seasonal feast: long term analysis of feeding behaviour in the spotted hyena (*Crocuta crocuta*). *Afr. J. Ecol.* **37**, 149–160.

- Davidson, A. D., Hamilton, M. J., Boyer, A. G., Brown, J. H. & Ceballos, G. 2009 Multiple ecological pathways to extinction in mammals. *Proc. Natl Acad. Sci. USA* **106**, 10702–10705.
- DeVault, T. L., Rhodes, O. E., & Shivik, J. A. 2003 Scavenging by vertebrates: behavioral, ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234.
- Dudley, J. P. 1996 Record of carnivory, scavenging and predation for *Hippopotamus amphibius* in Hwange National Park, Zimbabwe. *Mammalia* **60**, 486–488.
- Ebenman, B. & Jonsson, T. 2005 Using community viability analysis to identify fragile systems and keystone species. *Trends Ecol. Evol.* **20**, 568–575.
- Fisher, D. O. & Owens, I. P. F. 2004 The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391–398.
- Fritz, S. A., Bininda-Emonds, O. & Purvis, A. 2009 Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**, 538–549.

- Gasaway, W. C., Mossestad, K. T. & Stander, P. E. 1991 Food acquisition by spotted hyenas in Etosha National Park, Namibia: predation versus scavenging. *Afr. J. Ecol.* **29**, 64–75.
- Gaston, K. J. & Blackburn, T. M. 1995 Birds, body size and the threat of extinction. *Phil. Trans. R. Soc. Lond. B.* **347**, 205–212.
- Harrington, F. H. 1978 Ravens attracted to wolf howling. *Condor* **80**, 236–237.
- Hawkins, C. P. & MacMahon, J. A. 1989 Guilds: the multiple meanings of a concept. *Annu. Rev. Entomol.* **34**, 423–451.
- Houston, D. C. 1979 The adaptations of scavengers. In *Serengeti: Dynamics of an ecosystem* (ed. A. R. E. Sinclair & M. Norton-Griffiths), pp. 263–286. Chicago: University of Chicago Press.
- Lee, T. M. & Jetz, W. 2010 Unraveling the structure of species extinction risk for predictive conservation science. *Proc. R. Soc. Lond. B.* **278**, 1329–1328.
- Long, P. R., Székely, T., Kershaw, M. & O’Connell, M. 2007 Ecological factors and human threats both drive wildfowl population declines. *Anim. Conserv.* **10**, 183–191.



- McCann, K., Hastings, A. & Huxel, G. R. 1998 Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.
- Morris, D. W., Kotler, B. P., Brown, J. S., Sundararaj, V. & Ale, S. B. 2009 Behavioral indicators for conserving mammal diversity. *Ann. N.Y. Acad. Sci.* **1162**, 334–356.
- Neutel, A. M., Heesterbeek, J. A. P. & Ruiters, P. C. 2002 Stability in real food webs: weak links in long loops. *Science* **296**, 1120–1123.
- O’Grady, J. J., Reed, D. H., Brook, B. W. & Frankham, R. 2004 What are the best correlates of predicted extinction risk? *Biol. Conserv.* **118**, 513–520.
- Petchey, O. L. & Gaston, K. J. 2002 Extinction and the loss of functional diversity. *Proc. R. Soc. Lond. B.* **269**, 1721–1727.
- Pimm, S. L., Jones, H. L. and Diamond, J. 1988 On the risk of extinction. *Am. Nat.* **132**, 757–785.
- Pimm, S. L., Russell, J. G., Gittleman, J. L. & Brooks, T. M. 1995 The future of biodiversity. *Science* **269**, 347–350.
- Purvis, A., Gittleman, J. L., Cowlshaw, G. & Mace, G. M. 2000 Predicting

extinction risk in declining species. *Proc. R. Soc. Lond. B.* **267**, 1947–1952.

Regan, H. M., Lupia, R., Drinnan, A. N. and Burgman, M. A. 2001 The currency and tempo of extinction. *Am. Nat.* **157**, 1–10.

Root, R. B. 1967 The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* **37**, 317–350.

Soulé, M. 1985 What is conservation biology? *BioScience* **35**, 727–734.

Stahler, D., Heinrich, B. & Smith, D. 2002 Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Anim. Behav.* **64**, 283–290.

Stein, B. A. 2002 States of the Union: Ranking America's biodiversity. Virginia: NatureServe.

Tømmeraas, P. J. 1989 Carrion feeding in the gyrfalcon *Falco rusticolus*: a review. *Fauna Norvegica Series C Cinclus* **12**, 65–77.

Wilson, E. O. 2000 On the future of conservation biology. *Conserv. Biol.* **14**, 1–3.

Wilton, M. L. 1986 Scavenging and its possible effects upon predation – a selective review of literature. *Alces* **22**, 155–180.

## **2 A tale of two critters: identifying cooperative behavioural interactions and co-extirpation risk between scavenger species**

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### **2.1 INTRODUCTION**

Despite widespread research on intrinsic (biological) and extrinsic (environmental) associations with conservation status (Purvis *et al.* 2000; Cardillo *et al.* 2005; Lee & Jetz 2010), little has been done to assess the effects of species interactions on co-extinctions, secondary extinctions or extinction cascades (Petchey & Gaston 2002; Fowler 2010). These extinctions occur when the loss of one species from an ecological community results in other community members that are trophically reliant on processes influenced by the removed species declining in abundance or becoming extinct (Diamond 1989; Koh *et al.* 2004; Fowler 2010). A related idea is that of secondary extirpations where declines in, or the absence of, a keystone predator in an area results in the subsequent loss of species from the community (Ebenman & Jonsson 2005). The loss of an individual species can therefore result in the disruption of critical connections among interacting species within a community (Dunne *et al.* 2002). Species interactions also contribute to the general maintenance of ecological and species diversity with the disappearance of strongly interactive species potentially leading to changes in ecosystem composition, structure and diversity (Soulé & Terborgh 1999; Soulé *et al.* 2005). These indirect changes can have important effects on

patterns of regional conservation statuses of species. Species loss in communities and the subsequent effects on other species is therefore an important and growing area of conservation and biodiversity research. The cascading losses of species due to the initial loss of an interactive species could be a major source of biodiversity loss both in the present and the future (Koh *et al.* 2004).

Many guilds are characterized by widespread, indirect interactions among species, representing what can be called “weak links”. These weak links can have important stabilizing effects on communities, and therefore serve an important function in maintaining species diversity (Polis & Strong 1996; Bengtsson *et al.* 1997, Naeem & Li 1997; McCann *et al.* 1998; Berlow 1999). Failure to recognize and account for species dependencies and co-extirpation effects in assessments of conservation risk may result in biased estimates of extinction risk (Poulin 1998; Windsor 1998; McKinney 1999). Understanding why the loss of certain species triggers a cascade of species declines and extirpations is critical to predicting extinction risk. A focus on weak links between species can help identify community organization and the impact of species loss (Berlow 1999), as well as reveal which animals may act as the keystone species.

Weak links are common within the scavenger guild, and are important to the function of the overall community. It is increasingly clear that these linkages are essential for maintaining the stability and persistence of the community. Missing or critically declining species may have severe repercussions across trophic levels

(McCann 1998; Neutel 2002). The fluctuating nature of carrion resources is likely to influence not just the intensity, but also the nature of species interactions among different trophic levels (DeVault 2003). It would be expected that because carrion resources are heterogeneous in space and time (DeVault 2003), obligate scavengers would benefit from interactions with other scavengers and predators in the community and that some of these linkages may be strong enough to cause extinction (extirpation) cascades. For example, common ravens (*Corvus corax*) are known to commonly associate with gray wolf (*Canis lupus*) packs as a strategy to locate fresh carrion (Harrington 1978; Stahler *et al.* 2002). In many American states, common ravens and gray wolves are both extirpated, suggesting a connection between the loss of one species and subsequent extirpation of another (Figure 2.1).

Here I test the strength of relationships (correlations) between the conservation statuses of different North American (north of Mexico) scavenger species within the same scavenging guild for five major biomes of North America. I examine whether behavioral interactions help explain significant positive correlations between scavenger conservation status, suggesting the possible presence of co-risk and co-extirpation processes. Although both species may be sensitive to the same anthropogenic threats, extinction cascades – where the loss of one species leads to increased risk for the other species – may also be a factor.

## **2.2 METHODS**

### ***2.2.1 Species Selection***

The scavenging guild in North America includes a large array of mammalian and avian species with considerable diversity in ecology, life history and tolerance to anthropogenic impacts. I included all avian and mammalian scavengers found in Canada and the U.S.A. (excluding Hawaii) that are known to at least occasionally consume carrion (Table 2.1 and 2.2). For the purpose of this study, I defined a scavenger as a vertebrate species that is known to be at least partially carnivorous in its feeding habits and is part of ecologically relevant behavioural interactions with other scavenger species in relation to carrion resources. As many of these species are considered charismatic, they are relatively well known and well described in the literature allowing for a literature assessment of behavioural interactions and potential responses to anthropogenic threats.

### ***2.2.2 Conservation Status***

The conservation status for each species was queried at a sub-national (S-rank) scale (i.e. states in the U.S.A. and provinces in Canada) from NatureServe, a network of biological inventories operating in the United States and Canada (Stein 2002) that is internationally recognized and widely used to prioritize species conservation (O'Grady *et al.* 2004). All assessments of conservation status were obtained in July 2010. Conservation status in NatureServe is categorized into the following five numerical ranks: critically imperiled (S1), imperiled (S2), vulnerable (S3), apparently secure (S4), and secure (S5), with the

additional non-numerical ranks of possibly extirpated (SH), presumed extirpated (SX) and unranked (SNR) (Table 2.3) (Stein 2002). I viewed NatureServe categories as a continuous spectrum of risk (Purvis *et al.* 2000) and converted all ranked species to an ordinal index of conservation risk from 1 to 7 (Table 2.3), with the level of imperilment increasing with the numerical value (i.e. 1 representing a secure species and 7 representing a species that is presumed extirpated). Data deficient (SU) and undesignated species (SNR) were excluded from the analysis.

### **2.2.3 Statistical Analyses**

Spearman's rank correlations ( $r_s$ ) were used to identify statistical associations between conservation statuses of species for all the states and provinces where both species historically (extirpated status) and currently occur. Species were categorized into ecological groups according to the following biomes to keep species associations ecologically meaningful: 1) Arctic/northern forest; 2) Pacific/intermountain west; 3) Prairie/grassland; 4) Eastern deciduous; and 5) Southwest desert. I only report positive correlations between paired species, and interpret them as a potential signal of a weak linkage between species. Species that had no significant correlation with other species or fewer than 10 observations were not included in subsequent examinations of weak linkages among paired species. All correlation analyses were performed using STATA (StataCorp 2009) statistical software using the *spearman* command.



#### **2.2.4 Species connections**

Significant ( $p \leq 0.05$ ) Spearman's rank correlations between species pairings for each biome were separated into strong ( $r_s \geq 0.7$ ), moderate ( $r_s \geq 0.4$ ) and weak ( $r_s \geq 0.2$ ) 'connections' (see Appendix 1 Tables 5.3, 5.4 and 5.5 for full values). A count of 'connections' was made for each species to rank their overall importance.

### **2.3 RESULTS**

There were few strong connections between species, with the majority of strong connections involving large carnivores such as the gray wolf, cougar (*Puma concolor*), grizzly bear (*Ursus arctos*) or American black bear (*Ursus americanus*). When moderate to weak connections were considered, the number of linkages increased substantially, with patterns emerging across and within biomes. Figure 2.2 illustrates the associations between highly interactive species for each biome. As expected, large carnivores such as the gray wolf, grizzly and black bears were the most connected species. The common raven, however, was the most interactive species within and across biomes, with most connections involving mammalian scavengers (Tables 2.4 and 2.5). The common raven was defined by a combination of weak, moderate and strong connections, largely to mammalian scavengers. Only the American black bear rivaled the common raven in the number of species connections, with all other species sharing approximately half the number of connections observed between the common raven and other scavenger species (Table 2.5).

## 2.4 DISCUSSION

### 2.4.1 *Gray wolf*

The gray wolf has become one of the better-known North American terrestrial animals widely considered as a keystone species, particularly following its highly publicized reintroduction to Yellowstone National Park. There is substantial support for the idea that wolves, like other keystone species, have impacts on other species beyond what would be expected from considering their biomass or abundance, and their loss from an ecosystem results in cascading effects to other ecosystem components (Simberloff 1998). These effects influence community structure and biodiversity, ultimately resulting in positive effects for the many species indirectly affected by wolves as the result of weak links or interactions (Ripple *et al.* 2001; Ripple & Beschta 2004; White & Garrott 2005). Coyotes (*Canis latrans*), common ravens, black-billed magpies (*Pica hudsonica*), bald eagles (*Haliaeetus leucocephalus*), grizzly bears and American black bears and numerous other species – specific to individual biomes – regularly utilize carrion created by gray wolves. For example, in Riding Mountain National Park in southeastern Saskatchewan, Canada, over 30 species of avian and mammalian scavengers used wolf kills (Wilmers *et al.* 2003). The importance of gray wolf provided carrion has a positive effect on litter sizes in coyotes (Crabtree & Sheldon 1999), increased reproductive rate in common ravens, black-billed magpies and bald eagles (Newton *et al.* 1982) and larger body size and litter size in grizzly bears (Blanchard 1987). Top predators, such as the gray wolf, therefore provide critical carrion resources for other scavenging species, effectively

generating a safety net of resources for members of the scavenging guild (Wilmers *et al.* 2003).

Given the evidence for these community relationships with the gray wolf, positive connections with many of the scavenger species are likely to be the result of behavioural interactions with wolves. However, as a large (and often controversial) mammalian carnivore, like several of the species to which it is connected, the gray wolf is sensitive to anthropogenic disturbances and increased human presence (Carroll *et al.* 2000). As such, I cannot assume all the connections seen in this study are the result of behavioural interactions. While the evidence for the far-reaching trophic and behavioural effects of gray wolf presence within an ecosystem is compelling, it remains to be determined as to which connections are simply due to shared responses to human impacts on the landscape.

#### **2.4.2 Grizzly bear**

The grizzly bear has long been considered an indicator of sensitive ecological systems, regularly suggested as an “umbrella species” for many ecosystems (Noss *et al.* 1996; Carroll *et al.* 2000; Peterson 2001). Conservation plans have frequently relied on the idea that the large area of habitat required to protect viable populations of grizzly bears will, by default, also protect sufficient habitat for other species with smaller area requirements (Noss *et al.* 1996; Nielsen 2011). Grizzly bears are also unique in that they regularly scavenge carrion and also prey

upon other species, but are highly omnivorous and derive much of their diet from non-animal (protein) sources (Mattson 1997). This suggests multiple directionalities in the connections seen in this study, with grizzlies relying on carrion from other large predators (e.g. wolves), providing carrion to other scavengers (e.g. ravens) and acting as a habitat-protecting umbrella species. Grizzly bears are especially dependent on spring carrion, with female bears that have access to reliable carrion sources attaining larger body and litter sizes than those bears who encounter carrion less frequently (Blanchard 1987). This again suggests that some of the connections in this study are the result of the grizzly bears' reliance on carrion from other predators.

Like other large mammalian carnivores, grizzly bears are sensitive to landscape changes and human activities (Carroll *et al.* 2000; Nielsen *et al.* 2006, 2008). I cannot, therefore, discount that several of the correlations seen between grizzly bears and other scavengers are the result of shared responses to anthropogenic impacts. However, the trophic interactions mentioned above provide support for the hypothesis of a positive behavioural or indirect interaction with the scavenging behaviours of grizzlies.

### **2.4.3 *American black bear***

The black bear is the second most interactive species overall and for the four biomes where it occurs. I am uncertain why the black bear demonstrates this many interactions – it is generally not considered a keystone, umbrella or

indicator species (Mitchell & Powell 2003) like many of the other highly connected species in this study. As black bears are highly omnivorous and relative habitat generalists, their direct influences on other species and ecosystem processes are more difficult to quantify (Noss *et al.* 1996). The array of species connected to the black bear also have vastly different life histories, behaviours and responses to human impacts. It is therefore difficult to attribute the black bear's high connectivity with scavengers as one of shared threat responses.

Perhaps weak links between black bears and other scavenger species have been overlooked, or the relationships are due to similar sensitivities with other species to anthropogenic factors. As it stands, previous research favours species such as gray wolves and grizzly bears as more suitable focal species. This uncertainty may simply indicate the need for a better understanding of the directionality of these interactions and if and how external, anthropogenic factors may influence pairings. Examining interactions involving the black bear within the scavenging guild may yield new insight as to its value in protecting ecosystems.

#### ***2.4.4 North American river otter***

When compared to its marine cousin, the North American river otter (*Lontra canadensis*) has received little attention with regards to its behavioural connections and associated interactions with other species. My results, however, suggest that the otter may mimic the sea otter with several behaviour connections to multiple terrestrial species. The river otter was the third most connected species

in North America, and was one of the top connected species in four of the five biomes examined. Preliminary work by Beazley & Cardinal (2004) has identified the river otter as displaying characteristics that potentially qualify the species as an keystone and umbrella species, with the otter also suggested as the best focal species for use as an indicator of habitat quality. Indicator species are those “organisms whose characteristics (presence or absence, population density, dispersion, reproductive success) are used as an index of attributes too difficult, inconvenient or expensive to measure for other species or environmental conditions of interest” (Landres *et al.* 1988). River otters are sensitive to anthropogenic disturbance and also to environmental stressors such as acidification and pollution (Beazely & Cardinal 2004). Their aquatic habitat requirements make them unique among the mammalian scavengers examined.

Overall, the otter had almost equal connectivity between avian and mammalian scavengers, the lowest connectivity with mammals for the top species considered overall. This could be a reflection of not just the habitat preference of otters, but also their diet. Primarily piscivorous, otters may provide important aquatic scavenging opportunities for avian and mammalian species alike that would otherwise be largely unavailable to many of the terrestrial species, representing an important linkage between the two ecosystems. Given its degree of connectivity and sensitivity to human disturbance and environmental stressors, I suggest the river otter represents a potential indicator species with multiple linkages to mammalian and avian scavengers.

#### **2.4.5 Common raven**

Common ravens are highly intelligent, opportunistic omnivores (Heirich 1995). As a result, many studies have been conducted to evaluate their feeding habits, tolerances of human activity and overall cleverness (Vucetich 2004; Marzluff & Neatherlin 2006; White 2006). Ravens are not often thought of as an indicator, umbrella or keystone species. Ravens are typically considered a generalist consumer, but in the presence of carrion, they behave more like specialized scavengers (Stahler *et al.* 2002; Selva & Fortuna 2007). In times of significantly reduced carrion availability, ravens have been known to experience declines (Mueller *et al.* 2009). These shortages of carrion can be due to the absence of top predators such as the gray wolf, with their absence associated with subsequent declines in raven numbers (Mueller *et al.* 2009). Common ravens are extirpated or considered at risk throughout much of Eastern and the Midwestern U.S.A. where wolves have been extirpated or are at risk.

As the raven is predominantly connected to mammalian predators, it is unlikely that these connections are related to shared responses to anthropogenic effects. Unlike many predator populations, raven populations increase with human activity (Marzluff & Neatherlin 2006). It may be that the raven represents a threshold species for ecosystems – their absence potentially signifying the major loss of functionality within a community, ravens do not appear to be limited by dispersal abilities or sensitivities to human activity, so there is support for the

hypothesis of critical linkages with other species. Ravens may therefore play a pivotal role in identifying ecosystems in crisis.

#### ***2.4.6 Patterns in scavenger co-extirpations***

It was difficult to disentangle the effects of true behavioral interactions from the shared impacts of anthropogenic effects, particularly for associations between carnivores that are known to be sensitive to human activity. However, in the case of the raven, approximately two-thirds of its connections were with mammalian carnivores. It is unlikely that an avian opportunist with a substantial dispersal ability and high tolerance for human activity would be affected in a similar way as other species that are sensitive to anthropogenic factors, particularly larger mammalian carnivores. As a result, one may hypothesize that the weak links seen between common ravens and other scavenger and predatory species do reflect behavioral connections that affect the health of an ecosystem, where functional interactions occur to the overall mutual benefit of all species involved. It is particularly resounding that in each of the five biomes of North America, the raven consistently demonstrated the highest number of paired linkages. This finding provides further merit to the idea that the status of an ecologically pivotal, highly interactive species, is perhaps more indicative of the integrity of an ecosystem than any other single species (Noss *et al.* 1996).

Large, mammalian carnivores are most often selected as focal species for use in regional conservation planning due to their large home range requirements, low



population densities, low fecundity and other traits that lower their ecological resistance to anthropogenic impacts (Weaver *et al.* 1996). This approach is not without flaws – large carnivores are difficult and costly to monitor given that they occur at low densities, with many being habitat generalists that do not select a habitat based on biodiversity values, but rather for a sufficient prey base and security from human persecution (Noss *et al.* 1996; Linnell *et al.* 1998; Simberloff 1998). If ecosystem indicators are required for conservation planning, practical alternatives can be found among smaller carnivore species such as the river otter, or, as my results indicate, other vertebrates such as the common raven. The common raven would also be easier to detect and monitor than the more elusive carnivores.

Given the complexities of conservation risk among species and sub-national units, factoring out the effects of human activity and determining the directionality of connections was beyond the scope of this study. My goal was to use an exploratory analysis to rank scavenger species that have significant associations with other species, which may signify “weak links” formed through behavioural interactions. Using existing information on interactions between species from previous studies, I was able to speculate as to which connections may be the result of shared responses to anthropogenic effects versus true behavioral interactions, and therefore identify focal species for future behavioural studies.

To my knowledge, this study is the first of its kind to consider species behavioural interactions and “weak links” among species in the context of conservation risk. Further analyses should attempt to factor out the effects of shared responses to anthropogenic impacts to reveal spurious and real, behavioural interactions between species. The detection of the gray wolf-common raven interaction supports the contention that some of these patterns are relevant for understanding subsequent interactions between other scavenger species.

#### **2.4.7 Conclusions**

Species interactions are often functionally extinct long before the species themselves are absent from a community (Soulé *et al.* 2005). This raises the question of the relative importance of maintaining a viable minimum population of certain species (current conservation paradigm) versus protecting a functional ecosystem, and as a result, the ecological effectiveness of species interactions. As it stands, research, policy and management rarely consider cooperative interspecies interactions. Ignoring these connections, however, risks further ecological degradation with disappearances of species and decreases in the diversity and resilience of already unraveling ecosystems (Soulé *et al.* 2005). As an increasing number of species and communities face growing pressure from human activity, it is imperative that conservation and management decisions are made with not just the best, but also the most holistic science possible. I suggest that reintroduction efforts for a species should consider its interactions and connections to other species before implementation, and where possible,

reintroduce the functionally interacting animals important for the reintroduced species.

## 2.5 REFERENCES

- Beazely, K. & Cardinal, N. 2004 A systematic approach for selecting focal species for conservation in the forests of Nova Scotia and Maine. *Environ. Conserv.* **31**, 81–101.
- Bengtsson, J., Jones, J. & Setälä, H. 1997 The value of biodiversity. *Trends Ecol. Evol.* **12**, 334–336.
- Berlow, E. L. 1999 Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–334.
- Blanchard, B. M. 1987 Size and growth patterns of the Yellowstone grizzly bear. *Int. C. Bear* **7**, 99–107.
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O., Sechrest, W., Orme, C. D. & Purvis, A. 2005. Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241.
- Carroll, C., Noss, R. F. and Paquet, P.C. 2001 Carnivores as focal species for conservation planning in the rocky mountain region. *Ecol. Appl.* **11**, 961–980.
- Crabtree, R. L. & Sheldon, J. W. 1999 The ecological role of coyotes on

Yellowstone's northern range. *Yellowstone Science* **7**, 15–23.

Davies, K. F., Margules, C. R. & Lawrence, J. F. 2004 A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* **85**, 265–271.

Davies, T. J., Fritz, S. A., Greyner, R., Orme, C. D. L., Bielby, J., Bininda-Emonds, O. R. P. *et al.* 2008 Phylogenetic trees and the future of mammalian biodiversity. *Proc. Natl. Acad. Sc. USA* **103**, 11556–11563.

DeVault, T. L., Rhodes, O. E., & Shivik, J. A. 2003 Scavenging by vertebrates: behavioral, ecological and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* **102**, 225–234.

Diamond, J. M. 1989 The present, past and future of human-caused extinctions. *Phil. Trans. R. Soc. Lond. B.* **325**, 469–477.

Ebenman, B. & Jonsson, T. 2005 Using community viability analysis to identify fragile systems and keystone species. *Trends Ecol. Evol.* **20**, 568–575.

Fowler, M. S. 2010 Extinction cascades and the distribution of species interactions. *Oikos* **119**, 864–873.

Harrington, F. H. 1978 Ravens attracted to wolf howling. *Condor* **80**, 236–237.

- Koh, L. P., Dunn, R. R., Sodhi, N. S., Colwell, R. K., Proctor, H. C. & Smith, V. S. 2004 Species co-extinctions and the biodiversity crisis. *Science* **305**, 1632–1634.
- Landres, P. B., Verner, J. and Thomas, J. W. 1988 Ecological uses of vertebrate indicator species: a critique. *Conserv. Biol.* **2**, 316–328.
- Lee, T. M. & Jetz, W. 2010 Unraveling the structure of species extinction risk for predictive conservation science. *Proc. R. Soc. Lond. B.* **278**, 1329–1328.
- Linnell, J. D. C., Swenson, J. E., Landa, A. and Kvam, T. 1998 Methods for monitoring European large carnivores – a worldwide review of relevant experience. *Norwegian Institute for Nature Research Oppdragsmelding* **549**, 1–38.
- Mattson, D. J. 1997 Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. *Biol. Conserv.* **81**, 161–177.
- McCann, K., Hastings, A. & Huxel, G. R. 1998 Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.
- McKinney, M. L. 1999 High rates of extinction and threat in poorly studied taxa.

*Conserv. Biol.* **13**, 1273–1281.

Mueller, T., Selva, N., Pugacewicz, E. & Prins, E. 2009 Scale-sensitive landscape complementation determines habitat suitability for a territorial generalist.

*Ecography* **32**, 345–353.

Mitchell, M. S. & Powell, R. A. 2003 Response of black bears to forest management in the southern Appalachian Mountains. *J. Wildlife Manage.*

**67**, 692–705.

Marzluff, J. M. & Neatherlin, E. 2006 Corvid response to human settlements and campgrounds: causes, consequences, and challenges for conservation.

*Biol. Conserv.* **130**, 301–314.

Naeem, S. & Li, S. 1997 Biodiversity enhances ecosystem reliability. *Nature*

**390**, 507–509.

Neutel, A. M., Heesterbeek, J. A. P. & Ruiters, P. C. 2002 Stability in real food webs: weak links in long loops. *Science* **296**, 1120–1123.

Newton, I., Davis, P. E. & Davis, J. E. 1982 Ravens and buzzards in relation to sheep-farming and forestry in Wales. *J. Appl. Ecol.* **19**, 681–706.

- Nielsen, S. E. 2011 Relationships between grizzly bear source-sink habitat and prioritized biodiversity sites in Central British Columbia. *BC J. Ecosys. Manag.* **12**, 136–147.
- Nielsen, S. E., Boyce, M. S. & Stenhouse, G. S. 2006 A habitat-based framework for grizzly bear conservation in Alberta. *Biol. Conserv.* **130**, 217–229.
- Nielsen, S. E., Boyce, M. S., Beyer, H., Huettmann, F. & Stenhouse, G. S. 2008 Can natural disturbance-based forestry rescue a declining population of grizzly bears? *Biol. Conserv.* **141**, 2193–2207.
- Noss, R.F., Quigley, H. B., Horncocker, M. G., Merrill, T. and Paquet, P. C. 1996 Conservation biology and carnivore conservation in the Rocky Mountains. *Conserv. Biol.* **10**, 949–963.
- O’Grady, J. J., Reed, D. H., Brook, B. W. & Frankham, R. 2004 What are the best correlates of predicted extinction risk? *Biol. Conserv.* **118**, 513–520.
- Petchey, O. L. & Gaston, K. J. 2002 Extinction and the loss of functional diversity. *Proc. R. Soc. Lond. B.* **269**, 1721–1727.
- Peterson, D. Grizzly bears as a filter for human use management in Canadian Rocky Mountain national parks. *USDA For. Serv. Proc.* **5**, 354–361.



- Polis, G. A. & Strong, D. R. 1996 Food web complexity and community dynamics. *Am. Nat.* **147**, 813–846.
- Poulin, R. 1998 Comparison of three estimators of species richness in parasite component communities. *J. Parasitol.* **84**, 485–490.
- Purvis, A., Gittleman, J. L., Cowlshaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B.* **267**, 1947–1952.
- Ripple, W. J., Larsen, E. J., Renkin, R. A. & Smith, D. W. 2001 Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biol. Conserv.* **102**, 227–234.
- Ripple, W. J. & Beschta, R. L. 2004 Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *Forest. Ecol. Manag.* **200**, 161–181.
- Selva, N. & Fortuna, M. A. 2007 The nested structure of a scavenger community. *Proc. R. Soc. Lond. B.* **274**, 1101–1108.
- Simberloff, D. 1998 Flagships, umbrellas, and keystones: is single-species

management passé in the landscape era? *Biol. Conserv.* **83**, 247–257.

Soulé, M. E. & Terborgh, J. 1999 Protecting nature at regional and continental scales: a conservation biology program for the new millennium. *BioScience* **49**, 809–817.

Soulé, M. E., Estes, J. A., Miller, B. and Honnold, D. L. 2005 Strongly interacting species: conservation policy, management, and ethics. *BioScience* **55**, 168–176.

Stahler, D., Heinrich, B. & Smith, D. 2002 Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Anim. Behav.* **64**, 283–290.

StataCorp. 2009 *Stata statistical software*, Release 11. Texas: StataCorp LP.

Stein, B. A. 2002 States of the Union: Ranking America's biodiversity. Virginia: NatureServe.

Weaver, J. L., Paquet, P.C. & Ruggiero, L. F. 1996 Resilience and conservation of large carnivores in the Rocky Mountains. *Conserv. Biol.* **10**, 964–976.

White, P. J. & Garrott, R. A. 2005 Yellowstone's ungulates after wolves –

expectations, realizations, and predictions. *Biol. Conserv.* **125**, 141–152.

Wilmers, C. C., Crabtree, R. L., Smith, D. W., Murphy, K. M. and Getz, W. M.  
2003 Trophic facilitation by introduced top predators: grey wolf subsidies  
to scavengers in Yellowstone National Park. *J. Anim. Ecol.* **72**, 909–916.

Windsor, D. A. 1998 Most of the species on Earth are parasites. *Int. J. Parasitol.*  
**28**, 1939–1941.

Table 2.1 Mammalian species of the North American scavenging guild examined for positive conservation status correlations with other scavenger species.

CLASS MAMMALIA		
Family	Scientific name	Common name
Didelphidae	<i>Didelphis virginiana</i>	Virginia opossum
Canidae	<i>Canis latrans</i>	Coyote
	<i>Canis lupus</i>	Gray wolf
	<i>Canis rufus</i>	Red wolf
	<i>Vulpex lagopus</i>	Arctic fox
	<i>Vulpes macrotitus</i>	Kit fox
	<i>Vulpes velox</i>	Swift fox
	<i>Vulpes vulpes</i>	Red fox
	<i>Urocyon cinereoargenteus</i>	Gray fox
Ursidae	<i>Urocyon littoralis</i>	Island gray fox
	<i>Ursus americanus</i>	American black bear
	<i>Ursus arctos</i>	Grizzly bear
Mustelidae	<i>Ursus maritimus</i>	Polar bear
	<i>Martes americana</i>	American marten
	<i>Martes pennanti</i>	Fisher
	<i>Mustela erminea</i>	Ermine
	<i>Mustela frenata</i>	Long-tailed weasel
	<i>Mustela nigripes</i>	Black-footed ferret
	<i>Mustela nivalis</i>	Least weasel
	<i>Mustela vison</i>	American mink
	<i>Gulo gulo</i>	American wolverine
	<i>Taxidea taxus</i>	American badger
Mephitidae	<i>Lontra canadensis</i>	North American river otter
	<i>Spilogale gracilis</i>	Western spotted skunk
	<i>Spilogale putorius</i>	Eastern spotted skunk
	<i>Mephitis macroura</i>	Hooded skunk
	<i>Mephitis mephitis</i>	Striped skunk
Procyonidae	<i>Conepatus mesoleucus</i>	Hog-nosed skunk
	<i>Bassariscus astutus</i>	Ringtail
	<i>Procyon lotor</i>	Raccoon
Felidae	<i>Nasua narica</i>	White-nosed coati
	<i>Puma concolor</i>	Cougar
	<i>Leopardus pardalis</i>	Ocelot
	<i>Leopardus wiedii</i>	Margay
	<i>Herpailurus yagouaondi</i>	Jaguarundi
	<i>Lynx canadensis</i>	Canadian lynx
	<i>Lynx rufus</i>	Bobcat
<i>Panthera onca</i>	Jaguar	

Table 2.2 Avian species of the North American scavenging guild examined for positive conservation status correlations with other scavenger species.

CLASS AVES		
Family	Scientific name	Common name
Cathartidae	<i>Coragyps atratus</i>	Black vulture
	<i>Cathartes aura</i>	Turkey vulture
	<i>Gymnogyps californianus</i>	California condor
Accipitridae	<i>Haliaeetus leucocephalus</i>	Bald eagle
	<i>Circus cyaneus</i>	Northern harrier
	<i>Buteo lineatus</i>	Red-shouldered hawk
	<i>Buteo swainsoni</i>	Swainson's hawk
	<i>Buteo albicaudatus</i>	White-tailed hawk
	<i>Buteo jamaicensis</i>	Red-tailed hawk
	<i>Buteo lagopus</i>	Rough-legged hawk
Falconidae	<i>Aquila chrysaetos</i>	Golden eagle
	<i>Caracara cheriway</i>	Crested (Northern) caracara
	<i>Falco peregrinus</i>	Peregrine falcon
Laridae	<i>Falco rusticolus</i>	Gryfalcon
	<i>Stercorarius pomarinus</i>	Pomarine jaeger
	<i>Stercorarius longicaudus</i>	Long-tailed jaeger
	<i>Larus ridibundus</i>	Black headed gull
	<i>Larus canus</i>	Mew gull
	<i>Larus californicus</i>	California gull
	<i>Larus argentatus</i>	Herring gull
	<i>Larus thayeri</i>	Thayer's gull
	<i>Larus glaucooides</i>	Iceland gull
	<i>Larus occidentalis</i>	Western gull
	<i>Larus glaucescens</i>	Glaucous-winged gull
	<i>Larus hyperboreus</i>	Glaucous gull
	<i>Larus marinus</i>	Great black-backed gull
	<i>Rissa tridactyla</i>	Black-legged kittiwake
	<i>Rhodostethia rosea</i>	Ross's gull
<i>Xema sabina</i>	Sabine's gull	
<i>Pagophila eburnea</i>	Ivory gull	
Strigidae	<i>Nyctea scandiaca</i>	Snowy owl
Corvidae	<i>Perisoreus canadensis</i>	Gray jay
	<i>Cyanocitta cristata</i>	Blue jay
	<i>Aphelocoma californica</i>	Western scrub jay
	<i>Aphelocoma coerulescens</i>	Florida scrub jay
	<i>Aphelocoma ultramarina</i>	Mexican jay
	<i>Nucifraga columbiana</i>	Clark's nutcracker
	<i>Pica hudsonica</i>	Black-billed magpie
	<i>Pica nuttalli</i>	Yellow-billed magpie
	<i>Corvus brachyrhynchos</i>	American crow
	<i>Corvus caurinus</i>	Northwestern crow
	<i>Corvus imparatus</i>	Tamaulipas (Mexican) crow
<i>Corvus ossifragus</i>	Fish crow	
<i>Corvus cryptoleucus</i>	Chihuahuan raven	
<i>Corvus corax</i>	Common raven	

Table 2.3 Definitions for interpreting NatureServe conservation status ranks at the sub-national (S-rank) level (Stein 2002) and associated ordinal conversions of S-ranks.

S-rank status	Definition	Ordinal rank
S1	Critically imperiled	5
S2	Imperiled	4
S3	Vulnerable	3
S4	Apparently secure	2
S5	Secure	1
SH	Possibly extirpated	6
SX	Presumed extirpated	7
SU	Unrankable	-
SNR	Unranked	-

Table 2.4 Species with the highest overall connections in all biomes of North America and the percent of those connections that are with mammalian species.

Species	Total species connections	% Mammalian connections
Common raven	20	65
American black bear	19	63
North American river otter	16	56
Gray wolf	14	57
Grizzly bear	13	69

Table 2.5 Most highly interactive species from each North American biome, showing total number and percent of connections for all species and total number and percent connections for mammalian species only within each biome.

	Species	Species connections	% Connected	Mammalian connections	% Mammalian connections
Arctic/ Northern Forest (30 species)	Common raven	20	66.7	13	65.0
	Am. black bear	19	63.3	12	63.2
	Gray wolf	14	46.7	8	57.1
	Grizzly bear	13	43.3	9	69.2
	N.A. river otter	13	43.3	9	69.2
Pacific/ Intermountain West (33 species)	Common raven	20	60.6	13	65.0
	Black bear	19	57.6	12	63.2
	Gray wolf	13	39.4	7	53.8
	Grizzly bear	13	39.4	9	69.2
	N.A. river otter	12	36.4	9	75.0
Prairie/ Grassland (32 species)	Common raven	16	50.0	11	68.8
	Am. black bear	15	46.9	10	66.7
	Gray wolf	12	37.5	6	50.0
	Grizzly bear	12	37.5	9	75.0
	N.A. river otter	11	34.4	7	63.6
Eastern deciduous (31 species)	Common raven	14	45.2	10	71.4
	Am. black bear	13	41.9	9	69.2
	N.A. river otter	13	41.9	7	53.8
	Gray wolf	10	32.3	5	50.0
Southwest desert (16 species)	Common raven	9	56.3	6	66.7
	Gray wolf	7	43.8	3	42.9
	Cougar	6	37.5	3	50.0



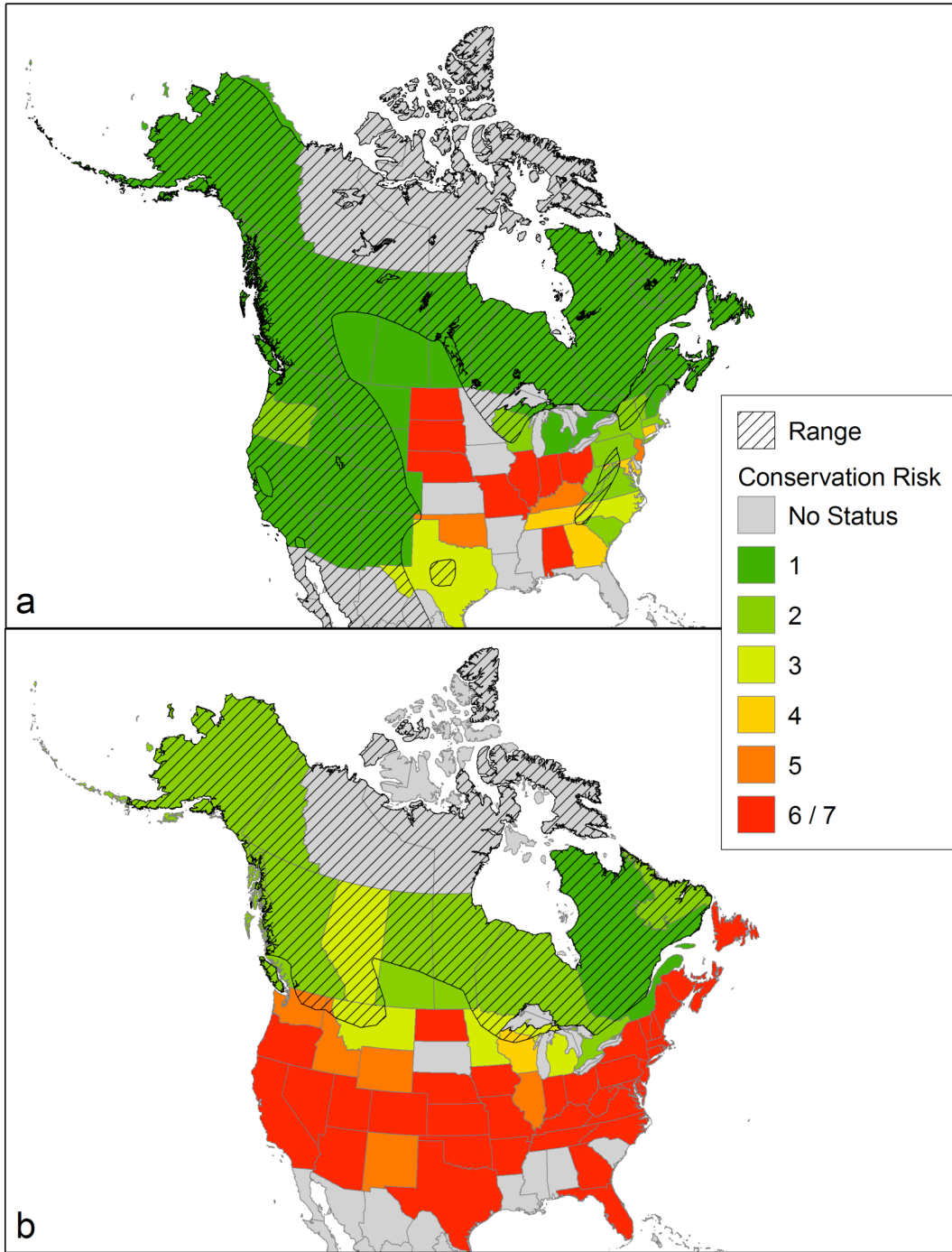


Figure 2.1 Example of sub-national variation in conservation status (ordinal rank) for common ravens (a) and gray wolves (b) in North America. Green sub-national units represent secure (S5 status) with conservation risk increasing to the red, sub-national units where the species are extirpated (SH or SX). Grey sub-national units are unranked. Species range is depicted as cross-hatched polygons.

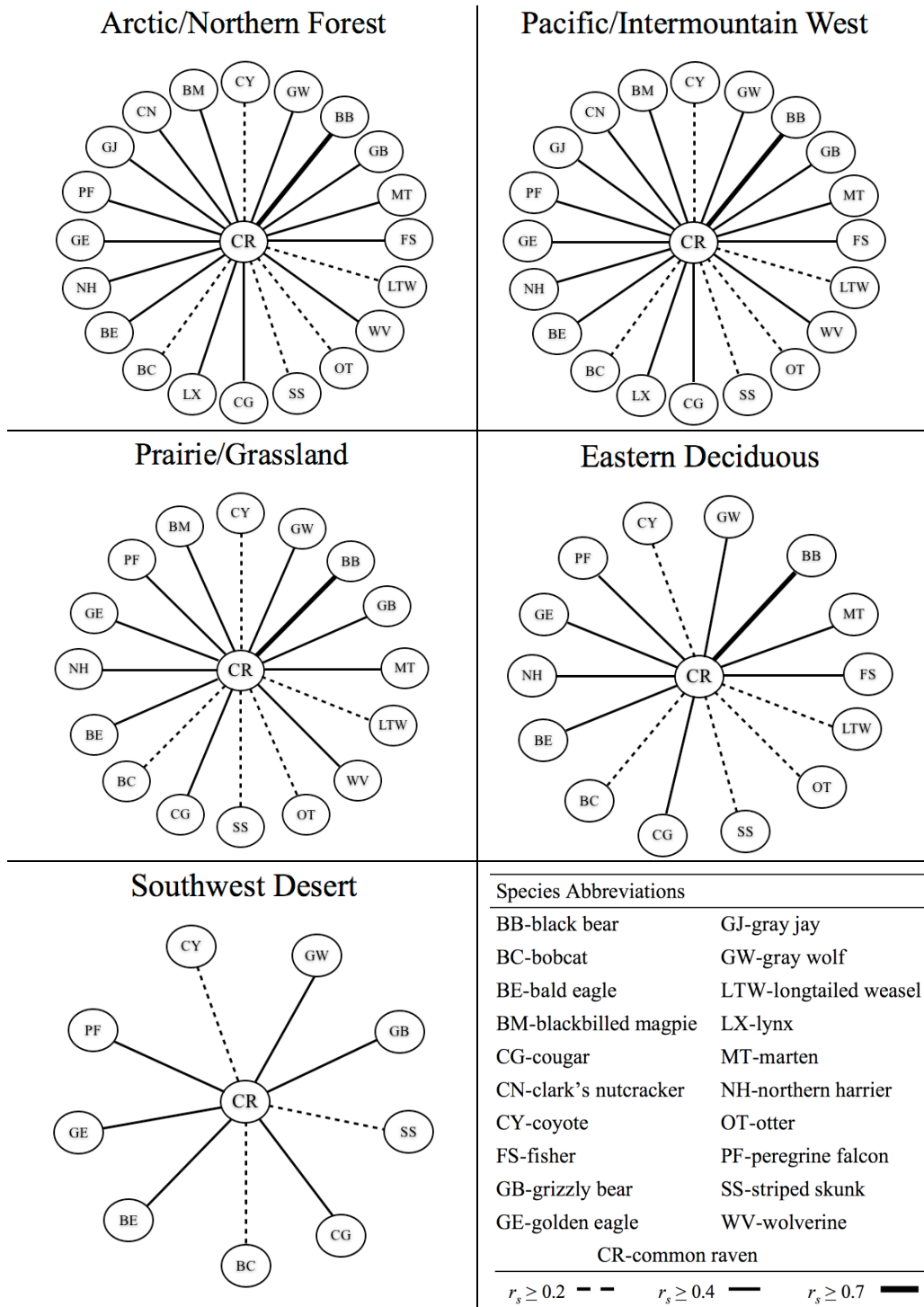


Figure 2.2 Species constellation diagrams for North American biomes. Line thickness signifies strength of correlation between conservation statuses of the common raven and connected species. All Spearman's rank correlations are statistically significant to at least  $p \leq 0.05$ . See appendix for full table of correlation rho ( $r_s$ ) values and associated  $p$ -values.

### **3 Planning Noah's Ark for the 21<sup>st</sup> century: what factors determine the conservation risk of North American mammalian and avian scavengers?**

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#### **3.1 INTRODUCTION**

Current patterns of species extinction risk are phylogenetically nonrandom at multiple spatial scales, with threats often clustered among species sharing similar traits (Bennett & Owens 1997; Russell *et al.* 1998; Purvis *et al.* 2000; Cardillo *et al.* 2008; Davies *et al.* 2008; Safi & Petteerolli 2010). Previous studies have demonstrated that the level of species' risk is often strongly associated with ecological and life history traits such as range size, body size, fecundity, sociality and trophic position (Gaston & Blackburn 1995; Bennett & Owens 1997, Purvis *et al.* 2000; Reynolds *et al.* 2005; Collen *et al.* 2006; Cardillo *et al.* 2008, Liow *et al.* 2009). These particular traits may make certain species more susceptible to decline (Purvis *et al.* 2005). Identifying species with those traits may help predict future extinction risk and thus result in more proactive conservation efforts.

A growing body of evidence suggests that consideration of not just biology (e.g. life history traits) and geography (e.g. range characteristics), but also anthropogenic factors, as well as their interrelationships, better predict patterns of extinction risk (Brashares 2003; Cardillo *et al.* 2005; Davidson *et al.* 2009). Clarifying the relevance and relative importance of anthropogenic factors in conjunction with biological variables across taxonomic groups, ecological guilds and geographic regions will help explain current species conservation status,

predict future at risk species and make conservation efforts as effective as possible (Cardillo *et al.* 2004; Long *et al.* 2007; McKenzie *et al.* 2007). Given that ranges of species do not follow political or national borders, they experience a range of heterogeneity in anthropogenic footprints. Acknowledging this variation will help clarify species conservation statuses and future management actions.

Most studies of extinction risk have focused on the spatial scale (extent and grain) of analyses to range-wide, global patterns, with few examining regional (sub-national) patterns in risk where management decisions are made and interpretations of anthropogenic footprints and activities are more meaningful (Bennett and Owens 1997; Purvis *et al.* 2000; Brashares 2003; Collen *et al.* 2006; McKenzie *et al.* 2007; Cardillo *et al.* 2008). These studies have also generally limited their analysis to a taxonomic class (e.g. Mammalia) or order (e.g. Carnivora or Primate), as opposed to an ecologically functional group (Purvis *et al.* 2000; Cardillo *et al.* 2008; Fritz *et al.* 2009). In this study, I examine how ecological and life history (including behavioral) traits and anthropogenic effects influence sub-national variation in conservation status (ordinal ranking) of an ecological guild – scavenger species in Mammalia (37 species) and Aves (43 species) – across Canada and the U.S.A.. Specifically, I first evaluate which of the following four main hypothesized factors most affect conservation status of mammalian versus avian scavengers in North America: 1) geography (range size); 2) life history; 3) behaviour; and 4) anthropogenic footprints. I then develop a multivariate model combining each of the four main drivers of conservation risk

for both taxonomic classes. Based on these results I evaluate similarities and differences between mammalian and avian scavengers and determine how these factors influence the probability of being a secure, vulnerable, imperiled or extirpated species.

## **3.2 METHODS**

### **3.2.1 *Scavenger species***

The scavenging guild in North America includes a large array of mammalian and avian species with considerable diversity in ecology, life history and tolerance of anthropogenic impacts. This guild therefore provides an opportunity for investigating variations in conservation status due to differences in biological (intrinsic) and landscape (extrinsic) factors at scales that acknowledge landscape heterogeneity within the range of a species. I included all avian (43 species) and mammalian species (37 species) found in Canada and the U.S.A. (excluding Hawaii) that consume carrion on at least an occasional basis (Table 3.1 and 3.2). For the purpose of this study, I defined a scavenger as a vertebrate species that is known to be at least partially carnivorous in its feeding habits and is part of ecologically relevant behavioural interactions with other scavenger species in relation to carrion resources. As mammalian and avian species are considered charismatic, they are relatively well known and well described in the literature allowing for extensive querying of information on natural history, ecology, behavioural interactions and potential responses to anthropogenic threats.

### **3.2.2 Conservation status (response variable)**

The conservation status for each species was queried at a sub-national (S-rank) scale (i.e. states in the U.S.A. and provinces in Canada) from NatureServe, a network of biological inventories operating in the United States and Canada (Stein 2002) that is internationally recognized and widely used to prioritize species conservation (O'Grady *et al.* 2004). All assessments of conservation status were obtained in July 2010. Conservation statuses from NatureServe are categorized into the following ranks: critically imperiled (S1), imperiled (S2), vulnerable (S3), apparently secure (S4), and secure (S5), with the additional non-numerical ranks of possibly extirpated (SH), presumed extirpated (SX) and unranked (SNR) (Table 3.3) (Stein 2002). I viewed NatureServe categories as a continuous spectrum of risk (Purvis *et al.* 2000) and converted all ranked species to an ordinal index of conservation risk that ranged from 1 to 7 (Table 3.3), with the level of imperilment increasing with numerical value (i.e. 1 representing a secure species and 7 representing a species that is presumed extirpated). Data deficient (SU) and undesignated species (SNR) were excluded from my analyses. See Table 3.4 and 3.5 for a frequency table of ordinal conservation ranks for mammalian and avian scavenger species in North America.

### **3.2.3 Biological (intrinsic) factors**

Peer-reviewed literature and reference books were used to compile a database identifying ecological, life history and behavioral traits for each species (Table 3.6 for summary of variables considered; see Appendix 1 for full reference list of

sources used to construct databases). I considered geographic range size for each species within North America. Range maps for mammalian scavengers of North America were based on Patterson *et al.* (2007), while range maps for avian scavengers were based on Ridgely *et al.* (2007) (see Figure 3.1 for an example of species current range map and conservation statuses across North America). Both these datasets are available at the NatureServe online website and represent extant and in some cases formerly occupied (recently extirpated) ranges for each species. Range sizes for each species were measured in ArcGIS using a Lambert Azimuthal Equal Area projection.

Life history traits that I considered included average adult body mass for males and females (kilograms), annual reproductive rate (litter/clutch size per year), mass specific productivity (reproductive rate per kilogram body mass), litter/clutch size (young per year) and gestation/incubation period (in days). For behavioural traits, I considered circadian activity patterns for mammals (diurnal [1] or non-diurnal [0, i.e. nocturnal, crepuscular no pattern]), migratory behaviour for birds (migratory [1] or non-migratory [0]), sociality (social [1] or non-social [0]), mate fidelity (monogamous [1] or non-monogamous [0, i.e. polygynous, polygynandrous, polygyny/polygynandry and monogamy common]) and diet composition (carnivorous [1] or non-carnivorous [0, i.e. omnivory common]).

### **3.2.4 Anthropogenic (extrinsic) factors**

As intrinsic factors alone do not determine the conservation status of a species, measurements of extrinsic components of the environment in the form of anthropogenic threats need to be considered. Environmental exposure to different anthropogenic factors varies across space, and as such, I measured the average and variability (standard deviation) of different indices of anthropogenic footprint for each species at a sub-national scale (i.e. in the range of the species within a state or province; Table 3.7 for summary of variables used). My anthropogenic indices included the Last of the Wild Human Influence Index (Sanderson *et al.* 2002) and the Anthromes classification and its associated estimates of human population density (Ellis *et al.* 2010). The Human Influence Index measured human influence on terrestrial ecosystems for the year 2000 from settlements, access, land transformations and electric power infrastructure (Ellis and Ramankutty 2008). Anthromes (anthropogenic biomes) on the other hand, reflect land use patterns in the year 2000 that described direct human interactions with ecosystems, including urban village, cropland, rangeland (pastures) and semi-natural area anthromes. For my analyses, I focused on rural agricultural footprints by using the amount of cropland and rangeland. Similar to numerous other analyses of species extinction risk, I also used human population density (mean and standard deviation) (Woodroffe 2000; Cardillo *et al.* 2004; Cardillo *et al.* 2008) at the sub-national scale for each species for the area where the species occurred. If my range map for a species did not overlap a sub-national unit where



it was ranked, such as in extirpated range, I used the extent of the sub-national unit to define anthropogenic footprints.

### **3.2.5 Statistical analyses**

I evaluated conservation risk for North American scavengers at the sub-national scale using two approaches: 1) analysis of the ordinal ranks of conservation status using ordered logistic regression; and 2) individual analyses of the different conservation statuses (0 or 1) using logistic regression. In both cases I predicted conservation risk of avian or mammalian species based on their ecological traits (range size or diet), life history traits, behavioural traits and anthropogenic footprints. For the ordered logistic regression analysis, the ordinal rank of conservation risk ranged from a low of 1 (S5 – secure) to a high of 6 (SH – possibly extirpated and SX – presumed extirpated were combined into a single category). For logistic regression analyses I considered the probability a species was in one of the four following conservation status categories (i.e. a 0 or 1 state): secure (S5), vulnerable (S4/S3), imperiled (S2/S1) and extirpated (SX/SH). In doing so, I made no assumption about linear responses of conservation risk across the ordinal classes (1 to 6). All analyses were performed in STATA (StataCorp 2009 College Station, Texas) under the command *ologit* and *logit*. To account for non-independence among observations within a species (i.e. multiple sub-national observations for each species), I used the *cluster* option in STATA to estimate robust (inflated) standard errors with species identity (a unique numeric code per species) used to categorize the unit of clustering. Because I was interested in

identifying similarities or conversely comparing differences among mammalian and avian responses to factors affecting conservation status, I analyzed each taxonomic class separately.

I used Akaike Information Criterion (AIC) to evaluate support for individual hypotheses (Burnham & Anderson 2002). Specifically, I compared ecological, life history, behaviour and anthropogenic hypotheses using AIC and Akaike weights ( $w_i$ ). Because I had multiple measurement variables for some of the hypothesized factors, I also evaluated support for models within a hypothesized group. Because many factors within a hypothesized group were correlated, I limited my analyses to the following ten uncorrelated variables (Pearson correlations ( $r$ ) of all pair wise comparisons being less than |0.7|): range size, diet, female body mass, annual reproductive rate, mate fidelity, sociality, human influence index, human population density, amount of cropland and amount of rangeland. I also simplified one of the ecological (diet) and two of the behavioural variables (mate fidelity and sociality) into binary variables that represented whether the species was primarily carnivorous or primarily omnivorous in their diet, monogamous or non-monogamous mate fidelity and whether the species was social or non-social (solitary). From the set of ten predictor variables, I developed eight *a priori* models (Table 3.8) describing conservation risk, including a null model that contained a simple constant (i.e. mean value) term for conservation risk. For each candidate model, I report pseudo- $R^2$ , AIC values and Akaike weights ( $w_i$ ).

Following these initial analyses, I generated a single multivariate composite model that combined the most commonly supported factors within each hypothesized group in order to include all four hypothesized factors (i.e. ecological, life history, behaviour and anthropogenic footprint) into a single model. I used odds ratios ( $\beta_{OR}$ ), standardized coefficients ( $\beta_{StdXY}$ ) and pseudo- $R^2$  values to evaluate the direction and magnitude of responses in conservation risk by taxonomic class (Aves versus Mammalia) for each factor. Finally, I evaluated the strength of individual factors by taxonomic class for the multivariate composite model across conservation status categories (logistic regression results) based on standardized coefficients (i.e.  $\beta_{StdXY}$  coefficients reported as a function of standard deviation changes in both the X [explanatory] and Y [response] variables).

### **3.3 RESULTS**

#### ***3.3.1 Predictors of conservation status for avian scavengers in North America***

Diet (carnivorous or non-carnivorous) was the most supported individual hypothesized factor affecting ordinal conservation status (ranking) of avian scavengers having an Akaike weight ( $w_i$ ) of 0.996, explaining 4.82% of the variation (pseudo- $R^2$ ) in conservation rankings of species (Table 3.9). Life history traits of body mass and reproductive rates were the next most supported hypothesized factor with an Akaike weight ( $w_i$ ) of 0.004 and a 4.45% variance explained. Although Akaike weights did not suggest strong support for other individual factors (candidate models), all other models were more supported than

the null model predicting constant conservation status among species. Behaviour, specifically sociality (solitary or non-solitary species) and mate fidelity (monogamous or non-monogamous species) explained 3.05% of the variation in conservation status of avian scavengers.

Surprisingly, anthropogenic factors (human influence index, variation in human population density, percent pasture and percent cropland) were only marginally more supported than a null model, explaining less than 1% of the variation in conservation status. The effects of human activity were more pronounced when conservation risk was separated into different status categories (Figure 3.3).

Anthropogenic effects became more important when considering species with an imperiled or extirpated ranking ( $R^2 = 3.8\%$  and  $R^2 = 2.3\%$ , respectively). The ordinal multivariate model for avian scavengers that included range size (geography), life history, behaviour and anthropogenic factors explained 8.62% of the variation in conservation status, while variance explained in logistic regression models describing individual statuses ranged from a low of 6.22% for vulnerable (S4/S3) species, to a high of 19.54% for secure (S5) species (Table 3.11).

Female body mass did not significantly explain ordinal conservation risk in avian scavengers, although there was a positive trend between body mass and conservation risk ( $\beta_{OR} = 2.332$ ,  $SE = 1.448$ ,  $p = 0.173$ ;  $\beta_{StdXY} = 0.203$ ). However, when considering individual statuses, significant effects of body mass on

conservation status were apparent. For secure (S5) species, increases in body mass resulted in a four-fold reduction in being a secure ranked species ( $\beta_{OR} = 0.259$ ,  $SE = 0.126$ ,  $p = 0.006$ ;  $\beta_{StdXY} = -0.307$ ). For behavioural factors, monogamous species were nearly five times less likely to be at risk than non-monogamous species ( $\beta_{OR} = 0.214$ ,  $SE = 0.145$ ,  $p = 0.023$ ;  $\beta_{StdXY} = -0.193$ ) and four times less likely to have an imperiled (S2/S1) ranking than non-monogamous species ( $\beta_{OR} = 0.235$ ,  $SE = 0.162$ ,  $p = 0.036$ ;  $\beta_{StdXY} = -0.185$ ). Predominantly carnivorous species did not statistically relate to conservation risk, although there was a positive trend between a carnivorous diet and ordinal conservation risk ( $\beta_{OR} = 1.959$ ,  $SE = 1.018$ ,  $p = 0.196$ ;  $\beta_{StdXY} = 0.160$ ) and an imperiled ranking ( $\beta_{OR} = 1.836$ ,  $SE = 1.012$ ,  $p = 0.270$ ;  $\beta_{StdXY} = 0.147$ ). Range size did not significantly predict ordinal conservation risk ( $\beta_{OR} = 0.554$ ,  $SE = 0.304$ ,  $p = 0.281$ ;  $\beta_{StdXY} = -0.129$ ), although it was related to species having a secure ranking, increasing the likelihood by a factor of two and a half per unit change in range size ( $\beta_{OR} = 2.475$ ,  $SE = 1.085$ ,  $p = 0.039$ ;  $\beta_{StdXY} = 0.188$ ).

The human influence index (HII) was positively related to ordinal conservation risk ( $\beta_{OR} = 1.045$ ,  $SE = 0.019$ ,  $p = 0.016$ ;  $\beta_{StdXY} = 0.190$ ), with its effect most apparent on imperiled (S2/S1) species with a 7.8% increase in being an imperiled species per unit change in the HII ( $\beta_{OR} = 1.078$ ,  $SE = 0.022$ ,  $p < 0.001$ ;  $\beta_{StdXY} = 0.329$ ). Avian scavengers were less likely to be imperiled as variability in the amount of cultivated land increased ( $\beta_{OR} = 0.971$ ,  $SE = 0.013$ ,  $p = 0.022$ ;  $\beta_{StdXY} = -0.134$ ). There was a positive relationship between percent rangeland and ordinal

conservation risk of avian scavengers with risk increasing by 1% per percent increase in rangeland ( $\beta_{OR} = 1.010$ ,  $SE = 0.005$ ,  $p = 0.035$ ;  $\beta_{StdXY} = 0.096$ ). The effect of rangeland was most influential for secure (S5) species ( $\beta_{OR} = 0.988$ ,  $SE = 0.006$ ,  $p = 0.035$ ;  $\beta_{StdXY} = -0.114$ ). No significant effects of reproductive rate, sociality or variability in human population density were found for either ordinal conservation risk or individual analyses of conservation status for avian scavengers.

### ***3.3.2 Predictors of conservation status for mammalian scavengers in North America***

Range size was the most supported hypothesized factor affecting the conservation status of mammalian scavengers with an Akaike weight ( $w_i$ ) of 0.955, explaining 2.98% of the variation (pseudo- $R^2$ ) in ordinal conservation rankings of species (Table 3.11). Life history traits of body mass and reproductive rates were the second most supported hypothesized factor at an Akaike weight ( $w_i$ ) of 0.045. While the other candidate models did not receive as strong of support as range characteristics, all the other models were more supported than a null model predicting constant conservation status among species. In particular, diet and a full complex of anthropogenic factors (human influence index, variability in human population density, variability in percent cultivated land and the amount of rangeland) explained variability in the conservations status of mammalian scavengers. Mammals were more influenced by human impacts than birds, with anthropogenic effects alone accounting for up to 1.6% of the variability in

conservation risk. As seen previously with avian scavengers, anthropogenic effects also became more important for mammalian scavengers when considering those species with an imperiled or extirpated ranking ( $R^2 = 6.60\%$  and  $R^2 = 6.17\%$ , respectively) (Figure 3.3). The ordinal multivariate model for mammalian scavengers that included range size, life history, behaviour and anthropogenic factors explained 13.5% of the variation in conservation status, while variance explained in logistic regression models describing individual statuses ranged from a low of 2.6% for vulnerable (S4/S3) species, to a high of 32.18% for extirpated (SH/SX) species (Table 3.12).

For the multivariate model, range size was a significant predictor of ordinal conservation risk and individual statuses in mammalian scavengers. As range size decreased by one unit (log scale), species were nearly 14 times more likely to be at risk in ordinal ranking ( $\beta_{OR} = 0.071$ ,  $SE = 0.047$ ,  $p < 0.001$ ;  $\beta_{StdXY} = -0.369$ ), eight and a half times more likely to have an imperiled (S2/S1) ranking status ( $\beta_{OR} = 0.117$ ,  $SE = 0.055$ ,  $p < 0.001$ ;  $\beta_{StdXY} = -0.308$ ) and seven times more likely to have an extirpated (SH/SX) ranking ( $\beta_{OR} = 0.140$ ,  $SE = 0.093$ ,  $p = 0.003$ ;  $\beta_{StdXY} = -0.237$ ). Female body mass was significant in explaining ordinal conservation risk ( $\beta_{OR} = 2.031$ ,  $SE = 0.448$ ,  $p = 0.001$ ;  $\beta_{StdXY} = 0.425$ ). As body mass increased by one unit (log scale), species were two times less likely to have a secure (S5) ranking ( $\beta_{OR} = 0.551$ ,  $SE = 0.116$ ,  $p = 0.004$ ;  $\beta_{StdXY} = -0.321$ ) and almost three times as likely to have an extirpated (SH/SX) ranking ( $\beta_{OR} = 2.709$ ,  $SE = 0.954$ ,  $p = 0.005$ ;  $\beta_{StdXY} = 0.518$ ). There was a significant positive relationship between a

carnivorous diet and conservation risk, with ordinal risk increasing by a factor of five for carnivorous mammalian scavengers ( $\beta_{OR} = 5.324$ ,  $SE = 3.937$ ,  $p = 0.024$ ;  $\beta_{StdXY} = 0.348$ ) by a factor of three for imperiled (S2/S1) mammalian scavengers ( $\beta_{OR} = 3.14$ ,  $SE = 1.703$ ,  $p = 0.035$ ;  $\beta_{StdXY} = 0.246$ ), and were six and a half times less likely to have a secure (S5) ranking ( $\beta_{OR} = 0.154$ ,  $SE = 0.092$ ,  $p = 0.002$ ;  $\beta_{StdXY} = -0.349$ ). Monogamy was negatively related to an imperiled (S2/S1) status in mammalian scavengers ( $\beta_{OR} = 0.314$ ,  $SE = 0.196$ ,  $p = 0.002$ ;  $\beta_{StdXY} = -0.224$ ).

For anthropogenic factors, the human influence index (HII) was significantly related to conservation risk, with ordinal risk increasing by 8.3% per unit increase in HII ( $\beta_{OR} = 1.083$ ,  $SE = 0.018$ ,  $p < 0.001$ ;  $\beta_{StdXY} = 0.290$ ) and by 13.8% for an extirpated (SH/SX) status ( $\beta_{OR} = 1.138$ ,  $SE = 0.027$ ,  $p < 0.001$ ;  $\beta_{StdXY} = 0.406$ ). Percent rangeland was significantly related to conservation risk, with ordinal risk increasing by 1.4% per percent increase in rangeland ( $\beta_{OR} = 1.014$ ,  $SE = 0.006$ ,  $p = 0.022$ ;  $\beta_{StdXY} = 0.129$ ), and by 1.0% for an imperiled (S2/S1) status ( $\beta_{OR} = 1.010$ ,  $SE = 0.008$ ,  $p = 0.001$ ;  $\beta_{StdXY} = 0.143$ ). As variability in human population density increased, ordinal conservation risk of mammalian scavengers declined ( $\beta_{OR} = 0.999$ ,  $SE = 0.0005$ ,  $p = 0.012$ ;  $\beta_{StdXY} = -0.095$ ), especially for an imperiled (S2/S1) status ( $\beta_{OR} = 0.9962$ ,  $SE = 0.002$ ,  $p = 0.029$ ;  $\beta_{StdXY} = -0.300$ ). Likewise, variability in human population density increased the likelihood of having a secure (S5) status ( $\beta_{OR} = 1.002$ ,  $SE = 0.0004$ ,  $p < 0.001$ ;  $\beta_{StdXY} = 0.117$ ). No significant effect of reproductive rate, sociality or variability in the amount of



cultivated land was found for either ordinal conservation risk or individual analyses of conservation status for mammalian scavengers.

### **3.3.3 Differences in conservation risk for avian and mammalian scavengers**

Avian and mammalian scavengers experienced similar responses in their ordinal conservation risk for amount of rangeland ( $\beta_{StdXY} = 0.096, p = 0.035$  and  $\beta_{StdXY} = 0.129, p = 0.022$  respectively) and sociality ( $\beta_{StdXY} = -0.106, p = 0.499$  and  $\beta_{StdXY} = -0.127, p = 0.103$  respectively) (Figures 3.2 and 3.3). A number of important differences, however, were apparent between the two groups of scavengers. The negative relationship between range size and conservation risk was three times greater for mammals ( $\beta_{StdXY} = -0.369, p < 0.001$ ) compared with birds ( $\beta_{StdXY} = -0.129, p = 0.281$ ), while the effect of female body mass was twice that for mammals ( $\beta_{StdXY} = 0.425, p = 0.001$ ) as compared to birds ( $\beta_{StdXY} = 0.203, p = 0.173$ ) (Figure 3.2). A carnivorous diet was two times more influential in increasing conservation risk in mammals ( $\beta_{StdXY} = 0.348, p = 0.024$ ) than birds ( $\beta_{StdXY} = 0.160, p = 0.196$ ) (Figure 3.3). Likewise, conservation risk was negatively related to variability in human population density for both birds and mammals, but the effect was three times greater for mammals ( $\beta_{StdXY} = -0.095, p = 0.012$ ) than birds ( $\beta_{StdXY} = -0.032, p = 0.245$ ) (Figure 3.4). The positive relationship between conservation risk and the human influence index was one and a half times greater for mammals ( $\beta_{StdXY} = 0.290, p < 0.001$ ) than birds ( $\beta_{StdXY} = 0.190, p = 0.016$ ) (Figure 3.4). Finally, monogamy was negatively related to conservation risk of avian scavengers ( $\beta_{StdXY} = -0.193, p = 0.023$ ), while no

significant effect of monogamy was found for mammals ( $\beta_{StdXY} = 0.035$ ,  $p = 0.729$ ) (Figure 3.3). There was no significant relationship between reproductive rate or amount of cultivated land and conservation risk for both birds ( $\beta_{StdXY} = -0.128$ ,  $p = 0.352$  and  $\beta_{StdXY} = -0.059$ ,  $p = 0.197$  respectively) and mammals ( $\beta_{StdXY} = -0.060$ ,  $p = 0.609$  and  $\beta_{StdXY} = -0.230$ ,  $p = 0.525$  respectively) (Figure 3.2 and 3.4).

### **3.4 DISCUSSION**

#### **3.4.1 Avian Class**

Large body size predisposes a species to decline, as this trait is associated with K-selected life histories where species have lower reproductive rates and smaller population sizes (Pimm *et al.* 1988; Gaston & Blackburn 1995; Bennett & Owens 1997). Despite this general rule, associations between body mass and conservation risk are not always supported (Pimm 1988; Laurance 1991; Brashares 2003; Collen *et al.* 2006). I found that body size was, however, inversely related to secure (S5) statuses and positively related to extirpated (SH/SX) statuses of North American avian scavengers.

Monogamy has been linked to increased conservation risk, as monogamous species are more vulnerable to changes in the proportion of breeding females in a population as the result of demographic stochasticity or human influences (Greene *et al.* 1998; Legendre *et al.* 1999). I found a negative relationship between monogamy and ordinal conservation risk for avian scavengers. The effects were

non-linear, however, when examined for individual status categories, with monogamy positively associated with both a secure (S5) and extirpated (SH/SX) status. Breeding monogamy has been linked to increased nesting success and decreased nest predation due to the presence of two parents (Slagsvold & Lifjeld 1994), and it may also reduce mate search costs (females) and competition for breeding opportunities (males). The discrepancy between prior examinations of conservation risk and monogamy with my results, as well as the assumed benefits of monogamy, indicates that there may be species-specific or unexamined interactive effects with other factors influencing the effect of monogamy on avian scavengers. In general, monogamy has rarely been used for predicting conservation risk despite the potential for strong associations. My findings indicate that the effects of mating systems on conservation status within the avian family warrant more attention.

### **3.4.2 Mammalian Class**

Similar to previous studies that have examined the effects of range size on conservation risk of mammals (Fisher & Owens 2004; Cardillo *et al.* 2008, Fritz *et al.* 2009), species range size was the strongest predictor of conservation risk. Large ranges, in theory, permit larger sized populations that can act as buffers against anthropogenic impacts and environmental stochasticity (Cardillo *et al.* 2008). The effect of range size may therefore exceed the importance of intrinsic biological differences among taxonomic groups and/or anthropogenic threats (Cardillo *et al.* 2008). Small ranges may also often indicate habitat specificity,

which should lower a species tolerance for habitat modifications, thus increasing the probability of conservation risk (Purvis *et al.* 2000).

The association between carnivory and increased conservation risk in this study highlights the importance of recognizing a species' dependencies on additional components and interactions within an ecosystem. Generalist species that are often defined as having broad diets should be less sensitive than highly carnivorous species, especially those species that are highly predatory, as they are vulnerable not just to extirpations in prey species, but also to factors affecting prey species habitats (Fisher *et al.* 2003; Boyles & Storm 2007; Hockey & Curtis 2009). Wilson and Willis (1975) suggested that large bodied specialists were among the first to be lost from ecological guilds, and indeed, specialization is one of the more fundamental concepts for explaining extinction risk (McKinney 1997). Specialization is also associated with other risk-promoting traits (e.g. high trophic level, low fecundity, low abundance), as supported by Brown's "niche breadth hypothesis" (1995). This hypothesis stipulates that a species broadly adapted for one parameter is also broadly adapted in other parameters (Brown 1995), which would likely include omnivorous diets, habitat generality, temperature tolerance and so on. There is also evidence that specialized species are more vulnerable simply due to the fact they most often have smaller population sizes and range sizes, lower tolerances to change and narrow niches (Lawton 1995; McKinney 1997). The influence of diet type on conservation risk

in mammals in particular, indicates the importance of recognizing a species dependence on other components of the ecosystem.

Body size (mass) patterns in mammal species are associated with other life history traits including small litter size, low population density and longer gestation periods (Fritz *et al.* 2009). All these factors reduce the ability of a species to compensate for increased mortality, generally as a result of anthropogenic impacts, and as such, lead to increased conservation risk (Fritz *et al.* 2009). Large mammals also tend to have large range sizes, thus making them more likely to encounter threats (Woodroffe and Ginsberg 1998). Cardillo *et al.* (2005) found that larger bodied species were more likely to be predisposed to decline as the result of intrinsic, biological traits. My findings agree with the general theory that increased body mass in mammals is associated with increased conservation risk for mammalian scavengers in North America (McKenzie *et al.* 2007; Cardillo *et al.* 2008; Davidson *et al.* 2009), although this is inconsistent with some other studies (Laurance 1991; Bennett & Owens 1997; Davies 2000; Brashares 2003). Similar to birds, body size often unifies many different life history traits and is likely to interact with other important variables. The interactions between body mass and other biological factors and conservation risk are still not fully understood. Using body mass to infer mechanisms of conservation risk should therefore be done with caution until there is a better understanding of its linkages to other factors.

#### **3.4.4 Anthropogenic Effects**

Of the four anthropogenic factors tested, the human influence index (Sanderson *et al.* 2002) was the most consistent and important predictor of species conservation status for avian and mammalian scavengers in North America. The use of this composite measure of anthropogenic impacts has also been supported by Lee & Jetz (2010). Areas of higher human influence, as signified by the index, therefore generally indicate areas where species are likely to be at risk (Sanderson *et al.* 2002; Laliberte & Ripple 2004).

The effects of variability in human population density were more pronounced in mammalian scavengers than avian scavengers. Previous literature has suggested strong positive relationships between human population density and conservation risk in both birds and mammals (Kerr & Currie 1995; Woodroffe 2000; Brashares *et al.* 2001; Cardillo *et al.* 2008). Human population density, however, does not necessarily signify human influence on the landscape and species residing in that area (Laliberte & Ripple 2004). Human population density alone, therefore, may not be a good indicator of conservation risk, as species sensitivity varies between regions and individual species. Accounting for the variability in human population density, as I have in this study, acknowledges that humans have not impacted all areas equally and that human population density is highly heterogeneous spatially. The patchiness of human population density should therefore be considered in other studies of conservation risk.

Anthropogenic effects alone were not the main drivers of conservation status for scavengers, although anthropogenic effects were more pronounced when examining individual statuses of scavengers, particularly for imperiled and extirpated species. An additive effect was also seen when all four hypothesized factors were considered. For example, when considered individually, diet in avian scavengers was the most supported hypothesized factor affecting ordinal conservation status. In the multivariate model that considered all four hypothesized factors, however, diet was no longer statistically related to conservation risk. This highlights the importance of including both environmental and biological attributes when considering a species' vulnerability and current conservation status. Anthropogenic effects were less important for avian scavengers than for mammalian scavengers. Birds have great dispersal abilities and the capacity to move quickly from disturbance, making them less vulnerable to many anthropogenic impacts (Miserendino *et al.* 2011). The unique life history and behavioural traits of birds played a much larger role in determining their level of risk than in mammals.

Overall, range size and life history traits (specifically body mass) were the most important predictors of conservation status. These findings demonstrate the additive effects that create large taxonomic and geographic variations in species conservation status, and emphasize the importance of incorporating intrinsic and extrinsic factors in analyses of species' risk.

### **3.4.5 Conclusions**

Synergistic combinations of anthropogenic (extrinsic) factors and species traits (intrinsic factors) determine species conservation status. My study ranks the importance of these factors for avian and mammalian scavengers in North America. Life history and behavioral traits played a more important role in determining conservation risk of avian scavengers, while range size, female body mass and anthropogenic indices were more important in determining conservation risk of mammalian scavengers. Understanding these taxonomic differences in conservation status and how these factors synergistically affect conservation risk will aid with more effective protection and management of communities across the landscape.

Selecting the appropriate intrinsic variables and measures of human impact, and adequately representing the complexity of their interactions remain a challenge. This study is the first of my knowledge to focus on patterns of conservation risk for a functional group rather than a taxonomic grouping. Further work is needed to examine similarities/differences for other guilds/functional groups.

Understanding the biological and anthropogenic mechanisms that result in different conservation statuses, and utilizing this knowledge to predict which species may be become threatened in the future given projected threats, will be important for providing more proactive conservation actions and help to prioritize those actions given limited resources.



### 3.5 REFERENCES

- Bennett, P. M. & Owens, I. P. F. 1997 Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proc. R. Soc. Lond. B.* **264**, 401–408.
- Boyles, J. G. & Storm, J. J. 2007 The perils of picky eating: dietary breadth is related to extinction risk in insectivorous bats. *PLoS Biol.* **7**, e672.
- Brashares, J. S. 2003 Ecological, behavioral and life history correlates of mammal extinctions in West Africa. *Conserv. Biol.* **17**, 733–743.
- Burhnam, K.P. & Anderson, D. R. 2002 *Model selection and multi-model inference: a practical information-theoretic approach*, 2nd edn. New York: Springer.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J. & Mace, G. M. 2004 Human population density and extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914.
- Cardillo, M., Mace, G. M., Jones, K. E., Bielby, J., Bininda-Emonds, O., Sechrest, W., Orme, C. D. & Purvis, A. 2005. Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241.

- Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. & Purvis, A. 2008 The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. Lond. B.* **275**, 1441–1448.
- Collen, B., Bykova, E., Ling, S., Milner-Gulland, E. J. & Purvis, A. 2006 Extinction risk: a comparative analysis of Central Asian vertebrates. *Biodivers. Conserv.* **15**, 1859–1871.
- Davidson, A. D., Hamilton, M. J., Boyer, A. G., Brown, J. H. & Ceballos, G. 2009 Multiple ecological pathways to extinction in mammals. *Proc. Natl Acad. Sci. USA* **106**, 10702–10705.
- Davies, K. F., Margules, C. R. & Lawrence, J. F. 2000 Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**, 1450–1461.
- Davies, T. J., Fritz, S. A., Greyner, R., Orme, C. D. L., Bielby, J., Bininda-Emonds, O. R. P. *et al.* 2008 Phylogenetic trees and the future of mammalian biodiversity. *Proc. Natl. Acad. Sc. USA* **103**, 11556–11563.
- Ellis, E. C., Goldewijk, K. K., Siebert, S. Lightman, D. & Ramankutty, N. 2010 Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecol. Biogeogr.* **19**, 589–606.

- Ellis, E. C. & Ramankutty, N. 2008 Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* **6**, 439–447.
- Fisher, D. O., Blomberg, S. P. & Owens, I. P. F. 2003 Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. *Proc. R. Soc. Lond. B.* **270**, 1801–1808.
- Fisher, D. O. & Owens, I. P. F. 2004 The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391–398.
- Fritz, S. A., Bininda-Emonds, O. & Purvis, A. 2009 Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecol. Lett.* **12**, 538–549.
- Gaston, K. J. & Blackburn, T. M. 1995 Birds, body size and the threat of extinction. *Phil. Trans. R. Soc. Lond. B.* **347**, 205–212.
- Greene, C., Umbanhowar, M. M. & Caro, T. 1998 Animal breeding systems, hunter selectivity, and consumptive use in wildlife conservation. In *Behavioral Ecology and Conservation Biology* (ed. T. Caro), pp. 271–305. Oxford: University Press.

- Hockey, P. A. & Odette, C. E. 2009 Use of basic biological information for rapid prediction of the response of species to habitat loss. *Conserv. Biol.* **23**, 64–71.
- Laliberte, A. S. & Ripple, W. J. 2004 Range contractions of North American carnivores and ungulates. *BioScience* **54**, 123–138.
- Laurance, W. F. 1991 Ecological correlates of extinction proneness in Australian tropical rainforest mammals. *Conserv. Biol.* **5**, 79–89.
- Lawton, J. H. 1995 Population dynamic principles. In *Extinction Rates* (eds. Lawton J. H. & May, R. M), pp. 147–163. Oxford: University Press.
- Lee, T. M. & Jetz, W. 2010 Unraveling the structure of species extinction risk for predictive conservation science. *Proc. R. Soc. Lond. B.* **278**, 1329–1328.
- Legendre, S., Clobert, J., Moller, A. P. and Sorci, G. 1999 Demographic stochasticity and social mating system in the process of extinction of small populations: the case of passerines introduced to New Zealand. *Am. Nat.* **153**, 449–463.
- Liow, L. H., Fortelius, M., Lintlaakso, K., Mannila, H. & Stenseth, N. C. 2009 Lower extinction risk in sleep-or-hide mammals. *Am. Nat.* **173**, 264–272.

- Long, P. R., Székely, T., Kershaw, M. & O'Connell, M. 2007 Ecological factors and human threats both drive wildfowl population declines. *Anim. Conserv.* **10**, 183–191.
- McKenzie, N. L., Burbidge, A. A., Baynes, A., Brereton, R. N., Dickman, C. R., Gordon, G., Gibson, L. A., Menkhorst, P. W., Robinson, A. C., Williams, M. R. & Woinarski, J. C. 2007 Analysis of factors implicated in the recent decline of Australia's mammal fauna. *J. Biogeogr.* **34**, 597–611.
- McKinney, M. L. 1997 Extinction, vulnerability and selectivity: combining ecological and palaeontological views. *Annu. Rev. Ecol. Syst.* **28**, 495–516.
- Miserendino, M. L., Casaux, R., Archangelsky, M., Di Prinzio, C. Y., Brand, C. & Kutschker, A. M. 2011 Assessing land-use effects on water quality, in-stream habitat, riparian ecosystems and biodiversity in Patagonian northwest streams. *Sci. Total Environ.* **409**, 612–624.
- O'Grady, J. J., Reed, D. H., Brook, B. W. & Frankham, R. 2004 What are the best correlates of predicted extinction risk? *Biol. Conserv.* **118**, 513–520.
- Patterson, B. D., Ceballos, G., Sechrest, W., Tognelli, M. F., Brooks, T., Luna, L.,

Ortega, P., Salazar, I. & Young, B. E. 2007 *Digital distribution maps of the mammals of the Western hemisphere*, version 3.0. Virginia: NatureServe.

Pimm, S. L., Jones, H. L. & Diamond, J. 1988 On the risk of extinction. *Am. Nat.* **132**, 757–785.

Price, S. & Gittleman, J. 2007 Hunting to extinction: biology and regional economy influence extinction risk and the impact of hunting in Artiodactyls. *Proc. R. Soc. Lond. B.* **274**, 1845–1851.

Purvis, A., Gittleman, J. L., Cowlishaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B.* **267**, 1947–1952.

Purvis, A., Cardillo, M., Greyner, R. & Collen, B. 2005 Correlates of extinction risk: phylogeny, biology, threat and scale. In *Phylogeny and Conservation* (ed. A. Purvis, J. L. Gittleman & T. Brookes), pp. 295–316. Cambridge: University Press.

Reed, J. M. 1999 The role of behavior in recent avian extinctions and endangerments. *Conser. Biol.* **13**, 232–241.

- Reynolds, J. D., Dulvy, N. K., Goodwin, N. B. & Hutchings, J. A. 2005 Biology of extinction risk in marine fishes. *Proc. R. Soc. Lond. B.* **272**, 2337–2344.
- Ridgely, R. S., Allnutt, T. F., Brooks, T., McNicol, D. K., Mehlman, D. W., Young, B. E. & Zook, J. R. 2007 *Digital distribution maps of the birds of the Western hemisphere*, version 3.0. Virginia: NatureServe.
- Safi, K. & Pettorelli, N. 2010 Phylogenetic, spatial and environmental components of extinction risk in carnivores. *Global Ecol. Biogeogr.* **19**, 352–362.
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. W. & Woolmer, G. 2002 The human footprint and the last of the wild. *BioScience* **52**, 891–904.
- Saunders, D., Hobbs, R. & Margules, C. 1991 Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* **5**, 18–32.
- Slagsvold, T. & Lifjeld, J. T. 1994 Polygyny in birds: the role of competition between females for male parental care. *Am. Nat.* **143**, 59–94.
- StataCorp. 2009 *Stata statistical software*, Release 11. Texas: StataCorp LP.

Stein, B. A. 2002 States of the Union: Ranking America's biodiversity. Virginia: NatureServe.

Wilcox, B. & Murphy, D. 1985 Conservation strategy: the effects of fragmentation on extinction. *Am. Nat.* **125**, 879–887.

Wilson, E. O. and Willis, E. O. 1975 Applied biogeography. In *Ecology and Evolution of communities* (ed. M. L. Cody & J. M. Diamond), pp. 522–534. Cambridge: Belknap.

Woodroffe, R. 2000 Predators and people: using human densities to interpret declines of large carnivores. *Anim. Conserv.* **3**, 165–173.

Woodroffe, R. & Ginsberg, J. R. 1998 Edge effects and the extinction of populations inside protected areas. *Science.* **280**, 2126–2128.



Table 3.1 Mammalian species of the North American scavenging guild considered in this study, with the number of sub-national observations representing the number of jurisdictions (states and provinces) the species is ranked in.

CLASS MAMMALIA			
Family	Scientific name	Common name	No. of sub-national observations
Didelphidae	<i>Didelphis virginiana</i>	Virginia opossum	36
Canidae	<i>Canis latrans</i>	Coyote	48
	<i>Canis lupus</i>	Gray wolf	15
	<i>Canis rufus</i>	Red wolf	16
	<i>Vulpes lagopus</i>	Arctic fox	7
	<i>Vulpes macrotitus</i>	Kit fox	9
	<i>Vulpes velox</i>	Swift fox	9
	<i>Vulpes vulpes</i>	Red fox	54
	<i>Urocyon cinereoargenteus</i>	Gray fox	40
	<i>Urocyon littoralis</i>	Island gray fox	1
Ursidae	<i>Ursus americanus</i>	American black bear	49
	<i>Ursus arctos</i>	Grizzly bear	9
	<i>Ursus maritimus</i>	Polar bear	6
Mustelidae	<i>Martes americana</i>	American marten	25
	<i>Martes pennanti</i>	Fisher	20
	<i>Mustela erminea</i>	Ermine	34
	<i>Mustela frenata</i>	Long-tailed weasel	51
	<i>Mustela nigripes</i>	Black-footed ferret	13
	<i>Mustela nivalis</i>	Least weasel	28
	<i>Mustela vison</i>	American mink	50
	<i>Gulo gulo</i>	American wolverine	15
	<i>Taxidea taxus</i>	American badger	28
	<i>Lontra canadensis</i>	North American river otter	50
Mephitidae	<i>Spilogale gracilis</i>	Western spotted skunk	13
	<i>Spilogale putorius</i>	Eastern spotted skunk	21
	<i>Mephitis macroura</i>	Hooded skunk	3
	<i>Mephitis mephitis</i>	Striped skunk	50
	<i>Conepatus mesoleucus</i>	Hog-nosed skunk	1
Procyonidae	<i>Bassariscus astutus</i>	Ringtail	12
	<i>Procyon lotor</i>	Raccoon	51
	<i>Nasua narica</i>	White-nosed coati	3
Felidae	<i>Puma concolor</i>	Cougar	20
	<i>Leopardus pardalis</i>	Ocelot	1
	<i>Herpailurus yagouaondi</i>	Jaguarundi	1
	<i>Lynx canadensis</i>	Canadian lynx	23
	<i>Lynx rufus</i>	Bobcat	49
	<i>Panthera onca</i>	Jaguar	3

Table 3.2 Avian species of the North American scavenging guild considered in this study, with the number of sub-national observations representing the number of jurisdictions (states and provinces) the species is ranked in.

CLASS AVES			
Family	Scientific name	Common name	Number of sub-national observations
Cathartidae	<i>Coragyps atratus</i>	Black vulture	20
	<i>Cathartes aura</i>	Turkey vulture	50
	<i>Gymnogyps californianus</i>	California condor	4
Accipitridae	<i>Haliaeetus leucocephalus</i>	Bald eagle	59
	<i>Circus cyaneus</i>	Northern harrier	52
	<i>Buteo lineatus</i>	Red-shouldered hawk	35
	<i>Buteo swainsoni</i>	Swainson's hawk	24
	<i>Buteo albicaudatus</i>	White-tailed hawk	1
	<i>Buteo jamaicensis</i>	Red-tailed hawk	55
	<i>Buteo lagopus</i>	Rough-legged hawk	7
	<i>Aquila chrysaetos</i>	Golden eagle	32
Falconidae	<i>Caracara cheriway</i>	Crested (Northern) caracara	4
	<i>Falco peregrinus</i>	Peregrine falcon	31
	<i>Falco rusticolus</i>	Gryfalcon	5
Laridae	<i>Stercorarius pomarinus</i>	Pomarine jaeger	2
	<i>Stercorarius longicaudus</i>	Long-tailed jaeger	3
	<i>Larus ridibundus</i>	Black-headed gull	1
	<i>Larus canus</i>	Mew gull	6
	<i>Larus californicus</i>	California gull	14
	<i>Larus argentatus</i>	Herring gull	29
	<i>Larus glaucoides</i>	Iceland gull	1
	<i>Larus occidentalis</i>	Western gull	3
	<i>Larus glaucescens</i>	Glaucous-winged gull	4
	<i>Larus hyperboreus</i>	Glaucous gull	4
	<i>Larus marinus</i>	Great black-backed gull	20
	<i>Rissa tridactyla</i>	Black-legged kittiwake	5
	<i>Rhodostethia rosea</i>	Ross's gull	1
<i>Xema sabina</i>	Sabine's gull	1	
Strigidae	<i>Nyctea scandiaca</i>	Snowy owl	5
Corvidae	<i>Perisoreus canadensis</i>	Gray jay	30
	<i>Cyanocitta cristata</i>	Blue jay	45
	<i>Aphelocoma coerulescens</i>	Florida scrub jay	1
	<i>Aphelocoma ultramarina</i>	Mexican jay	3
	<i>Nucifraga columbiana</i>	Clark's nutcracker	12
	<i>Pica hudsonica</i>	Black-billed magpie	22
	<i>Pica nuttalli</i>	Yellow-billed magpie	1
	<i>Corvus brachyrhynchos</i>	American crow	55
	<i>Corvus caurinus</i>	Northwestern crow	3
	<i>Corvus imparatus</i>	Tamaulipas (Mexican) crow	1
	<i>Corvus ossifragus</i>	Fish crow	22
<i>Corvus cryptoleucus</i>	Chihuahuan raven	6	
<i>Corvus corax</i>	Common raven	40	

Table 3.3 Definitions for interpreting NatureServe conservation status ranks at the sub-national (S-rank) level (Stein 2002) and associated ordinal conversions of S-ranks.

S-rank Status	Definition	Ordinal rank
S1	Critically imperiled	5
S2	Imperiled	4
S3	Vulnerable	3
S4	Apparently secure	2
S5	Secure	1
SH	Possibly extirpated	6
SX	Presumed extirpated	7
SU	Unrankable	-
SNR	Unranked	-

Table 3.4 Frequency of conservation risk (ordinal ranks) for 43 avian scavenger species in North America (north of Mexico).

Species (common name)	<i>Conservation risk (ordinal rank)</i>						<i>Total</i>
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	
American crow	51	1	1	2	0	0	55
Bald eagle	4	12	15	18	10	0	59
Black headed gull	0	0	1	0	2	0	3
Black-legged kittiwake	1	1	0	2	1	0	5
Black vulture	4	9	3	4	2	0	22
Black-billed magpie	14	4	4	0	0	0	22
Blue jay	43	2	0	0	0	0	45
California condor	0	0	0	0	1	3	4
California gull	5	4	1	4	0	0	14
Chihuahuan raven	0	3	1	1	1	0	6
Clark's nutcracker	7	5	0	1	0	0	13
Common raven	26	9	2	4	3	8	52
Crested (Northern) Caracara	0	1	0	1	2	1	5
Fish crow	8	6	4	3	1	0	22
Florida scrub jay	0	0	0	1	0	0	1
Glaucous gull	1	2	0	1	0	0	4
Glaucous-winged gull	3	0	0	1	0	0	4
Golden eagle	0	9	13	2	4	6	34
Gray jay	16	6	6	1	1	0	30
Great black-backed gull	9	3	4	2	3	0	21
Gyrfalcon	0	3	0	2	0	0	5
Herring gull	18	5	4	2	0	0	29
Iceland gull	0	1	0	0	0	0	1
Long-tailed jaeger	1	1	1	0	0	0	3
Mew gull	3	1	0	1	0	1	6
Mexican jay	2	1	0	0	0	0	3
Northern harrier	8	13	10	12	11	0	54
Northwestern crow	2	1	0	0	0	0	3
Peregrine falcon	0	1	8	14	21	3	47
Pomarine jaeger	1	0	1	0	0	0	2
Red-shouldered hawk	3	16	10	5	3	0	37
Red-tailed hawk	45	9	1	1	0	0	56
Ross's gull	0	0	0	0	1	0	1
Rough-legged hawk	3	1	3	0	1	0	8
Sabine's gull	1	0	0	0	0	0	1
Snowy owl	0	1	3	0	1	0	5
Swainson's hawk	1	8	8	6	2	0	25
Tamaulipas (Mexican) crow	0	0	1	0	0	0	1
Turkey vulture	23	22	3	3	0	0	51
Western gull	1	2	0	0	0	0	3
Western scrub jay	6	2	0	1	2	0	11
White-tailed hawk	0	1	0	0	0	1	2
Yellow-billed magpie	0	0	1	0	0	0	1
<i>Total</i>	<b>310</b>	<b>166</b>	<b>109</b>	<b>95</b>	<b>73</b>	<b>23</b>	<b>776</b>

Table 3.5 Frequency of conservation risk (ordinal ranks) for 37 mammalian scavenger species in North America (north of Mexico).

Species (common name)	<i>Conservation risk (ordinal rank)</i>						Total
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	
American badger	6	14	3	3	2	0	28
American black bear	28	8	8	3	4	9	60
American marten	10	6	6	4	3	7	36
American mink	41	8	4	0	0	0	53
American wolverine	1	1	5	6	5	17	35
Arctic fox	4	0	3	0	0	0	7
Black-footed ferret	0	0	0	0	7	6	13
Bobcat	19	19	8	1	2	0	49
Canadian lynx	5	4	2	1	11	7	30
Cougar	3	11	2	5	5	19	45
Coyote	45	6	0	0	0	0	51
Eastern spotted skunk	0	3	4	8	5	2	22
Ermine	26	5	4	0	0	1	36
Fisher	7	6	5	5	6	8	37
Gray fox	24	12	2	1	1	0	40
Gray wolf	1	7	4	1	5	38	56
Grizzly bear	0	1	3	1	3	16	24
Hog-nosed skunk	0	2	0	2	1	0	5
Hooded skunk	0	2	0	1	0	0	3
Island gray fox	0	0	0	0	1	0	1
Jagaurundi	0	0	0	0	1	0	1
Jaguar	0	0	0	0	2	2	4
Kit fox	0	2	4	0	3	0	9
Least weasel	6	7	7	6	2	1	29
Long-tailed weasel	30	10	8	2	1	0	51
North American river otter	17	17	12	6	3	1	56
Ocelot	0	0	0	0	1	3	4
Polar bear	0	1	2	3	0	0	6
Raccoon	46	4	1	0	0	0	51
Red fox	39	10	4	0	1	0	54
Red wolf	0	0	0	0	2	14	16
Ringtail	1	4	4	0	1	2	12
Striped skunk	46	4	0	0	0	0	50
Swift fox	0	0	4	3	5	2	14
Virginia opossum	32	5	0	1	1	0	39
Western spotted skunk	4	6	0	2	1	0	13
White-nosed coati	0	1	0	2	0	0	3
<i>Total</i>	<b>441</b>	<b>186</b>	<b>109</b>	<b>67</b>	<b>85</b>	<b>155</b>	<b>1,043</b>

Table 3.6 Biological factors considered in this study as predictors of conservation status for mammalian and avian scavengers in North America and examples of prior applications of these variables.

Category	Variable	Data type	Example application of use (reference)
Ecological	Range size	Continuous	Cardillo <i>et al.</i> 2008)
Life history	Female body mass	Continuous	Gaston & Blackburn 1995; Cardillo <i>et al.</i> 2008
	Reproductive rate	Continuous	Bennett & Owens 1997; O'Grady <i>et al.</i> 2004
	Gestation/incubation period	Continuous	Purvis <i>et al.</i> 2000
	Litter/clutch size	Continuous	Bennett & Owens 1997
	Condition of young at birth	Categorical	Lee & Jetz 2010
	Inter-birth interval	Categorical	Purvis <i>et al.</i> 2000
	Age of sexual maturity	Continuous	O'Grady <i>et al.</i> 2004
Behavioral	Circadian activity patterns	Categorical	Lee & Jetz 2010
	Annual activity patterns	Categorical	Liow <i>et al.</i> 2009
	Migratory behaviour	Categorical	Lee & Jetz 2010
	Territoriality	Categorical	Reed 1999
	Sociality	Categorical	Collen <i>et al.</i> 2006
	Mate fidelity	Categorical	Legendre <i>et al.</i> 2009; Brashares 2003
	Trophic position	Categorical	Purvis <i>et al.</i> 2000; Collen <i>et al.</i> 2006
	Diet composition	Categorical	Fisher <i>et al.</i> 2003
	Feeding style	Categorical	Lee & Jetz 2010
Degree of scavenging	Categorical	N/A	
Anthropogenic	Reintroduced populations	Categorical	N/A

Table 3.7 Anthropogenic factors considered as predictors of conservation status in analyses.

Variable	Source
Human Influence Index	Last of the Wild (Sanderson <i>et al.</i> 2002)
Cropland anthrome (%)	Anthromes (Ellis <i>et al.</i> 2010)
Rangeland anthrome (%)	Anthromes (Ellis <i>et al.</i> 2010)
Human population density	Anthromes (Ellis <i>et al.</i> 2010)
Harvested/Hunted	See appendix for database references

Table 3.8 Single factor *a priori* models used in analyses with associated variables.

Candidate Model	Variables
Range	Geographic range size
Diet	Predominantly carnivorous
Life history	Female body mass + reproductive rate
Behaviour	Monogamous + sociality
A1 (Humans)	Human influence index + population density
A2 (Agriculture)	% Cultivated land + % rangeland
A3 (Humans + agriculture)	Human influence index + population density + % cultivated land + % rangeland
Null (constant)	N/A



Table 3.9 Model fit (pseudo- $R^2$ ) and Akaike Information Criterion (AIC) comparisons for the null model and hypotheses describing conservation risk for North American avian scavengers (43 species and sub-national 776 observations) based on ordinal risk (ordered logistic regression) and four different levels of conservation status (logistic regression). Akaike weights ( $w_i$ ) describe the probability that the hypothesis is the most supported within the set of models tested and conservation status analysis. Bold font text highlights the most supported model. Add 4 degrees of freedom for the ordered logistic regression model.

Candidate Models*	df (k)	Ordinal risk (1 – 6)			Conservation risk											
					Secure (S5 [1])			S3/S4 (2-3)			S1/S2 (4-5)			Extirpated (6–7)		
		$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$
Range size	2	0.12	2423.8	0.000	0.12	1046.9	0.000	0.03	1012.7	0.000	0.36	811.9	0.000	0.36	210.4	0.000
<b>Carnivorous diet</b>	2	<b>4.82</b>	<b>2310.4</b>	<b>0.996</b>	<b>11.60</b>	<b>927.1</b>	<b>0.896</b>	2.85	984.2	0.063	<b>5.48</b>	<b>770.4</b>	<b>0.984</b>	0.34	210.5	0.000
<b>Life history</b>	3	4.45	2321.5	0.004	11.38	931.4	0.104	<b>3.59</b>	<b>978.8</b>	<b>0.937</b>	2.61	795.7	0.000	<b>12.59</b>	<b>187.1</b>	<b>1.000</b>
B (monogamy + social)	3	3.05	2355.2	0.000	6.22	985.2	0.000	0.87	1006.2	0.000	4.70	778.7	0.016	1.75	209.5	0.000
A1 (Humans)	3	0.64	2413.4	0.000	0.50	1045.0	0.000	0.52	1009.7	0.000	3.05	792.1	0.000	0.90	211.3	0.000
A2 (Agriculture)	3	0.13	2425.6	0.000	0.43	1045.7	0.000	0.28	1012.2	0.000	0.0	816.8	0.000	1.78	209.5	0.000
A3 (Humans + Ag)	5	0.93	2410.3	0.000	1.12	1042.6	0.000	0.78	1011.1	0.000	3.88	789.4	0.000	2.23	212.6	0.000
Null (constant)	1	0.00	2424.8	0.000	0.00	1046.2	0.000	0.00	1011.0	0.000	0.00	812.8	0.000	0.00	209.2	0.000

\*Models include variables range (range size), diet (predominantly carnivorous), behaviour (sociality + monogamy), life history (female body mass + reproductive rate), A1 (human influence index + human population density), A2 (% cultivated land + % rangeland) and A3 (human influence index + human population density + % cultivated land + % rangeland).

Table 3.10 Model fit (pseudo- $R^2$ ) and Akaike Information Criterion (AIC) comparisons for the null model and hypotheses describing conservation risk for North American mammalian scavengers (37 species and sub-national 1043 observations) based on ordinal risk (ordered logistic regression) and four different levels of conservation status (logistic regression). Add 4 degrees of freedom for the ordered logistic regression model. Akaike weights ( $w_i$ ) describe the probability that the hypothesis is the most supported within the set of models tested. Bold font text highlights the most supported model. Bold font text highlights the most supported model. Add 4 degrees of freedom for the ordered logistic regression model.

Candidate Models*	df (k)	Ordinal risk (1 – 6)			Conservation risk											
					Secure (S5 [1])			S3/S4 (2 – 3)			S1/S2 (4 – 5)			Extirpated (6 – 7)		
		$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$	$R^2$	AIC	$w_i$
<b>Range size</b>	2	<b>2.98</b>	<b>3193</b>	<b>0.955</b>	<b>8.27</b>	<b>1307.5</b>	<b>1.000</b>	0.05	1245.9	0.001	<b>7.22</b>	<b>807.7</b>	<b>0.996</b>	1.14	870.7	0.000
<b>Carnivorous diet</b>	2	1.62	3237.0	0.000	4.29	1364.0	0.000	<b>1.17</b>	<b>1231.9</b>	<b>0.928</b>	2.05	852.4	0.000	0.49	876.4	0.000
<b>Life history</b>	3	2.85	3198.6	0.045	3.65	1375.1	0.000	0.82	1238.2	0.040	0.21	870.4	0.000	<b>13.20</b>	<b>767.0</b>	<b>1.000</b>
B (monogamy + social)	3	0.05	3290.5	0.000	0.02	1426.6	0.000	0.28	1245.0	0.001	1.01	863.5	0.000	1.80	866.9	0.000
A1 (Humans)	3	0.75	3267.3	0.000	1.52	1405.3	0.000	0.73	1239.4	0.022	3.65	840.6	0.000	5.38	835.5	0.000
A2 (Agriculture)	3	0.65	3270.6	0.000	1.83	1400.9	0.000	0.24	1245.5	0.001	4.43	833.8	0.000	1.25	871.7	0.000
A3 (Humans + Ag)	5	1.62	3243.0	0.000	3.55	1380.6	0.000	0.84	1242.0	0.006	6.60	819.0	0.004	6.17	832.7	0.000
Null (constant)	1	0.0	3288.0	0.000	0.0	1423.0	0.000	0.0	1244.5	0.002	0.0	868.2	0.000	0.0	878.7	0.000

\*Models includes variables range (range size), diet (predominantly carnivorous), behaviour (sociality + monogamy), life history (female body mass + reproductive rate), A1(human influence index + human population density), A2 (% cultivated land + % rangeland) and A3 (human influence index + human population density + % cultivated land + % rangeland).

Table 3.11 Model coefficients (reported as odds ratios [ $\beta_{OR}$ ] and robust standard errors [S.E.]) describing conservation risk for North American avian scavengers (43 species and sub-national 776 observations) based on the four main hypothesized factors and model type. Ordered logistic regression was used to estimate ordinal ranking of conservation risk, while logistic regression was used to estimate probability of four different conservation statuses.

Predictor variable	Ordinal risk (1 – 6)		Conservation risk							
	$\beta_{OR}$	S.E.	Secure (S5 [1])		S4/S3 (2 – 3)		S2/S1 (4 – 5)		Extirpated (6)	
	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.
<i>Ecology &amp; Geography</i>										
Range size	0.554	0.304	2.475	1.085	0.549	0.186	0.806	0.415	1.861	2.206
Carnivory	1.959	1.018	0.458	0.245	1.796	0.795	1.836	1.012	0.618	1.062
<i>Life history</i>										
Body mass (female)	2.332	1.448	0.259	0.126	1.155	0.443	1.284	0.769	23.2	34.2
Reproductive rate	0.864	0.136	1.173	0.158	0.806	0.086	0.883	0.173	1.426	0.355
<i>Behaviour</i>										
Monogamous species	0.214	0.145	6.02	3.879	0.56	0.213	0.235	0.162	(omitted)	
Social species	0.636	0.426	1.531	1.111	1.037	0.383	0.547	0.342	3.086	3.48
<i>Anthropogenic environment</i>										
Human Influence Index (HII)	1.045	0.019	0.972	0.021	0.973	0.021	1.078	0.022	1.042	0.04
% Cultivated land (StDev)	0.987	0.01	1.005	0.011	1.011	0.009	0.971	0.013	1.034	0.033
% Rangeland (Avg)	1.01	0.005	0.988	0.006	1.004	0.005	1.009	0.006	1.005	0.015
Population density (StDev)	0.9997	0.0002	1.0003	0.0004	1.0003	0.0005	0.9994	0.0003	0.9987	0.0013
Model fit (pseudo- $R^2$ )	8.62		19.54		6.22		11.57		16.43	

Table 3.12 Model coefficients (reported as odds ratios [ $\beta_{OR}$ ] and robust standard errors [S.E.]) describing conservation risk for North American mammalian scavengers (37 species and sub-national 1043 observations) based on the four main hypothesized factors and model type. Ordered logistic regression was used to estimate ordinal ranking of conservation risk, while logistic regression was used to estimate probability of four different conservation statuses.

Predictor variable	Ordinal risk (1 – 6)		Conservation risk							
	$\beta_{OR}$	S.E.	Secure (S5 [1])		S4/S3 (2 – 3)		S2/S1 (4 – 5)		Extirpated (6)	
	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.	$\beta_{OR}$	S.E.
<i>Ecology &amp; Geography</i>										
Range size	0.071	0.047	82.83	90.41	0.963	0.263	0.117	0.055	0.14	0.093
Carnivory	5.324	3.937	0.154	0.092	1.732	0.458	3.14	1.703	4.536	4.874
<i>Life history</i>										
Body mass (female)	2.031	0.448	0.551	0.116	0.92	0.084	1.317	0.196	2.709	0.954
Reproductive rate	0.956	0.085	1.076	0.089	0.957	0.042	1.024	0.066	0.85	0.143
<i>Behaviour</i>										
Monogamous species	1.201	0.636	0.855	0.451	1.107	0.434	0.314	0.12	2.587	2.131
Social species	0.508	0.211	1.904	1.008	0.708	0.388	0.806	0.274	0.569	0.56
<i>Anthropogenic environment</i>										
Human Influence Index (HII)	1.083	0.018	0.927	0.015	1.004	0.02	1.029	0.024	1.138	0.027
% Cultivated land (StDev)	0.994	0.009	1.015	0.01	0.991	0.007	0.97	0.016	1.023	0.012
% Rangeland (Avg)	1.014	0.006	0.982	0.007	1.001	0.004	1.015	0.004	1.01	0.008
Population density (StDev)	0.9988	0.0005	1.0017	0.0004	0.9988	0.0007	0.9962	0.0017	1.0005	0.0006
Model fit (pseudo- $R^2$ )	13.5		26.25		2.6		16.19		32.18	

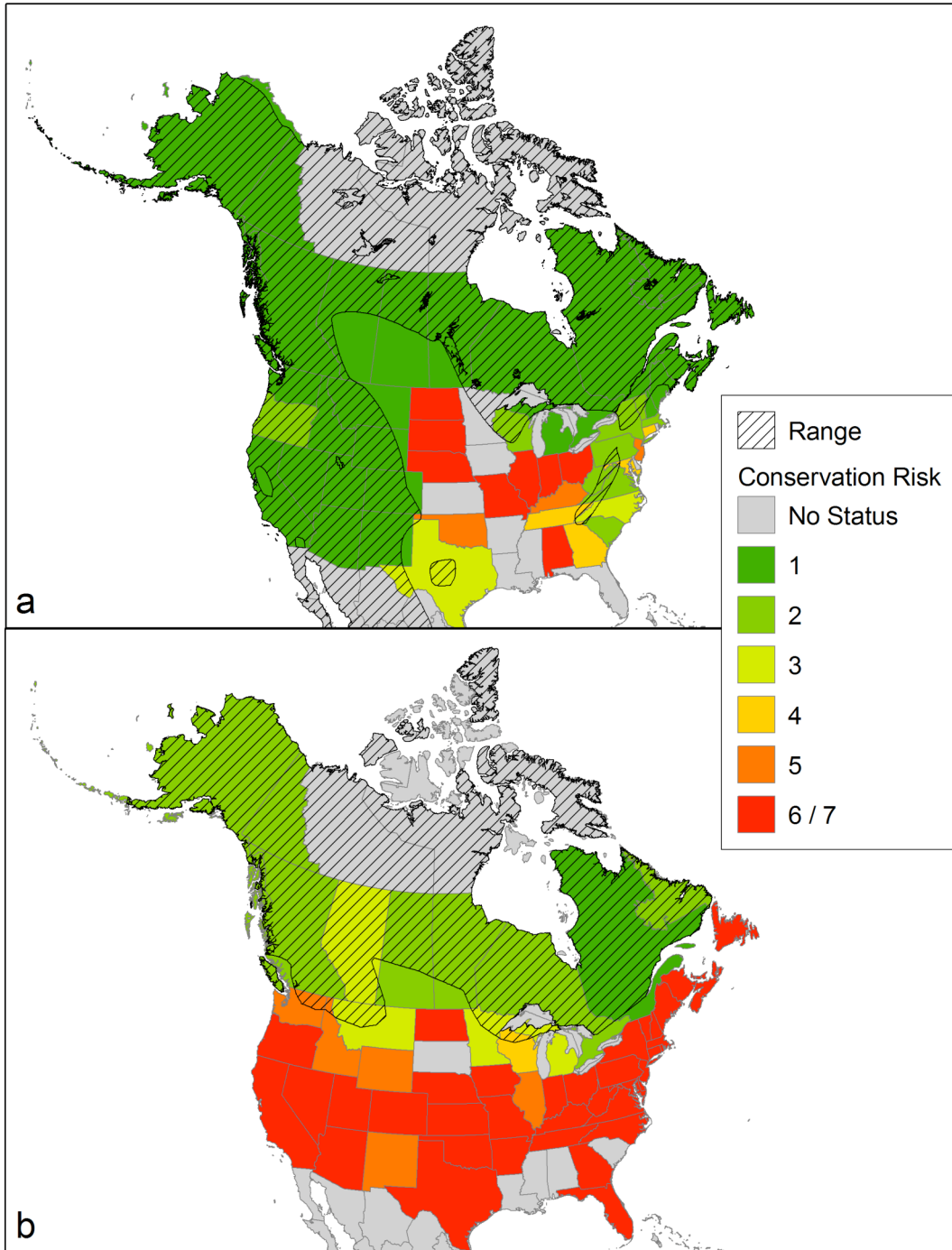


Figure 3.1 Example of sub-national variation in conservation status (ordinal rank) for common ravens (a) and gray wolves (b) in North America. Green sub-national units represent secure (S5 status) with conservation risk increasing to the red, sub-national units where the species are extirpated (SH or SX). Grey sub-national units are unranked. Species range is depicted as cross-hatched polygons.

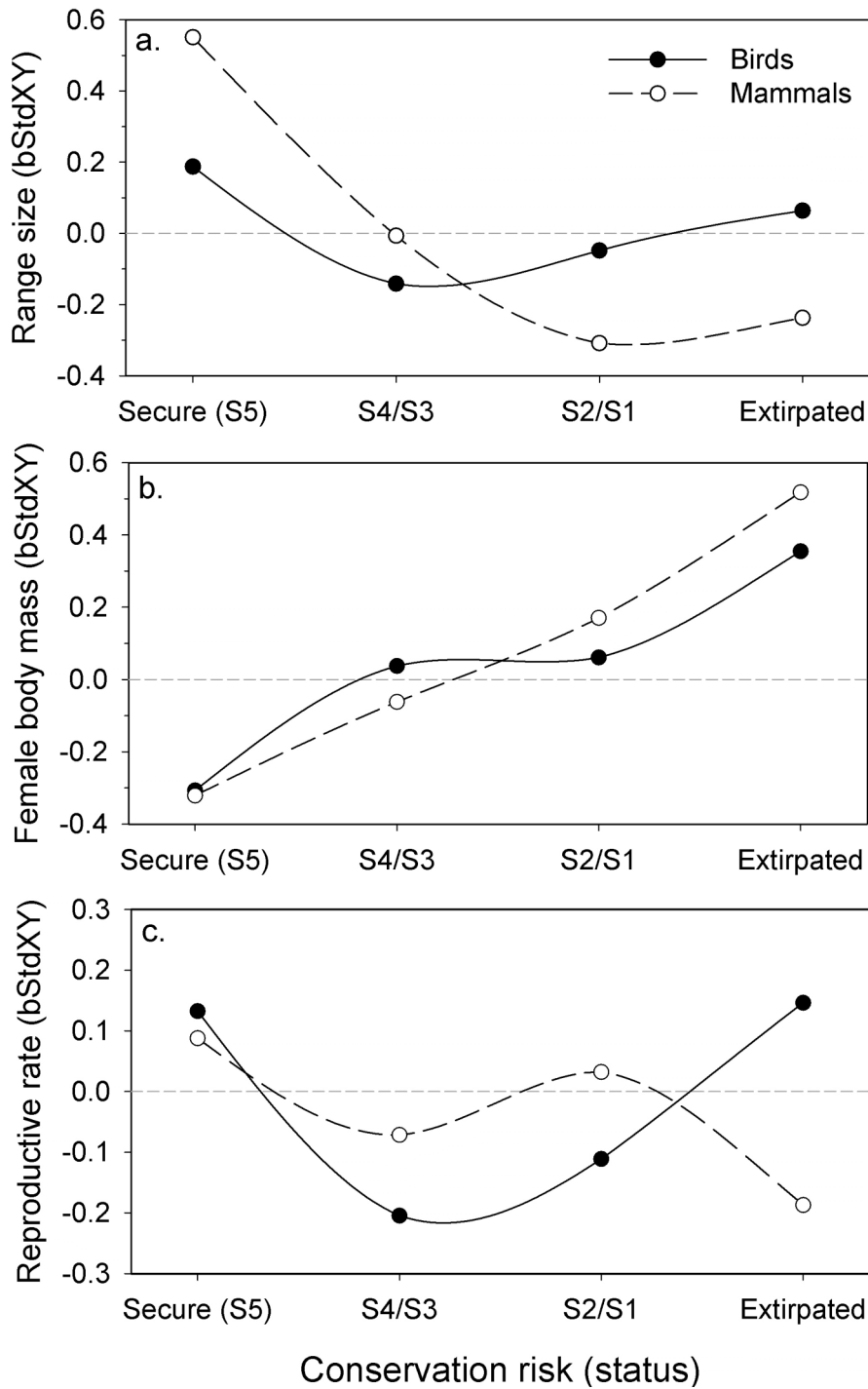


Figure 3.2 Effects of ecological (range size) and life history traits (female body mass and reproductive rate) by avian and mammalian taxa on four different ordinal categories of conservation risk ranging from secure (S5) to extirpated. Graphed responses are expressed as standardized coefficients (bStdXY) in both the response (Y) and predictor variables (X) variables. For instance, a 1 standard deviation increase in range size results in a nearly 60% (standardized) increase in secure status of mammals.

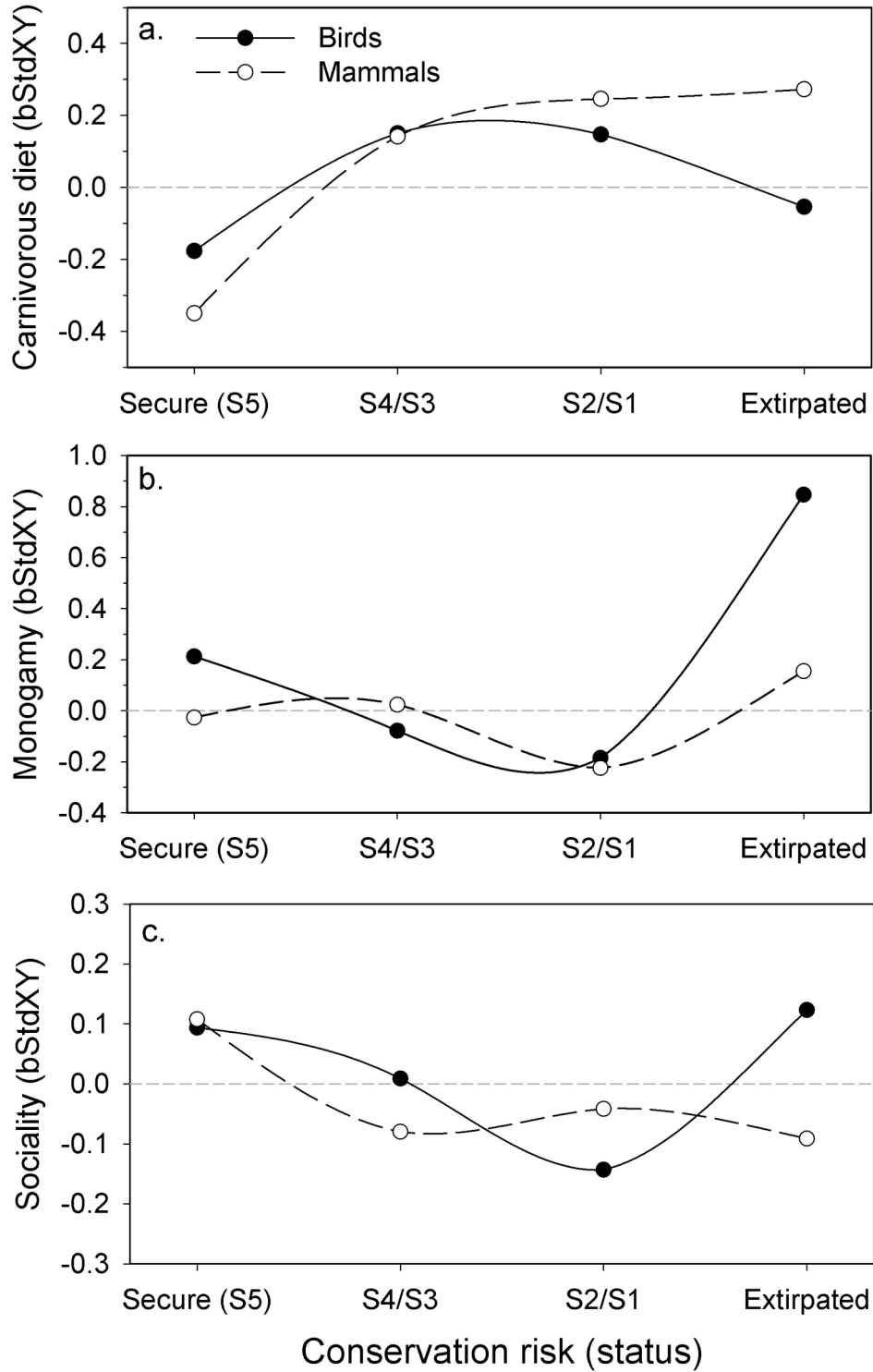


Figure 3.3 Effects of diet (predominantly carnivorous diet) and behaviour (monogamy and sociality) by avian and mammalian taxa on four different ordinal categories of conservation risk gradient ranging from secure (S5) to extirpated. See figure 3.2 for description of bStdXY.

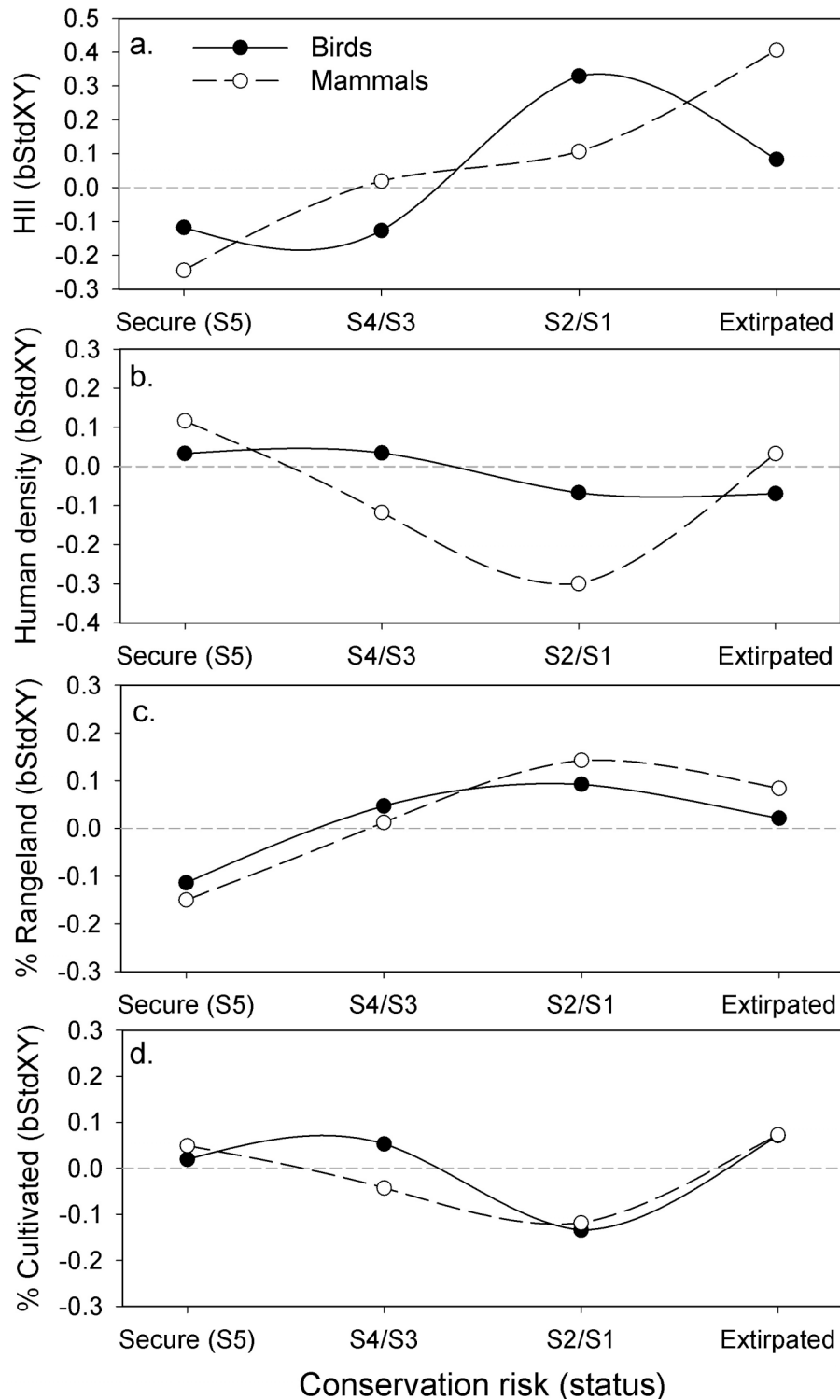


Figure 3.4 Effects of anthropogenic footprints (human influence index, variation in human population density, % rangeland and variation in % cultivated land) by avian and mammalian taxa on four different ordinal categories of conservation risk ranging from secure (S5) to extirpated. See figure 3.2 for description of bStdXY.



## 4 Summary, implications, limitations and recommendations

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### 4.1 SUMMARY

#### 4.1.1 *Species interactions*

Using a Spearman Rank correlation, I tested the strength of cooperative relationships between the conservation statuses of different species within the same scavenging guild for five major biomes of North America. Five highly interactive species emerged, suggesting the presence of behavioural interactions that contribute to conservation risk. The gray wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) were among the most trophically interactive species, supporting previous arguments that these animals may serve as keystone or umbrella species (Simberloff 1998, Peterson 2001). The American black bear (*Ursus americanus*), North American river otter (*Lontra canadensis*) and common raven (*Corvus corax*) were also all found to be highly trophically interactive. The most connected species overall and within each biome – the common raven – was perhaps the most surprising. The raven may, therefore act as a sentinel species for other avian or mammalian scavengers, regardless of ecosystem (biome). Its absence indicates a loss of functionality for the overall scavenging guild, and likely the rest of the ecosystem, thus helping to identify ecosystems in crisis. These findings emphasize the importance of considering not just strong behavioural effects between species, but also weak links that may have important stabilizing effects on communities and thus species diversity (Polis & Strong

1996; Bengtsson *et al.* 1997, Naeem & Li 1997; McCann *et al.* 1998; Berlow 1999).

#### **4.1.2 *Correlates of risk***

Conservation risk varies across species and regions as the result of intrinsic and extrinsic factors. I evaluated how variability in intrinsic, biological and extrinsic, anthropogenic factors influenced the conservation risk of 43 avian and 37 mammalian North American scavengers. Life history and behavioral traits played a more important role in determining sub-national conservation risk of avian scavengers, while range size and female body mass (potentially in conjunction with the degree of human influence on the landscape) were more important in determining sub-national conservation risk of mammalian scavengers. While conservation risk for avian and mammalian scavengers was influenced by many of the same factors, the magnitude of those effects on predicting conservation risk often differed between the classes, suggesting the importance of recognizing major taxonomic differences in functional groups of species. The additive effect of all four hypothesized factors (life history, ecological and behavioural traits and anthropogenic effects) were considered, however, increased the explanatory power of the models, suggesting the presence of synergistic effects between intrinsic, biological factors and extrinsic, anthropogenic factors.

## 4.2 IMPLICATIONS

Behavioural interactions between species, both cooperative and agonistic, have yet to be examined as a predictor of extinction risk. No studies to date fully explain the variation in conservation risk by way of intrinsic, biological and extrinsic, environmental and anthropogenic factors that are perceived as the main drivers of extinction risk. This could be in part due to the failure to account for interactions and dependencies between species. Even in large, multi-species datasets that examine conservation status and extinction risk, such as in Chapter 3, the intrinsic traits and extrinsic impacts are still on an individual species basis, thus ignoring the importance of interspecific interactions on conservation risk of a species. As demonstrated in Chapter 2, communities and ecosystems are complex and interconnected and a species' life history or response to anthropogenic effects is far from the only factor influencing the conservation risk faced by that species. This should emphasize the importance of not just understanding the complex behavioural interactions that take place between species in a community, but also accounting for these interactions in future studies to avoid missing critical, explanatory linkages.

Globally, the human population continues to increase, and with it, so too does the level of threat faced by many species. As a result, now more than ever, it is critical that we identify the underlying mechanisms behind the current patterns of conservation statuses and associated risk of species, and make full use of intrinsic and extrinsic factors to predict which species may decline in the future due to

escalating human pressure (Cardillo *et al.* 2004, 2008). Nonrandom losses of species from a community have negative consequences including, but not limited to, the reduced functional diversity of an assemblage (Petchey & Gaston 2002). Trophically, species in the scavenging assemblage are highly dependent on each other for multiple facets of scavenging behaviour - community assemblages are complex and interconnected, and the absence of a trophic link can have detrimental effects. These linkages may also make scavenging species sensitive to ecosystem alterations that modify the structure or composition of the community. Failing to account for these connections may reduce the success of conservation and management efforts. As a result, when in the process of rebuilding damaged ecosystems, we may need to consider reintroducing more than one species. Rather than focusing on species by species management and conservation, we should focus on rebuilding a functional community. This approach will likely be more successful in maintaining ecosystem functions and services, conserving biodiversity and protecting important species interactions (Morris *et al.* 2009). Understanding the biological and anthropogenic mechanisms that result in different conservation statuses and utilizing this knowledge to reliably predict which species may become threatened in the future allows biologists and managers to be proactive and holistic in their conservation decisions and the allocation of limited resources.

### 4.3 LIMITATIONS

Behavioural linkages between species in a community and how those connections influence risk are a critically understudied yet important component of conservation risk. As this study, to my knowledge, represents the first preliminary exploration of these effects, I did not have a basis to compare or guide my analyses and datasets. As a result, questions remain as to the directionality of relationships between species and how outside factors, such as anthropogenic effects, are involved in those connections. This study represents the starting point, illustrating key species that are highly interactive trophically, with the intent of providing the framework to make accurate, quantitative predictions about the future conservation status of species in subsequent studies.

Several different approaches have been used to assess the correlates of extinction risk. More commonly, studies have been using a method known as phylogenetically independent contrasts (Purvis *et al.* 2000; Cardillo *et al.* 2008). Phylogenetically independent contrasts acknowledge evolutionary similarities between closely related species given that many life history and behaviour traits are similar among these species. Phylogenetically independent contrasts account for non-independence (i.e. pseudoreplication) in data points (species) as the result of phylogenetic patterns (Bennett and Owens 1997). These contrasts, however, are dependent on the phylogeny used, with most phylogenies being imperfect. This results in the loss of information, thus affecting the identification of significant variables (Gage *et al.* 2004). Moreover, previous studies have found

that conventional regression analyses have yielded similar results to those derived from phylogenetically independent contrasts (Brashares 2003; Liow *et al* 2009). Given the debate that remains as to the “correct” type of analysis for these types of data sets, there is a real possibility that the discrepancies in what the best predictor variables are is at least partially the result of methodological differences.

Given the array of species considered in this study, it was not feasible to include all the possible life history, ecological, behavioural and anthropogenic factors that may influence conservation risk. Some variables of interest (e.g. migration, circadian activity patterns) were removed to ensure uniformity among results and to reduce multicollinearity problems. With an analysis of this scope and magnitude, it is difficult to consider all the potential variables and factors affecting conservation risk of species, and this may impact how much variation in species risk is explained by those factors considered.

#### **4.4 RECOMMENDATIONS**

This thesis has focused on a very specific functional group within a finite spatial scale. In the future, it will be important to examine other functional groups in communities, and to focus on different spatial scales, including a global scale analysis, to identify regional patterns across different ecosystems. While the options for selecting predictor variables seem endless, in a perpetually changing world, dominated by human impacts, it may become increasingly important to consider external correlates of extinction risk. Factors such as climate change,

disease and exotic/invasive organisms are likely to also affect the conservation risk faced by species in all ecosystems – in the future, this and other understudied factors may become more important to conservation risk. In addition, behavioural interactions, particularly weak ones, likely have significant effects on not just individual species, but communities and ecosystems as a whole. The loss of critical behavioural linkages between species in a community may result in co-extirpations and the loss of ecosystem stability and function. To ensure the best science is being used to form conservation and management plans, future studies examining patterns of conservation risk in communities must recognize both individual species factors and behavioral interactions between multiple species.

#### 4.5 References

- Bengtsson, J., Jones, J. & Setälä, H. 1997 The value of biodiversity. *Trends Ecol. Evol.* **12**, 334–336.
- Bennett, P. M. & Owens, I. P. F. 1997 Variation in extinction risk among birds: Chance or evolutionary predisposition? *Proc. R. Soc. Lond. B.* **264**, 401–408.
- Berlow, E. L. 1999 Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–334.
- Brashares, J. S. 2003 Ecological, behavioral and life history correlates of mammal extinctions in West Africa. *Conserv. Biol.* **17**, 733–743.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J. L., Bielby, J. & Mace, G. M. 2004 Human population density and extinction risk in the world's carnivores. *PLoS Biol.* **2**, 909–914.
- Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. & Purvis, A. 2008 The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. Lond. B.* **275**, 1441–1448.
- Fisher, D. O. & Owens, I. P. F. 2004 The comparative method in conservation



biology. *Trends Ecol. Evol.* **19**, 391–398.

Gage, G. S., Brooke, M. de L., Symonds, M. R. & Wege, D. 2004 Ecological correlates of the threat of extinction in Neotropical bird species. *Anim. Conserv.* **7**, 161–168.

Liow, L. H., Fortelius, M., Lintlaakso, K., Mannila, H. & Stenseth, N. C. 2009 Lower extinction risk in sleep-or-hide mammals. *Am. Nat.* **173**, 264–272.

McCann, K., Hastings, A. & Huxel, G. R. 1998 Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798.

Morris, D. W., Kotler, B. P., Brown, J. S., Sundararaj, V. & Ale, S. B. 2009 Behavioral indicators for conserving mammal diversity. *Ann. N.Y. Acad. Sci.* **1162**, 334–356.

Naeem, S. & Li, S. 1997 Biodiversity enhances ecosystem reliability. *Nature* **390**, 507–509.

Petchey, O. L. & Gaston, K. J. 2002 Extinction and the loss of functional diversity. *Proc. R. Soc. Lond. B.* **269**, 1721–1727.

Peterson, D. Grizzly bears as a filter for human use management in Canadian

Rocky Mountain national parks. *USDA For. Serv. Proc.* **5**, 354–361.

Polis, G. A. & Strong, D. R. 1996 Food web complexity and community. *Am. Nat.* **147**, 813–846.

Purvis, A., Gittleman, J. L., Cowlshaw, G. & Mace, G. M. 2000 Predicting extinction risk in declining species. *Proc. R. Soc. Lond. B.* **267**, 1947–1952.

Simberloff, D. 1998 Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol. Conserv.* **83**, 247–257.

## 5 Appendix 1

### 5.1 DATABASE REFERENCES

- Amstrup, S. C. 2003 Polar bear (*Ursus maritimus*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 587–610. Baltimore: John Hopkins University Press.
- Anderson, E. M. & Lovallo, M. J. 2003 Bobcat and lynx (*Lynx rufus* and *Lynx canadensis*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 758–788. Baltimore: John Hopkins University Press.
- Bechard, M. J. & Swem, T. R. 2002 Rough-legged Hawk (*Buteo lagopus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).
- Bechard, M. J., Houston, C. S., Sarasola, J. H. & England, A. S. 2010 Swainson's Hawk (*Buteo swainsoni*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Bednarz, J. C. & Raitt, R. J. 2002 Chihuahuan Raven (*Corvus cryptoleucus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Behrstock, R. A. 2001 Typical owls. In *The Sibley Guide to Bird Life and Behavior*, (ed. C. Elphick, J. B. Dunning & D. A. Sibley), pp. 336–338. New York: Random House.

Bekoff, M. & Gese, E. M. 2003 Coyote (*Canis latrans*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 476–481. Baltimore: John Hopkins University Press.

Boarman, W. I. & Heinrich, B. 1999 Common Raven (*Corvus corax*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Booms, T. L., Cade, T. J. & Clum, N. J. 2008 Gyrfalcon (*Falco rusticolus*), The

Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Buckley, N. J. 1999 Black Vulture (*Coragyps atratus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Buehler, D. A. 2000 Bald Eagle (*Haliaeetus leucocephalus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Copeland, J. P. & Whitman, J. S. 2003 Wolverine (*Gulo gulo*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 672–682. Baltimore: John Hopkins University Press.

Curry, R. L., Peterson, A. T. & Langen, T. A. 2002 Western Scrub-Jay (*Aphelocoma californica*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Cypher, B. L. 2003 Foxes (*Vulpes* species, *Urocyon* species and *Alopex lagopus*).

In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 511–546. Baltimore: John Hopkins University Press.

Dykstra, C. R., Hays, J. L. & Crocoll, S. T. 2008 Red-shouldered Hawk (*Buteo lineatus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Farquhar, C. 2009 White-tailed Hawk (*Buteo albicaudatus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Gardner, A. L. & Sunkist, M. E. 2003 Opossum (*Didelphis virginiana*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 3–29. Baltimore: John Hopkins University Press.

Gehrt, S. D. 2003 Raccoon (*Procyon lotor* and allies). In *Wild Mammals of*

*North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 611–634. Baltimore: John Hopkins University Press.

Gilchrist, H. G. 2001 Glaucous Gull (*Larus hyperboreus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Good, T. P. 1998. Great Black-backed Gull (*Larus marinus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Hatch, S. A., Robertson, G. J. & Baird, P. H. 2009. Black-legged Kittiwake (*Rissa tridactyla*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010)

Haven W., R. & Lee, D. S. 2000. Pomarine Jaeger (*Stercorarius pomarinus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

- Hayward, J. L. & Verbeek, N. A. 2008. Glaucous-winged Gull (*Larus glaucescens*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).
- Howell, S. N. & Jaramillo, A. 2006 Skuas, gulls, terns and skimmers. In *Complete birds of North America*, (ed. J. Alderfer), pp. 234–279. Washington: National Geographic Society.
- Humann, A. 2001 Hawks and allies, falcons and caracaras. In *The Sibley Guide to Bird Life and Behavior*, (ed. C. Elphick, J. B. Dunning & D. A. Sibley), pp. 289–308. New York: Random House.
- Jutglar, À. 1994 Family Cathartidae (New World Vultures). In *Handbook of the Birds of the World*, Vol. 2 (ed. J. del Hoyo, A. Elliott & J. Sargatal), pp. 24–41. Barcelona: Lynx Edicions.
- Kaufman, K. 1996 Lives of North American Birds. New York: Houghton Mifflin.
- Kirk, D. A. & Mossman, M. J.. 1998. Turkey Vulture (*Cathartes aura*), The Birds



of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Kochert, M. N., Steenhof, K., McIntyre, C. L. & Craig, E. H. 2002. Golden Eagle (*Aquila chrysaetos*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Koenig, W. & Reynolds, M. D. 2009. Yellow-billed Magpie (*Pica nuttalli*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Larivière, S. 2003 Mink (*Mustela vison*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 662–671. Baltimore: John Hopkins University Press.

Lewington, I. 1996 Family Laridae (Gulls). In *Handbook of the Birds of the World*, Vol. 3 (ed. J. del Hoyo, A. Elliott & J. Sargatal), pp. 572–623. Barcelona: Lynx Edicions.

- Lewington, I. & Willis, I. 1994 Family Accipitridae (Hawks and Eagles). In *Handbook of the Birds of the World*, Vol. 2 (ed. J. del Hoyo, A. Elliott & J. Sargatal), pp. 52–205. Barcelona: Lynx Edicions.
- Lindzey, F. G. 2003 Badger (*Taxidea taxus*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 683–691. Baltimore: John Hopkins University Press.
- Macwhirter, R. B. & Bildstein, K. L.. 1996. Northern Harrier (*Circus cyaneus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).
- Mallory, M. L., Stenhouse, I. J., Gilchrist, G., Robertson, G., Haney, J. C. & Macdonald, S. D. 2008. Ivory Gull (*Pagophila eburnea*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).
- McCormack, J. E. & Brown, J. L. 2008. Mexican Jay (*Aphelocoma ultramarina*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America

Online (July 2010).

Mcgowan, K. J. 2001 Crows and jays. In *The Sibley Guide to Bird Life and Behavior*, (ed. C. Elphick, J. B. Dunning & D. A. Sibley), pp. 408–415. New York: Random House.

Mcgowan, K. J. 2001. Fish Crow (*Corvus ossifragus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Melquist, W. E., Polechla, P. J. & Toweill, D. 2003 River otter (*Lontra canadensis*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 708–734. Baltimore: John Hopkins University Press.

Morrison, J. L. 1996. Crested Caracara (*Caracara cheriway*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Moskoff, W. & Bevier, L. R. 2002. Mew Gull (*Larus canus*), The Birds of North

America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology;  
Retrieved from the Birds of North America Online (July 2010).

Parmelee, D. F. 1992. Snowy Owl (*Bubo scandiacus*), The Birds of North  
America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology;  
Retrieved from the Birds of North America Online (July 2010).

Paquet, P. C. & Carbyn, L. N. 2003 Gray wolf (*Canis lupus*). In *Wild Mammals of  
North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A.  
Chapman), pp. 482–510. Baltimore: John Hopkins University Press.

Pelton, M. R. 2003 Black bear (*Ursus americanus*). In *Wild Mammals of  
North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A.  
Chapman), pp. 547–555. Baltimore: John Hopkins University Press.

Pierce, B. M. & Bleich, V. C. 2003 Mountain lion (*Puma concolor*). In *Wild  
Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C.  
Thompson & J. A. Chapman), pp. 744–757. Baltimore: John Hopkins  
University Press.

Pierotti, R. J. & T. P. Good. 1994. Herring Gull (*Larus argentatus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Pierotti, R. J. & Annett, C. A. 1995. Western Gull (*Larus occidentalis*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Powel, R.A., Buskirk, S. W. & Zielinski, W. J. 2003 Fisher and marten (*Martes pennanti* and *Martes americana*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 635–649. Baltimore: John Hopkins University Press.

Preston, C. R. & R. D. Beane. 2009. Red-tailed Hawk (*Buteo jamaicensis*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Quady, D. E.. 2006 Typical owls. In *Complete birds of North America*, (ed. J. Alderfer), pp. 321–334. Washington: National Geographic Society.

- Rosatte, R. & Larivière, S. 2003 Skunks (*Genera Mephitis, Spilogale and Conepatus*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 692–707. Baltimore: John Hopkins University Press.
- Schwartz, C. C., Miller, S. D. & Haroldson, M. A. 2003 Grizzly bear (*Ursus arctos*). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 556–5586. Baltimore: John Hopkins University Press.
- Small, B. & Quinn, D. 2009 Family Corvidae (Crows). In *Handbook of the Birds of the World*, Volume 14 (ed. J. del Hoyo, A. Elliott & D. A. Christie), pp. 494–642. Barcelona: Lynx Edicions.
- Snell, R. R. 2002. Iceland Gull (*Larus glaucoides*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).
- Snell, R. R. 2002. Thayer's Gull (*Larus glaucoides*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from

the Birds of North America Online (July 2010).

Snyder, H. 2001 New world vultures. In *The Sibley Guide to Bird Life and Behavior*, (ed. C. Elphick, J. B. Dunning & D. A. Sibley), pp. 183–186. New York: Random House.

Snyder, H. 2001 Hawks and allies, Falcons and caracaras. In *The Sibley Guide to Bird Life and Behavior*, (ed. C. Elphick, J. B. Dunning & D. A. Sibley), pp. 212–225. New York: Random House.

Snyder, N. F. & Schmitt, N. J. 2002. California Condor (*Gymnogyps californianus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Snyder, N. & Snyder, H. 2006 Raptors of North America. Minnesota: MBI Publishing.

Strickland, D. & Ouellet, H. 2011. Gray Jay (*Perisoreus canadensis*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of

Ornithology; Retrieved from the Birds of North America Online (July 2010).

Svendsen, G. E. 2003 Weasels and black-footed ferret (*Mustela* species). In *Wild Mammals of North America*, 2nd edn. (ed. G. A. Feldhamer, B. C. Thompson & J. A. Chapman), pp. 650–661. Baltimore: John Hopkins University Press.

Taylor, C. 2006 Hawks, kites, eagles and allies, caracaras and falcons. In *Complete birds of North America*, (ed. J. Alderfer), pp. 130–161. Washington: National Geographic Society.

Taylor, C. 2006 New world vultures. In *Complete birds of North America*, (ed. J. Alderfer), pp. 126–127. Washington: National Geographic Society.

Tomback, D. F. 1998. Clark's Nutcracker (*Nucifraga columbiana*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Trost, C. H. 1999. Black-billed Magpie (*Pica hudsonia*), The Birds of North



America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology;  
Retrieved from the Birds of North America Online (July 2010).

Tarvin, K. A., Woolfenden, & G. E.. 1999. Blue Jay (*Cyanocitta cristata*), The  
Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of  
Ornithology; Retrieved from the Birds of North America Online (July  
2010).

Verbeek, N. A. & R. W. Butler. 1999. Northwestern Crow (*Corvus caurinus*), The  
Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of  
Ornithology; Retrieved from the Birds of North America Online (July  
2010).

Verbeek, N. A. & C. Caffrey. 2002. American Crow (*Corvus brachyrhynchos*),  
The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of  
Ornithology; Retrieved from the Birds of North America Online (July  
2010).

White, C. M., Clum, N. J., Cade, T. J. & Hunt, W. G. 2002. Peregrine Falcon  
(*Falco peregrinus*), The Birds of North America Online (ed. A. Poole).

Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Wiley, R. H. & Lee, D. S.. 1998. Long-tailed Jaeger (*Stercorarius longicaudus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Willis, I. & Burn, H. 1994 Family Falconidae (Falcons and Caracaras). In *Handbook of the Birds of the World*, Vol. 2 (ed. J. del Hoyo, A. Elliott & J. Sargatal), pp. 216–277. Barcelona: Lynx Edicions.

Wilson, D. E. & Ruff, S. 1999 *The Smithsonian Book of North American Mammals*. Vancouver: UBC Press.

Winkler, D. W. 1996. California Gull (*Larus californicus*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Wood, C. L. 2006 Jays and crows. In *Complete birds of North America*, (ed. J.

Alderfer), pp. 417–429. Washington: National Geographic Society.

Woolfenden, G. E. & Fitzpatrick, J. W. 1996. Florida Scrub-Jay (*Aphelocoma coerulescens*), The Birds of North America Online (ed. A. Poole). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online (July 2010).

Table 5.1 All categorical variables included in database and considered during preliminary analyses as correlates of conservation risk.

Variable	Category	Database Code
NatureServe sub-national rank	S1	1
	S2	2
	S3	3
	S4	4
	S5	5
	Possibly extirpated	6
	Presumed extirpated	7
	Exotic	8
	Not ranked	9
	Unranked	0
Ordinal rank	Possibly extirpated	7
	Presumed extirpated	6
	S1	5
	S2	4
	S3	3
	S4	2
Global rank	S5	1
	EX	7
	EW	6
	CR	5
	EN	4
	VU	3
	NT	2
LC	1	
Global trend	Stable	0
	Increasing	1
	Decreasing	2
	Unset	3
Reintroduced	No	0
	Only reintro'd popn exist	1
	In some regions	2
Delayed implantation	No	0
	Yes	1
Condition of young at birth	Altricial	1
	Semi-altricial	2
	Semi-precocial	3
Interbirth interval (Litters/clutches per year)	Less than once every other year	1
	Every other year	2
	Reproduce each year	3
	Reproduce more than once per year	4

Variable	Category	Database Code
Migratory	Non-migratory	0
	Northern population migratory	1
	Local movement/short migrations	2
	Long distance migrations	3
Trophic position	1° predator	1
	2° predator	2
Feeding style	Primarily predatory	1
	Equally predatory and opportunistic	2
	Primarily opportunistic	3
Diet composition	Primarily carnivorous	1
	Omnivory common	2
	Highly omnivorous	3
Degree of scavenging	Obligate	1
	Significant/critical element	2
	Opportunistic, but not critical	3
	Rarely	4
Territoriality	Non-territorial	0
	Breeding territoriality only	1
	Year round territoriality (solitary)	2
	Year round territoriality (social)	3
	Foraging territoriality	4
Circadian activity patterns	No pattern	0
	Nocturnal	1
	Crepuscular	2
	Diurnal	3
Annual activity patterns	Year round	1
	Winter hibernation	2
	Winter torpor	3
Sociality	Primarily solitary/mated pairs	1
	Highly social family groups	2
	Winter/non-breeding sociality	3
	Some social grouping	4
	Highly gregarious (found in groups)	5
Mate fidelity	Monogamous	1
	Polygynous	2
	Polygynandrous	3
	All fidelities common	4
Harvested/hunted	No	0
	Yes	1

Table 5.2 All categorical variables included in database and considered during preliminary analyses as correlates of conservation risk.

Variable	Database unit
Average body length	Centimeters
Average mass	Grams
Average wingspan (birds)	Millimeters
Gestation/incubation period	Days
Average litter/clutch size	Young born/eggs laid
Age of independence	Months
Age of sexual maturity	Months
Age of first breeding event	Months
Age of first reproductive event	Months

Table 5.3 Strong species pairings ( $r_s \geq 0.7$ ) in the North American scavenging guild (\* $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ ).

Species 1	Species 2	Rho ( $r_s$ )
Gray wolf	American marten	0.756***
Gray wolf	Canadian lynx	0.812***
Gray fox	Ringtail	0.877***
American black bear	Common raven	0.783***
American marten	Canadian lynx	0.805***
Long-tailed weasel	Black-billed magpie	0.716***
American wolverine	Canadian lynx	0.742***
Ringtail	Peregrine falcon	0.872***
Cougar	Golden eagle	0.818***
Black vulture	Herring gull	0.863**

Table 5.4 Moderate strength species pairings ( $r_s \geq 0.4$ ) in the North American scavenging guild (\* $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ ).

Species 1	Species 2	Rho
Virginia opossum	Northern raccoon	0.507**
Virginia opossum	Black vulture	0.445*
Gray wolf	American black bear	0.521***
Gray wolf	Grizzly bear	0.636**
Gray wolf	Least weasel	0.466*
Gray wolf	American wolverine	0.633***
Gray wolf	Bald eagle	0.572***
Gray wolf	Northern harrier	0.536***
Gray wolf	Golden eagle	0.435*
Gray wolf	Gray jay	0.500**
Gray wolf	Common raven	0.564***
Red fox	Grizzly bear	0.540**
Red fox	Ermine	0.588***
Red fox	N. Am. river otter	0.402**
Red fox	Gray jay	0.473**
Gray fox	Eastern spotted skunk	0.487**
American black bear	Grizzly bear	0.594**
American black bear	American marten	0.668***
American black bear	Fisher	0.669***
American black bear	Ermine	0.590***
American black bear	Long-tailed weasel	0.452***
American black bear	American mink	0.411**
American black bear	American wolverine	0.446**
American black bear	N. Am. river otter	0.468***
American black bear	Cougar	0.456**
American black bear	Canadian lynx	0.595***
American black bear	Peregrine falcon	0.466**
American black bear	Bald eagle	0.450***
American black bear	Clark's nutcracker	0.638*
American black bear	Black-billed magpie	0.455*
Grizzly bear	Ermine	0.642**
Grizzly bear	American marten	0.542*
Grizzly bear	Long-tailed weasel	0.459*
Grizzly bear	American mink	0.473*
Grizzly bear	American wolverine	0.626**
Grizzly bear	N. Am. river otter	0.452*
Grizzly bear	Bald eagle	0.603**
Grizzly bear	Golden eagle	0.427*
Grizzly bear	Gray jay	0.640**
Grizzly bear	Common raven	0.443*
American marten	American wolverine	0.589***
American marten	Bald eagle	0.512**



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American marten	Northern harrier	0.564***
American marten	Gray jay	0.698***
American marten	Common raven	0.628***
Fisher	Least weasel	0.480*
Fisher	N. Am. river otter	0.603***
Fisher	Common raven	0.428*
Ermine	American mink	0.553***
Ermine	N. Am. river otter	0.652***
Ermine	Bald eagle	0.598***
Ermine	Red shouldered hawk	0.541*
Ermine	Herring gull	0.570**
Long-tailed weasel	Striped skunk	0.407**
Long-tailed weasel	Great black-backed gull	0.647**
Least weasel	Canadian lynx	0.541*
Least weasel	Bald eagle	0.466*
Least weasel	Northern harrier	0.457*
Black-footed ferret	Bobcat	0.668*
Black-footed ferret	Golden eagle	0.692**
American wolverine	Cougar	0.640***
American wolverine	Bald eagle	0.550***
American wolverine	Northern harrier	0.526**
American wolverine	Gray jay	0.579**
American wolverine	Common raven	0.630***
Badger	Bobcat	0.479**
N. Am. river otter	Canadian lynx	0.516**
N. Am. river otter	Black vulture	0.520*
N. Am. river otter	Herring gull	0.648***
N. Am. river otter	Great black-backed gull	0.451*
N. Am. river otter	Black-billed magpie	0.455*
N. Am. river otter	Fish crow	0.542**
Western spotted skunk	Cougar	0.554*
Eastern spotted skunk	Bobcat	0.635*
Eastern spotted skunk	Black vulture	0.661*
Striped skunk	Red-tailed hawk	0.475***
Raccoon	Black vulture	0.473*
Cougar	Bobcat	0.482**
Cougar	Northern harrier	0.514***
Cougar	Peregrine falcon	0.432**
Cougar	Clark's nutcracker	0.635*
Cougar	Black-billed magpie	0.636**
Cougar	Common raven	0.626***
Canadian lynx	Bald eagle	0.591***
Canadian lynx	Northern harrier	0.455*
Canadian lynx	Gray jay	0.563**
Canadian lynx	Common raven	0.597***
Bald eagle	Gray jay	0.479**

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Bald eagle	Common raven	0.433**
Northern harrier	Common raven	0.504***
Golden eagle	Common raven	0.409**
Peregrine falcon	Common raven	0.534***
Herring gull	Great black-backed gull	0.596**
Great black-backed gull	Gray jay	0.577*
Gray jay	Common raven	0.471**
Clark's nutcracker	American crow	0.560*
Clark's nutcracker	Common raven	0.589*
Black-billed magpie	Common raven	0.475*

Table 5.5 Weak species pairings ( $r_s \geq 0.2$ ) in the North American scavenging guild (\* $p \leq 0.05$ ; \*\*  $p \leq 0.01$ ; \*\*\*  $p \leq 0.001$ ).

Species 1	Species 2	Rho
Coyote	Gray wolf	0.302*
Coyote	American marten	0.389*
Coyote	Least weasel	0.392*
Coyote	Striped skunk	0.340*
Coyote	Canadian lynx	0.395*
Coyote	Common raven	0.359*
Gray wolf	Cougar	0.382*
Gray wolf	Peregrine falcon	0.312*
Red fox	American black bear	0.299*
Red fox	Long-tailed weasel	0.379**
Red fox	American mink	0.391**
Red fox	Canadian lynx	0.369*
American black bear	Northern harrier	0.341*
American black bear	Gray jay	0.370*
American marten	N. Am. river otter	0.376*
Fisher	Striped skunk	0.379*
Fisher	Peregrine falcon	0.370*
Ermine	Long-tailed weasel	0.394*
Ermine	Gray jay	0.389*
Long-tailed weasel	American mink	0.304*
Long-tailed weasel	Cougar	0.355*
Long-tailed weasel	Red-tailed hawk	0.296*
Long-tailed weasel	Common raven	0.366*
American mink	N. Am. river otter	0.329*
Badger	Northern harrier	0.391*
N. Am. river otter	Northern raccoon	0.358*
N. Am. river otter	Bald eagle	0.378**
N. Am. river otter	Common raven	0.376**
Striped skunk	Common raven	0.366*
Bobcat	Golden eagle	0.392*
Bobcat	Common raven	0.321*
Turkey vulture	Red-shouldered hawk	0.356*