

How do roads affect the habitat use of an assemblage of scavenging raptors?

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Abstract Scavengers may benefit from the availability of dead animals along roads that result from collisions with vehicles. However, roads are also considered risky places for many species. Animal habitat selection patterns usually balance energy intake with mortality risk. In this work we analyzed the foraging space use of an assemblage of diurnal scavenging raptors in relation to distance from roads in northwest Patagonia. We selected patches at different distances from roads, and placed a sheep carcass in each patch during the night ($n = 18$ carcasses in total). In general, carcasses near roads were detected by diurnal scavenging raptors much faster than those far from roads. Smaller raptors such as southern caracaras (*Caracara plancus*), chimango caracaras (*Milvago chimango*), and black vultures (*Coragyps atratus*), were commonly associated with roads both in terms of overall detections and scavenging activities. Southern and chimango caracaras proved to be very good at detecting carcasses, were faster to land in order to feed from them, and were found in greater numbers near roads than far from them. Even though Andean condors (*Vultur gryphus*) and black-chested buzzard-eagles (*Geranoaetus melanoleucus*) flew all over the area, they chose to feed far from roads. Our work emphasizes that some scavengers have taken advantage of the novel food resources provided by roads whereas others are reluctant to feed near them. Within a scenario of an increasing number of roads, some species can extend their distributions favoring competition and biotic homogenization processes within original communities. We highlight the importance of taking into account large flying scavengers in land-use planning.

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Introduction

Human development brings with it an increase in the number of roads to fulfill transport needs, but this increase has costly implications for nature (Forman et al. 2003). Roads may have no effect, may have negative effects, or even may benefit some species, especially those living in border areas or who are associated with human activities (Spellerberg 1998; Grilo et al. 2008). Roadside habitats usually contain a high abundance of small mammals especially along roads with wide verges (Adams and Geis 1983; Meunier et al. 2000). It has also been suggested that road verges may be selected as hunting sites due to the density of perches, which permit energetically economic hunting (Donázar et al. 1993; Meunier et al. 2000). Birds of prey may use this type of habitat for scavenging (Haug 1985; Watson 1986; Knight and Kawashima 1993) in addition to active hunting (Bourquin 1983; Fajardo et al. 1998).

Animal habitat selection patterns with respect to food resources usually balance energy intake with mortality risk (Grand and Dill 1999). An individual's risk of mortality varies across different habitats as it may be modified by the interplay of morphological and behavioral differences with the environmental characteristics of the habitat (Grand and Dill 1999). For example, roads may produce heterogeneous landscapes generating a differential distribution of birds in space due to differences in disturbance tolerance of the species (Marr et al. 1995; Bautista et al. 2004; Blumstein 2006; Speziale et al. 2008). Thus, it can be hypothesized that the distribution of species in heterogeneous habitats with respect to food quantity and mortality risk will depend upon each species' levels of energy requirements and perceived risk.

Birds that frequently feed near roads are probably used to traffic, which makes observations easier when conducting road censuses (Donázar et al. 1993; Travaini et al. 1995). It has been shown that roadside samples exaggerate the distribution and dominances in the avian communities (Hanowski and Niemi 1995; Keller and Fuller 1995). Therefore, the interpretation of data obtained by road censuses must be made carefully. A common explanation for this bias is the higher abundances of food along roads compared to inland habitats (Houston 1975; Knight and Kawashima 1993; Dean and Milton 2003). However, to our knowledge there are no studies comparing assemblages, abundances and behavior of scavenging raptors eating with respect to roads.

Carrion is an ephemeral and randomly distributed resource and its availability is critical for the survival of scavenging birds (Wallace and Temple 1987). However, roads, due to their supply of road kills, can generate a differential distribution of dead animals across a landscape. Carrion can only be considered a usable resource for scavenging birds if it is detected and eaten quickly enough. However, not every species takes the same risk of coming down to eat from human-created places like roads (Marr et al. 1995; Blumstein et al. 2005; Blumstein 2006). Feeding from such places can represent a high risk, especially for large species (Speziale et al. 2008).

Diurnal scavenging raptors in Patagonia usually aggregate along roads (Bellati 2000). Some of these species benefit from the introduced cattle carrion as well as by the introduction of other exotic species such as European hares (*Lepus europaeus*) and rabbits (*Oryctolagus cuniculus*) (Donázar et al. 1993). In this work we analyze the use of space for feeding by an assemblage of diurnal scavenging raptors in relation to the presence of roads

in northwest Patagonia. We propose that roads generate differential space use by scavengers in two different ways: (1) by expelling birds due to the disturbance they generate, and (2) attracting birds with the food they provide. We predict that scavengers used to human presence will feed more often by roads than the species not associated with anthropogenic disturbance. We apply five statistical models to investigate whether the roads have an effect on the habitat use of an assemblage of scavenger species in northwest Patagonia, Argentina.

Methods

Study area

We conducted our study in Río Negro and Neuquén provinces, in the northwest of Argentinean Patagonia (around 41°S and 71°W). The study area is hilly with ridges and cliffs belonging to the Patagonian phytogeographic province (Cabrera 1971). It is a typical steppe area with open vegetation dominated by grasses (*Festuca pallescens*, *Stipa speciosa*) and shrubs (*Mulinum spinosum*) (Cabrera 1971). We worked during two seasons in 2006: autumn (May to June) and spring (October to December). The prevailing climate is cold and rainy during autumn, but cool, windy, and mostly dry during spring (Paruelo et al. 1998). Our study sites were located near two roads surrounded mostly by rural areas with large farms dedicated to extensive sheep or cattle raising. Besides domestic livestock, there are increasing amounts of introduced mammals such as red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), and European hare (*Lepus europaeus*) mainly since the last century (Bellati 2000; Novaro and Walker 2005). Road-killed hares are commonly observed along roads (Donázar et al. 1993; Travaini et al. 1998), and legal and illegal hunting of deer and hares has increased in recent years. Thus, carcasses as a food source are abundant in the entire study area. Human density is low in the area; Río Negro and Neuquén provinces has 2.7 and 5 inhabitants/km² on average, respectively, but in rural areas the density is much lower.

Study species

We included in our work six obligate and facultative scavenging diurnal raptors: chimango caracara (*Milvago chimango*, 0.3 kg), southern caracara (*Caracara plancus*, 1.1–1.6 kg), black-chested buzzard-eagle (*Geranoaetus melanoleucus*, 2.0 kg), black vulture (*Coragyps atratus*, 1.1–1.9 kg), turkey vulture (*Cathartes aura*, 0.85–2.0 kg), and Andean condor (*Vultur gryphus*, female: 8–11 kg; male: 11–15 kg) (del Hoyo et al. 1994). The Andean condor is considered as a rare species, Near Threatened and included in CITES appendix I (CARPFS 1994; Bird Life International 2004; Lambertucci 2007). However, this area has one of the larger known populations of Andean condors within its distribution (Lambertucci et al. 2008). The other species are abundant and considered not threatened in this area (CARPFS 1994). We classified the six species in relation to their tolerance to human presence based on regional and local literature on the raptors' behavior and distribution (Donázar et al. 1993; del Hoyo et al. 1994; Travaini et al. 1998; Bellati 2000; Ferguson-Lees and Christie 2001; Yorio and Giaccardi 2002; Lambertucci 2007). Chimango caracara, southern caracara, and the two vultures were classified as tolerant of human disturbance while we classified the black-chested buzzard-eagle and Andean condor as not human-tolerant.

Experimental design

We monitored 18 carcasses during the study period. We placed two sheep carcasses simultaneously, one sited close to the roadside (near) and another at some distance from the road (far). ‘Far’ patches were located in open areas between 500 and 6,000 m from a road whereas ‘near’ patches were located up to 500 m from roads (following Clark and Karr 1979; Keller and Fuller 1995; Forman 2000; in concordance with Palomino and Carrascal 2007). We monitored both carcasses at the same time to diminish the possibility of unmeasured errors (e.g., weather conditions). Carcasses were placed during the night. Both types of patches had scattered vegetation, rock outcrops and offered sufficient opportunities for scavenging raptors to land and take off. Each carcass was monitored continuously from hides at least 300 m away from the sheep with the aid of binoculars (10 × 50) and telescopes (20 × 60 × 60), until the sheep was completely eaten, or up to a maximum of 14 days. If birds had not started eating in that time we abandoned the site and moved to monitor a new pair of carcasses. We obtained the sheep from livestock belonging to the farms where the experiments were set; hence, we did not increase the amount of food supply of the area.

We recorded every species flying, landing, and eating at each carcass, including the arrival sequence and number of species together at a carcass. We recorded the following variables per species: (1) detection time, which was the time it took from the sheep carcass being placed until an individual was flying low and directly over it, (2) time elapsed between detection and first feeding attempt, (3) total number of individuals flying over the sheep, counted from the time the sheep was placed until the experiment was finished and (4) total number of individuals eating at each carcass. We only registered a bird as a new individual if we could positively distinguish it from the previous one or if it arrived 15 min after the previously registered bird left the area.

Data analysis

In order to compare the time each species took to detect a carcass and the three-first species that ate the carcasses we divided the data into patches near and far from roads. We assessed the differences between the near and far patches as well as the differences between the individual species for each of the recorded variables using Mann–Whitney *U* and Kruskal–Wallis tests, as our data did not conform to parametric assumptions (Conover 1999).

We also made comparisons of the number of birds flying over or eating at the carcasses by using the exact distances from each sheep to the road. We assumed that the total number of birds observed (flying and landed) would follow a Poisson distribution given that the observations are discrete numbers and without an upper bound. From the total number of birds found near a carcass site, we modeled the fraction that actually landed and ate using a Binomial distribution,

$$\Pr\{g|N, p\} = \binom{N}{g} p^g (1 - p)^{N-g} \quad (1)$$

where *N* is the total number of birds found at a carcass site, *g* is the number that landed to eat and *p* is the per capita probability of landing.

Preliminary inspection of the data show an excess of zeros in the total number of birds compared to what would be expected for a Poisson distribution. Hence, for our subsequent analyses we used a “zero-inflated” Poisson distribution as follows:

$$\begin{aligned}\Pr\{k = 0\} &= (1 - v) + v \frac{\lambda^k \exp(-\lambda)}{k!}, \\ \Pr\{k > 0\} &= v \frac{\lambda^k \exp(-\lambda)}{k!}\end{aligned}\quad (2)$$

where v is a “detection probability” and λ is the usual Poisson parameter. Thus, the zeros in the data can be due to birds failing to encounter the carcass ($1 - v$) or as an outcome of the Poisson distribution $v\lambda^k \exp(-\lambda)/k!$

We then asked whether distance to roads affected the number of birds found at a carcass site and the probability of individuals landing to eat at these sites. To answer these questions we compared the fit of alternative models to our data using Akaike information criteria corrected by sample size AICc (Burnham and Anderson 1998). We contrasted the fit of the following alternative models:

1. constant detection probability (v), constant lambda and constant landing probability (p) (i.e. no effect of distance to road);
2. both lambda and landing probability changing with distance

$$\begin{aligned}\lambda &= \exp(a_d + b_d x) \\ \text{logit}(p) &= a_p + b_p x,\end{aligned}\quad (3)$$

3. a model that allowed for an “optimal” distance to road using a Ricker function

$$\begin{aligned}\lambda &= a_d x \exp(b_d x) \\ p &= a_p x \exp(b_p x)\end{aligned}\quad (4)$$

4. a combination of monotonic increase/decrease in lambda and optimal distance for landing probability

$$\begin{aligned}\lambda &= \exp(a_d + b_d x) \\ p &= a_p x \exp(b_p x)\end{aligned}\quad (5)$$

5. an optimal distance for lambda and a monotonic increase/decrease of landing probability

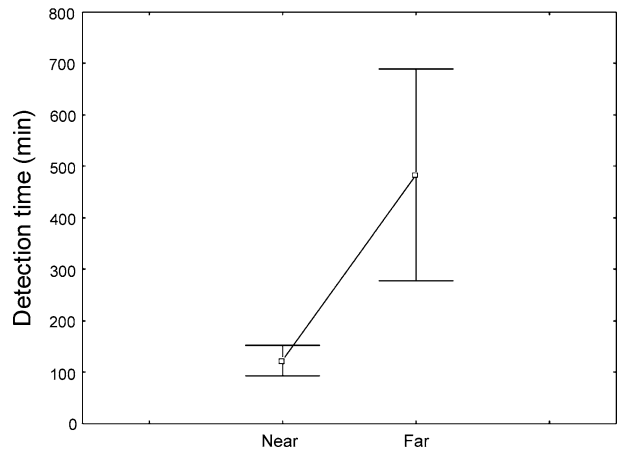
$$\begin{aligned}\lambda &= a_d x \exp(b_d x) \\ \text{logit}(p) &= a_p x + b_p x\end{aligned}\quad (6)$$

Models were fitted to data in *R* using maximum likelihood estimation with Ben Bolker’s *bbmle* package (<http://lib.stat.cmu.edu/R/CRAN/web/packages/bbmle/>).

Results

We monitored the carcasses a total of 1,791 h from sunrise to sunset (over 73 days—two sheep simultaneously). Birds ate from 16 of the 18 sheep carcasses. Although individuals of all 6 target species ate from the sheep carcasses, the assembly of species varied among sheep. We only registered turkey vultures during spring monitoring as they migrate

Fig. 1 Mean (\pm SE) time raptors needed to detect the sheep carcasses after we placed them near (<500 m) and far (≥ 500 m) from roads



northward and are not found in Patagonia during austral autumn and winter (Bildstein 2004). Due to the low information recorded for this species we only used these data for the comparison of the time species took to detect carcasses, the difference in time between detection and eating, and the sequence of the species eating. In addition to birds, we also occasionally had mammals feeding at the carcasses, including culpeo foxes (*Lycalopex culpaeus*), dogs (*Canis familiaris*) and a puma (*Puma concolor*).

Across all species, detection time was different between the near and far patches; scavengers detected carcasses in the near patches sooner than those in the far patches (Mann–Whitney *U*-test, $Z = 2.06$, $P = 0.039$, Fig. 1). Chimango caracara, Andean condor, and southern caracara were the first to detect sheep carcasses near roads 34, 33, and 22% of the times, respectively; carcasses more than 500 m from roads were detected first by Andean condors (89% of the time) and by turkey vultures (11% of the time). Southern and chimango caracaras generally ate first or second from carcasses near to roads. Meanwhile, away from roads, Andean condors mainly ate first and black-chested buzzard-eagle second. The third place for feeding near roads was shared by 5 of the 6 species, but far from roads we seldom saw three different scavenger species eating from a carcass (Table 1).

Table 1 Order of arrival at the carcass of the three-first scavenger species near (<500 m) and far (>500 m) from roads

Species	Near			Far		
	1°	2°	3°	1°	2°	3°
Chimango caracara	40 (3)	37.5 (3)		37.5 (3)		12.5 (1)
Southern caracara	60 (5)	25 (2)	12.5 (1)		25 (2)	
Black vulture			25 (2)			12.5 (1)
Turkey vulture		12.5 (1)	12.5 (1)			
Buzzard-eagle		12.5 (1)	12.5 (1)	12.5 (1)	37.5 (3)	12.5 (1)
Andean condor		12.5 (1)	12.5 (1)	50 (4)	12.5 (1)	
None			25 (2)		25 (2)	62.5 (5)

Percentages are based on the number of times a carcass was eaten (near $n = 8$ and far $n = 8$ carcasses). Numbers in brackets are the number of carcasses in which this species occupied this position

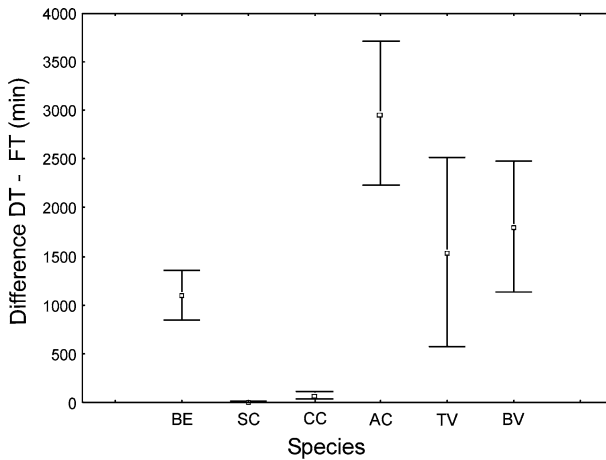


Fig. 2 Mean (\pm SE) time difference between detection time (DT) and feeding starting time (FT) for each scavenger species. BE (*black-chested buzzard-eagle*), SC (*southern caracara*), CC (*chimango caracara*), AC (*Andean condor*), TV (*turkey vulture*), and BV (*black vulture*)

Different species exhibited different degrees of feeding latency (Kruskal–Wallis test, $H = 18.94$, $P = 0.002$, Fig. 2). Southern caracaras and chimango caracaras spent similarly brief periods of time between detecting the carcass and starting to feed. On the other hand, eagles and vultures showed longer delays between detecting and eating, with Andean condors exhibiting the longest delay (Multiple comparisons of mean rank $P = 0.01$; Fig. 2).

Our constant, no effect model (model 1) had a bad fit for any of the species, indicating that roads do have an effect on the flying and feeding behavior of the assemblage of scavengers (Table 2). All the species tended to decline in numbers with increased distance to roads however the shape of this relation was different among species (Fig. 3a–e). The decrease in flying individuals of black vultures, southern caracaras and chimango caracaras was abrupt (Fig. 3c–e), while for Andean condors and black-chested buzzard-eagles the decline was more gradual (Fig. 3a–b). Moreover, if we only analyze carcasses up to 1,250 m from roads this trend was even smoother for eagles and even changed for condors (see Fig. S2, in the Electronic Supplementary Material (ESM)).

For every analyzed species, our model combining a monotonic increase/decrease in lambda and optimal distance for landing probability (model 4) best described the proportion of feeding birds in relation to total flying individuals at different distances to roads. However, there are important differences regarding this model among the five species. The optimum distance to eat (maximum in the curve) for black vulture (218 m), southern

Table 2 AICc table for all the models

	Model 1	Model 2	Model 3	Model 4	Model 5
Andean condor	1089.50	1043.36	1323.12	955.16	1411.33
Buzzard-eagle	368.34	334.23	464.79	328.98	470.04
Southern caracara	430.78	364.83	455.23	336.97	483.31
Chimango caracara	265.41	241.25	283.83	233.79	291.30
Black vulture	231.92	200.94	254.49	200.54	254.89

Lower AICc values indicated in bold (for AICc differences <2 models are considered equivalents)

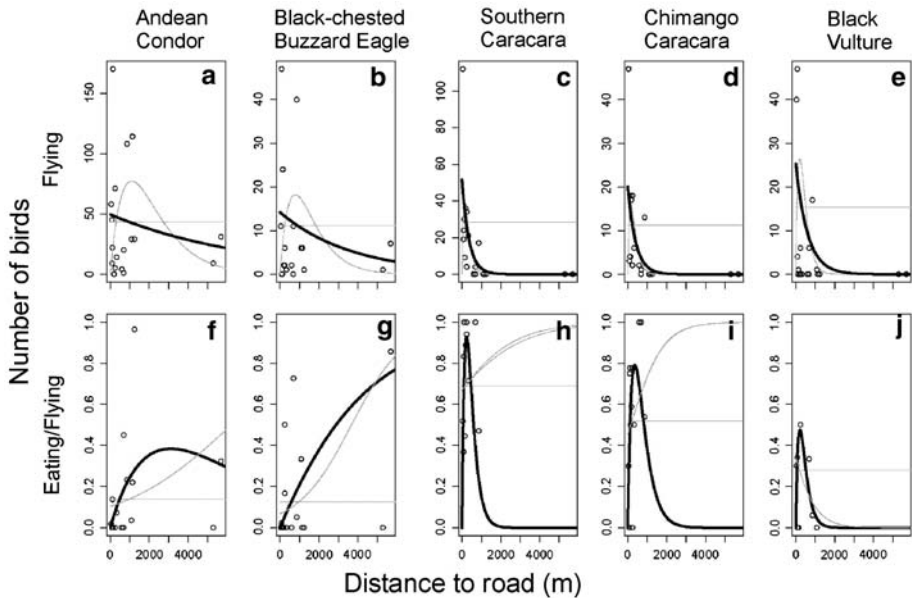


Fig. 3 Models of the number of raptors flying over (a–e) or proportion of birds eating related to the number of individuals flying (f–j) on each sheep carcass placed at different distances from roads (up to 6,000 m). Fitting curve of the best model (with lower AICc) is marked with a thicker line

caracara (235 m) and chimango caracara (365 m), was near roads showing an immediate decrease after that distance. For condors and eagles the optimum was far from roads (3,110–10,460 m, respectively, Fig. 3f–j). If we did not include the two furthestmost carcasses, which were the only data after the curve reaches its maximum, we observed a strong increment in the use of the carcasses with increasing distance from the road, without affecting the ranks of alternative models as assessed by AICc (see Fig. S2, in the ESM).

For black vultures, the model considering both lambda and landing probability changing with distance (model 2) was equivalent to model 4 in our analysis (Table 2). Therefore, we could not distinguish from our data if the incidence of vultures decreased directly with the distance to the road or increased for a short distance and then decreased quickly. Including only the carcasses up to 1,250 m from the road, the rank of the models are the same but we cannot distinguish between models 2 and 4 for the Andean condor as well as for black vultures (see Fig. S2, in the ESM). In this case, the proportion of Andean condors eating increased with the distance to the road without an optimum distance (see Table S1, in the ESM). Therefore, even though condors and eagles flew near roads more, or in similar numbers near to and far from the roads, they ate more often from carcasses further from roads. A contrasting behavior was observed for southern caracaras, chimango caracaras and black vultures. These species were seen more frequently flying and eating near to roads than away from them, even when we included all carcasses.

Discussion

We found differences between scavenger species in relation to flying and feeding activities at different distances from roads. Carcasses situated near roads were detected much faster

than those far from roads. Smaller raptors, such as southern caracaras, chimango caracaras and black vultures, were associated with roads both for searching and feeding activities. Southern and chimango caracaras appeared to be very good at detecting carcasses, were faster to go down to feed from them, and were found in greater numbers near roads than far from them. This might be due to the fact that these birds perch and wait near roads in order to have the opportunity of feeding from road-killed animals (Donázar et al. 1993; Dean and Milton 2003), and because they must eat quickly before bigger species arrive (Wallace and Temple 1987; Travaini et al. 1998). Small species can also be more tolerant to disturbance (traffic and human presence) than bigger birds (Blumstein et al. 2005). Roads can make birds vulnerable to collision and to being hunted, especially for large species that are slow to take off. Even though condors and eagles flew all over the area they chose to feed far from roads: flying over roads is not as risky as eating near them.

The distribution of bird species that breed or perch on trees can be influenced by tree distributions (Meunier et al. 2000; Sarasola and Negro 2006). However, in our study area the vegetation of the road verges was similar to the surroundings. Native trees are dispersed inland and are mainly associated to rocky outcrops or water courses. Exotic pine plantations are distributed throughout the region. Thus, it seems that this factor should not be the main one influencing the distribution of scavenging raptors with respect to roads.

There might be other factors affecting foraging decisions beyond disturbance created by the presence of roads including social interactions, birds' condition, hunger, or local effects (Beecham and Farnsworth 1998; Galef and Giraldeau 2001). The data variability we found is probably reflecting these factors. Even though we did not control all the factors that might be affecting the decisions that birds make, our results support the idea that the presence of roads clearly affects this assemblage of scavengers when making foraging decisions. On the other hand, the number of samples very far away from roads (between 1,250 and 6,000 m) was too low to draw clear conclusions about these places. However, although the models should be tested with more data in places far from roads, the optimal distance for feeding activities for condors and eagles was clearly greater than for the other species.

Differences in the time elapsed between detecting and eating from a carcass could also be attributed to differences in the birds' willingness to take risks (Lima and Dill 1990; Blumstein 2006). Once condors, vultures, and eagles detect the carcass they take a certain time period before they start feeding, or may not even feed at all. We generally saw condors and eagles flying or roosting in the surroundings of the carcass for long periods before they decided to start feeding. Our results showed that condors could be the first birds to detect food, especially far from roads. Therefore, condors are good at detecting food without the need for other birds. However, they did not eat without first assessing the environment (Donázar et al. 1999). On the other hand, southern and chimango caracaras were very fast to come down to eat after detecting a carcass. This might imply that they do not need to assess the environment surrounding the food as critically as the larger species, showing that smaller species are less fearful of taking risks.

The amount of food we placed was similar for each patch, whether near to or far from roads. Thus, the fact that smaller raptors quickly detected carcasses and fed mostly by roads may indicate that they are more used to obtaining food from roads and rely on roads as a source of food more than deciding to look for food inland. In addition, our results coincide with Grand and Dill's model (1999) in which better competitors (in this case large species *sensu* Wallace and Temple 1987) use less risky places. This may force smaller species (i.e., poor competitors) to choose more disturbed places, such as those created by humans, due to competition. From our data we can not conclude whether smaller raptors choose to feed by roads because of their benefits, if they are expelled from less risky places due to competition, or both.

Food is abundant in our study area and our results probably reflect this fact. High food abundance makes birds less willing to take unnecessary risks (Olsson et al. 2002). However, under a scenario of limited food, large scavengers will probably take higher risks in order to obtain an energy reward (Speziale et al. 2008). Thus, in areas poorer in food we predict a different pattern with larger species daring to feed by roads.

We found that the place where an item of food occurs seems to be very important for carrion eaters. Moreover, we documented that the sequence of arrival and eating, as well as the composition of an assemblage, can be influenced by the location of a carcass. The problems of roads when conducting road censuses have already been stated (e.g., Hanowski and Niemi 1995; Keller and Fuller 1995). In addition to those problems, we have proved that other bias created by roads have to be considered whenever carcasses are used as a tool; e.g., in the study of competence, hierarchies, facilitation, behavior experiments, management of endangered species, and reintroduction programs. If not, biased or unsuccessful results can be obtained.

Our work emphasizes that some scavengers could benefit from the extra food produced by roads while others may be disadvantaged by the presence of roads, or at least unwilling to take advantage of them. This might indicate that roads can have a detrimental effect on the feeding possibilities of some scavengers. Therefore, an interesting topic to be considered in future studies is the importance of roads as a dispersion vector for species used to traffic. The number of roads and amount of traffic are increasing in Patagonia, as in the entire world (Forman et al. 2003). This increase would favor an extension of the home range and abundances of a particular assemblage of species used to roads, which in turn, could cause a turnover of competitive abilities, i.e., causing smaller species to become better competitors than the bigger ones. A serious consequence derived from this possible outcome is the change in the original community of the area dissected by roads. This process, known as biotic homogenization, describes the gradual replacement of regionally distinct communities by cosmopolitan communities producing important ecological and evolutionary consequences (Olden et al. 2004). Competition for food between Andean condors and black vultures, which are increasing in human-modified areas, and possible biotic homogenization processes have already been proposed for Patagonia (Carrete et al. submitted). So, if the increment of roads favors an increase in the abundances of competitor species, a detrimental effect is very likely to arise, mainly for obligate scavenger species such as condors that are reluctant to feed by roads (Speziale et al. 2008). Consequences of roads for big scavengers and top predators birds should be acknowledged when designing conservation strategies.

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