
1. Introduction

Measuring how human activities may affect natural habitats is important for the assessment of environmental quality and for planning conservation strategies. In many cases, direct human disturbance can be a problem for animals, and road traffic is one example. Conservation biologists and managers in different parts of the world have been interested in the ecological effects on wildlife of roads and traffic (Spellerberg, 1998; Caro, 1999; Row et al., 2007; Bissonette and Adair,

2008; Eigenbrod et al., 2008). For example, car traffic diminishes habitat quality for breeding birds in forests over distances of 100–1500 m away from main roads in Netherlands (Reijnen et al., 1995). It also reduces species richness of insectivorous birds and abundances of passerines (Clark and Karr, 1979; Canaday, 1996). The complex road-traffic impact is generally greater than expected even on large bird species with large home ranges, often flying high above roads (van der Zande et al., 1980; Bautista et al., 2004). In this paper we aim to quantify the disturbance of roads on the Andean

condor (*Vultur gryphus*), one of the biggest flying birds of the world, with wingspan up to 3 m and 13 kg body mass (Ferguson-Lees and Christie, 2001).

Animal behaviour could provide a very useful tool for conservation (Sutherland, 1998; Buchholz, 2007). Behavioural responses can be used to assess the effects of anthropogenic disturbance (Skagen et al., 1991; Gill et al., 1996; Caro, 1999). For example, pink-footed geese (*Anser brachyrhynchus*) eat a lower percentage of food when they feed close to roads (Gill et al., 1996). Although behavioural studies are not the solution for every conservation problem, many practical and conceptual issues in conservation biology benefit from knowledge of individual behaviour (Gosling and Sutherland, 2000; Buchholz, 2007). As recently thoroughly reviewed (see summary by Kotler et al., 2007), behavioural indicators can be extremely useful to address many different topics in conservation biology. Specifically, suitably applied studies of foraging behaviour can give insights to habitat quality, population dynamics and even community ecology (Kotler et al., 2007; Olsson and Molokwu, 2007; Whelan and Jedlicka, 2007).

One important factor, which can be revealed through an individual's behaviour, is how foraging animals balance the risk of predation with the energy reward by making foraging decisions (Lima et al., 1985; Lima and Dill, 1990; Brown and Kotler, 2004). The cost of predation is often expected to be the factor most strongly influencing animal's behaviour (Brown, 1988, 1992). It involves the risk of predation (i.e. the probability of getting killed), the cost of getting killed (the expected fitness if surviving) and the marginal value of energy (i.e. the increase in fitness with one extra unit of energy gained; Brown, 1992; McNamara and Houston, 1994). More generally, the cost of predation could be termed a cost of catastrophic loss or injury (Brown and Kotler, 2004) as the risk of predation in many cases can also include other risks of getting killed or of disastrous injury.

Theory (Brown, 1988, 1992, 1999; Olsson and Holmgren, 1999) and numerous empirical studies (e.g. Kotler, 1997; Morris, 1997; Altendorf et al., 2001; Olsson et al., 2002; see also review by Brown and Kotler, 2004) have shown that several important behaviours can productively reveal how animals experience risks. These are particularly the time allocation pattern, measured by the patch residence time, the giving-up density (GUD; Brown, 1988), and the proportion of time spent vigilant while foraging (Caraco et al., 1980; Brown, 1999). In general, feeding time allocation will be directed towards safe and/or rewarding patches (e.g. Altendorf et al., 2001; Brown and Kotler, 2004), but in many cases there is a negative relation between profitability and safety (Gilliam and Fraser, 1987; Lima and Dill, 1990). Then the patch use will be a trade-off between food and safety. The GUD is the amount of food left behind in depletable food patches, when the foragers decide to abandon it and stop foraging, and can often be used as a surrogate for the quitting harvest rate (Brown, 1988; Olsson et al., 2001). Therefore, the GUD can be an extremely useful metric of the energy return demanded by the animal to remain in a patch under given circumstances (e.g. Kotler, 1997; Morris, 1997; Olsson et al., 2002; Brown and Kotler, 2004).

Andean condors have extremely low adult mortality rates, and can become very old. In zoos they can reach ages be-

tween 65 and 75 years (Kasielke and Wallace, 1990). Their reproductive rate is one of the lowest among all birds, with only one breeding attempt per 2–3 years, laying 1 egg each time, of which not all hatch and survive (Temple and Wallace, 1989; Lambertucci, in press; Lambertucci and Mastrantuoni, 2008). They only reach sexual maturity at the age of 6, although often do not reproduce before the age of 8, and the first eggs are generally infertile (Lint, 1959; Amadon, 1964; del Hoyo et al., 1994; Pavez and Tala, 1995). With such a slow reproductive rate, their marginal value of energy can be expected to be lower than for most other birds. Their cost of predation will therefore increase dramatically with even small increases in the risk of predation (Brown, 1992; Olsson et al., 2002), as fitness to such a large extent depends on survival. In addition, they are very vulnerable once they are on the ground, especially after eating, due to their difficulty to take off (Wallace and Temple, 1987; Donázar et al., 1999). Therefore, condors are predicted to be unusually reluctant to take any risks that might increase their mortality rate even slightly.

The distribution of Andean condors includes the Andes Mountains from Venezuela to the south of Argentina and Chile (del Hoyo et al., 1994). Currently it is considered Near Threatened worldwide (IUCN) and is listed in CITES I (Bird-Life International, 2004). It is threatened in Peru and endangered in Ecuador, Colombia and Venezuela (Lieberman et al., 1993; Cuesta, 2000; Koenen et al., 2000). Due to its natural history, it is very vulnerable and the main causes of population decline are related to humans (Lambertucci, in press). However, roads have not been considered as an important threat for this species, although condors may be killed by road traffic while feeding (S. Di Martino pers. comm.) and they can even be shot from roads (S.A.L. unpubl. data).

Condors are often the last members of the scavenger assemblage to arrive at a carcass after waiting hours, or even days, before they decide to approach it (Donázar et al., 1999; Houston, 2001). This behaviour reveals their extreme cautiousness. Some raptors might profit from road kills, but condors are generally not seen feeding near roads (Watson, 1986; Knight and Kawashima, 1993; Travaini et al., 1998; Bellati, 2000). The objective of this study is to analyze if the presence of roads affects Andean condors habitat use. Our hypothesis is that the disturbance from roads will affect how condors use the habitat for feeding. In order to test this, we set up a pair-wise design with standardized food patches. We simultaneously placed two sheep carcasses in pairs of patches far from roads and near them, to compare patch residence time, GUD and vigilance behaviour during foraging. We predict that, if disturbance from roads affect habitat quality in the hypothesized manner, (1) condors will spend less time in patches near roads than far away from them; (2) condors will abandon carcasses with more food (higher GUD) left on them near roads; (3) condors will try to reduce the risk of predation by scanning while feeding, so they will spend a higher proportion of the time scanning when feeding near roads. This is the first study to analyze habitat quality in relation to a human disturbance such as roads, by measuring and comparing condors' feeding behaviour.

2. Methods

2.1. Study area

We studied condors' feeding behaviour in the Río Negro and Neuquén provinces, in northwest Patagonia, Argentina, around 41°S and 71°W. The study was carried out in a mountain area. There are at least 196 condors in the study area (Lambertucci et al., 2008). It belongs to the Patagonian biogeographic province (Cabrera, 1971). It is a typical steppe area with open vegetation dominated by grasses like *Festuca pallens* and *Stipa speciosa* and bushes as *Mulinum spinosum* (Cabrera, 1971). Climate is cold and rainy during autumn but cool, windy and mostly dry during spring.

We worked during autumn (May–June) and spring (October–December) 2006, along three different roads; two gravel roads (road numbers 65 and 23), and one national paved road (road number 40S). The areas surrounding these roads are mostly sparsely populated rural land (0.6 inhabitants/km²) with large farms (average unit size 5000 ha) raising cattle or sheep extensively. In the area more than 1,600,000 sheep and over 450,000 cows are raised. Road traffic is approximately 100 vehicles/day on the gravel road 23, less than 100 on road number 65, and 1550 vehicles/day on the national 40S road (Lence, E., pers. comm.). No data is available about the number of road kills along those roads, but brown hare (*Lepus europaeus*) is the species most commonly found (pers. obs.).

2.2. Data collection and analysis

We made behavioural observations of condors feeding on sheep carcasses that we had placed in paired patches (26 patches in 13 pairs). Each pair was initiated by placing a sheep in each patch during the same night, and then the sheep were left in them for up to two weeks. Only one pair of patches had sheep in them at a time. One of the patches within each pair was situated near a road (distance 50–350 m) and the other one far from any road (distance 500–6000 m). In selecting the patches within the pairs we prioritised finding matched sites that were similar in all possible respects, such that they had rocky outcrops adjacent from which condors could assess the surroundings before feeding, scattered vegetation, and good possibilities to take off. In so doing, it was not possible to keep the distance between the roads and the patches and between the two patches in the pair, the same for all pairs. The distance between the patches in a pair was between 800 and 6000 m and the distance between different pairs was at least 2 km. This paired design avoids influences of variables like weather conditions and possible seasonal differences given that near and far patches were analyzed at the same time.

We monitored feeding at the 26 carcasses during the study period for a total of 54 days during autumn and 66 days in spring (2928 h in total: 1464 h in far and 1464 h in near patches). We obtained the carcasses from newly dead animals belonging to the farms where we performed the experiments; hence, our experiment did not increase the amount of food supply in the area. Each pair of patches was monitored for a period of nine days on average (5–14) starting from the morn-

ing after the carcasses were placed. We made the observations from hides, which were reached by foot before dawn, approximately 400 m away from the sheep with binoculars (10 × 50) and telescopes (20–60 × 60). No car was left in the surroundings of the hide or the experiment. If the Condors did not visit the pair in 14 days we changed to monitor a new pair of sheep carcasses. We recorded the following variables: detection time (time it took since the sheep carcass was placed until a condor was flying low right over it); patch residence time (average of total time per individual spent in the patch); total number of condors flying in the area (counted since the time the sheep was placed until the experiment was finished); total number of condors eating at each patch; and giving-up density. To estimate giving-up density we weighed the carcasses with a scale and we also visually estimated the remainder as a proportion of the whole sheep. Weighing was performed at night to avoid disturbing the condors. Given that we had a missing value, due to one sheep was taken as a whole by a puma, we converted the weights to the fraction remaining of the sheep; the estimation was done on a coarse semi-quantitative scale in steps of 10%. Condors were classified by age (adults or sub-adults/juveniles) and sex (del Hoyo et al., 1994). We only registered a condor as a new individual if we could positively distinguish it from the previous one or if it arrived at least 15 min after the previously registered bird left the area.

When the condors started foraging a patch, we noted their activity using a tape recorder. Focal sampling was conducted changing the focal individual every 5 min when more than one condor was feeding in the patch. We recorded the following behaviours: *Feeding*: head inside the carcass, head outside the carcass with a piece of food, or walking around the carcass looking down; *Scanning*: bill up, moving head to the sides; *Fighting* with other condors or other birds; *Resting*: either preening, or being inactive, not moving body or head. Even though feeding might involve some scanning too, there was not a visible scanning behaviour during those periods. We were not able to note if and when cars passed by on the roads as all focus was on the birds and from some hides the roads could not be seen. Therefore, we will not be able to separate between the effects of disturbance by the vehicles themselves and of the road as such.

Statistical analyses were performed using Fisher's exact test, sign test, paired t-test, and mixed linear effects modelling in lieu of a nested analysis of variance. Variables were log transformed when necessary to meet assumptions of normality. As can be seen from Figs. 4–6 there are a few outliers in the data, but these mostly act to make tests more conservative. We used SPSS 12.0.1 to analyze the data.

3. Results

Detection time (Fig. 1) and number of condors flying in the area (Fig. 2) were not different between patches near and far from roads ($t_{11} = 1.33$, $p = 0.21$, $t_{12} = 0.44$, $p = 0.7$). Seven out of the 13 pairs of patches were visited. The patch far from the road was used in all these cases, but the near patches were only used in four cases. This means that we observed condors feeding from a total of 11 carcasses. The number of

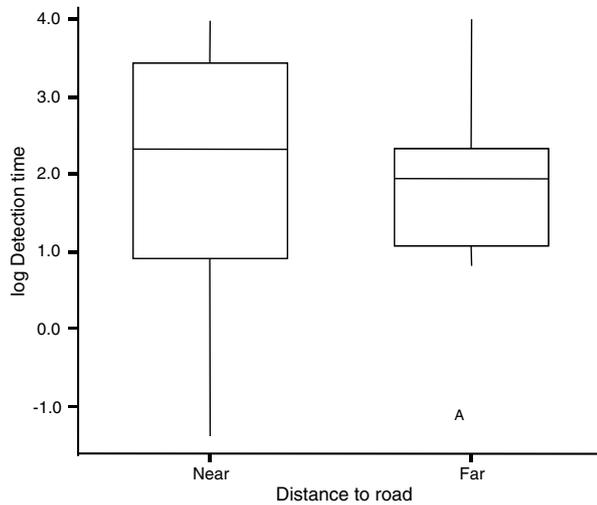


Fig. 1 – Time elapsed since the carcasses were put and a condor detected them in patches near to or far from roads (expressed as logarithm; $n = 26$). Box-plots, in which the central line shows the median, the box the third and fourth quartile ranges, and the whiskers (vertical lines) indicate the range of the data, excluding outliers.

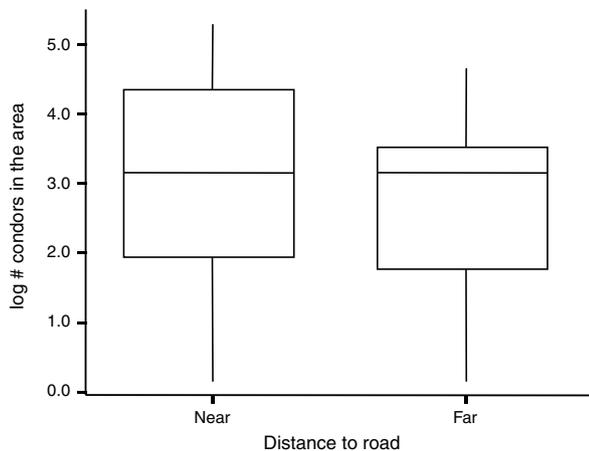


Fig. 2 – Comparison of the number of condors flying in the area surrounding patches near and far from roads (expressed as logarithm; $n = 26$). Box-plots show median and quartile ranges.

condors feeding in patches far from roads was higher than the number feeding in patches near them (Fig. 3; $t_6 = 4.22$, $p = 0.006$). In total, 100 condors fed in far patches but only six in near ones. The proportions of adults and juveniles, males and females were similar in patches at both distances to the roads (Fisher's exact test, $p = 0.7$ in both cases).

On average the condors started to use the near patches 28 h later than the far patches ($F_{1,4.01} = 9.33$, $p = 0.038$). Patch residence time was significantly higher in far than in near patches (geometric mean of difference between far and near patches 3.7 h, $t_6 = 2.72$, $p = 0.035$; Fig. 4). GUDs were higher in all patches near roads as compared to the paired patches far from roads (difference approximately 40%-units; 2-tailed sign test, $p = 0.031$; Fig. 5).

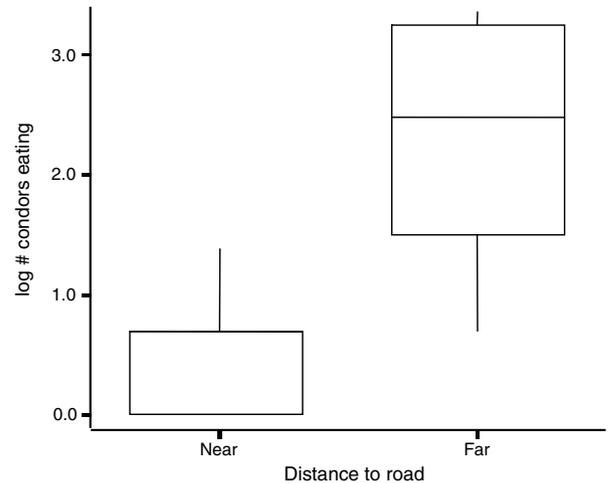


Fig. 3 – Number of condors that ate in near and far patches (expressed as logarithm). Box-plots show median and quartile ranges.

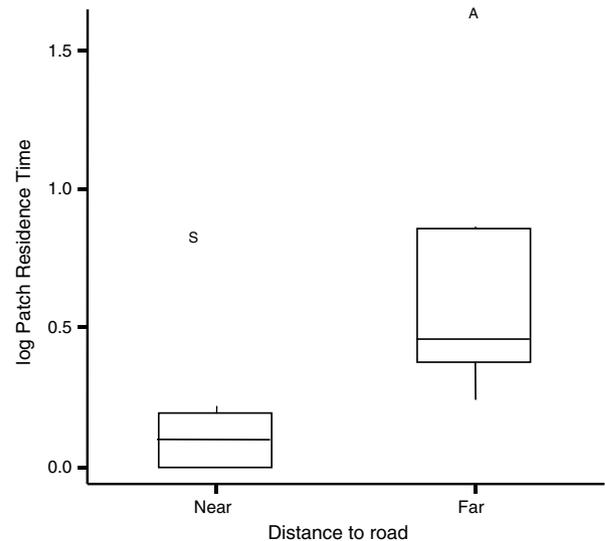


Fig. 4 – Average patch residence time per individual, in patches near and far from roads (expressed as logarithm). Box-plots show median and quartile ranges.

Condors spent more than twice as much time scanning when feeding near a road than when feeding in a patch far from any road ($F_{1,5.1} = 17.01$, $p = 0.009$; Fig. 6), but there was no difference between sexes or age groups (sex: $F_{1,7.7} = 0.607$, $p = 0.5$; age: $F_{1,3.6} = 0.061$, $p = 0.8$). The other behavioural variables are tightly correlated with the proportion of time scanning, and thus we do not analyze those separately, but only show them in Fig. 6.

4. Discussion

4.1. Use of behavioural indicators to assess disturbance

Condors are very cautious when deciding to feed, since once on the ground they are vulnerable (Pavez and Tala, 1995;

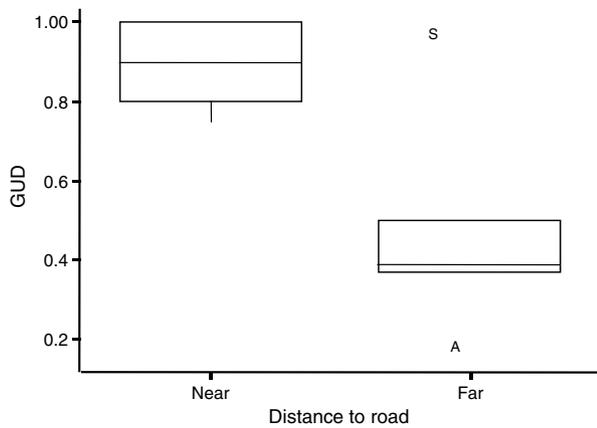


Fig. 5 – Giving-up density (GUD), expressed as 1-proportion of eaten sheep, for patches near and far from roads. Box-plots show median and quartile ranges.

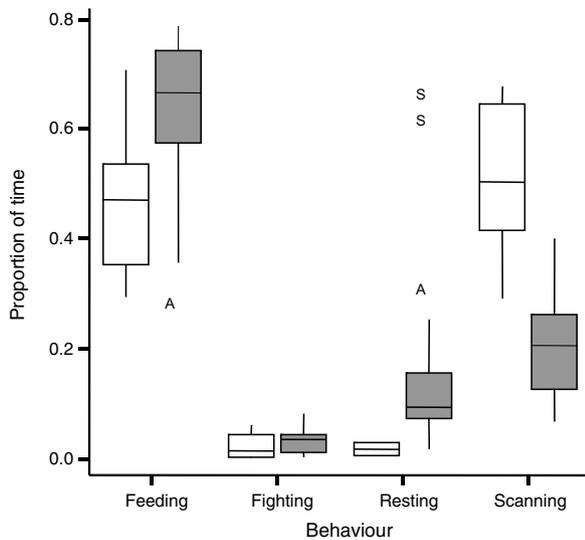


Fig. 6 – Proportion of time, out of the total time spent in a patch that condors spent on each type of behaviour. Shading indicates patch distance to roads: open boxes represents patches near and shaded boxes patches far from roads. Box-plots show median and quartile ranges.

Donázar et al., 1999). The condors discovered the dead sheep near roads as quickly as the ones far from the roads. Also, there were as many condors flying over the patches near roads as over the ones far from the roads. Still, the number of condors actually going down to feed was much higher in the patches far from the roads. Thus, this clearly shows that the decision of where to feed was made in a way consistent with the idea that Andean condors avoid roads.

Also the decision to leave the visited patches was affected by proximity to roads, in the predicted direction. The patch residence time per individual was longer in the patches far from the roads and the condors left lower GUDs in these patches. Considering the GUDs, we observed a consistent pattern in which a carcass was consumed (KLS and SAL, pers. obs). They generally started by opening the body under the armpits, eating the organs such as liver, heart and intestines

first. After that, they ate the large, soft muscles, and finally they took the smaller pieces of meat and removed tissue from the bones and skin. It is reasonable to assume that this pattern creates diminishing returns, i.e., depletion of the food patches. This implies that the lower GUDs in the patches far from the roads correspond to accepting lower intake rates in these patches, than near roads where GUDs were much higher.

Considering the decision about the amount of time to spend vigilant, the condors also behaved in agreement with the notion that they perceive a higher risk close to roads. By allocating more time to vigilance animals may be able to reduce the risk they take in a dangerous place (Lima and Dill, 1990; Brown, 1999). However, this reduction in risk often comes at the price of a reduction in energy gain. Thus, the benefit of feeding on an almost uneaten sheep near a road will be reduced if the condors, as they did, spend more time vigilant there.

Many practical and conceptual issues in conservation biology like reserves designs, responses to exploitation and disturbance as well as reintroduction programs can benefit from knowledge of individual behaviour (Caro, 1999; Sutherland and Norris, 2002; Olsson et al., 2002). Analysis of behaviour has been a powerful tool for the assessment of road effects on Andean condors. It has allowed us to positively distinguish the quality of feeding patches according to its distance to roads and their decisions about habitat selection. In this way food patches near roads seem to be of lower quality than patches at least 500 m away from roads. Thus our study supports the idea that behavioural analysis is a conservation tool that allows the assessment of environmental quality or degradation processes (Buchholz, 2007; Kotler et al., 2007; Whelan and Jedlicka, 2007).

We acknowledge that this type of study does not give a complete picture of the study species' habitat use, nor does it aspire to. Rather, we emphasize that studies of patch use and feeding behaviour are very powerful to understand key aspects of a species' habitat use and evaluation of its environment. This is because such studies can provide a very direct assay of the trade-offs between food acquisition and survivorship, which are two of the main determinants of fitness (Olsson and Holmgren, 1999; Olsson et al., 2002; Brown and Kotler, 2004; Holt and Kimbrell, 2007; Rosenzweig, 2007; Kotler et al., 2007).

This methodology could also help understanding the effects on individuals of different ages or sexes. Our results did not find an effect of age and sex on the differences found in condors' behaviour between good and bad patches. Even though the difference was not significant, (probably due few observations of some age categories) we observed that juveniles were more daring than adults. These groups could be expected to have different risk taking behaviour, as a consequence of different life-history traits. To make certain conclusions about any such differences larger sample sizes will be needed.

Even though the sample is small, the paired design increases the statistical power, and data from the matched pairs of patches is consistent for all the relevant variables and therefore our findings seem reliable. We can quite clearly conclude that Andean condors perceive roads as disturbing,

and that the effect is rather large. Our results indicate that they trade off energy for safety. However, exactly what about the roads that appears disturbing, i.e. whether the condors associate humans with hunting mortality, roads with traffic mortality, or if they are simply disturbed by noise or are xenophobic, is not possible to conclude from this study. In addition, disturbance is not the only effect of roads on wildlife (Spellerberg, 1998; Seiler, 2002; Forman et al., 2003) but appears to be the only effect of roads on condors. The landscape, mostly farms raising cattle extensively, with a low density of roads (0.06 km of road/km²) together with the ability of condors to fly high above roads make it likely that habitat loss and fragmentation is not a threat for this species yet. However, it is very important to study road effects more deeply in a healthy condor population during the near future to have reliable information for management plans in relation to this species and other big flying birds as endangered vultures.

4.2. Consequences of roads for Andean Condors

In comparison to some other areas, our study area might be relatively rich in food as it has a rather high density of domestic animals (Bellati, 2000). High food availability will emphasize the cost of predation, at a given risk (Olsson et al., 2002). However, scarcity of food is threatening condors in the northern part of their distribution (Wallace and Temple, 1988; Cuesta, 2000). In such poorer areas energy would be relatively more valuable, and that might lead condors in such areas to expose themselves to higher risks. This trade-off between energy intake and safety means that lower food availability might lead to an increased risk-associated mortality (McNamara and Houston, 1987).

An imminent problem is that like in many other areas of the world the number of roads and traffic is increasing in the study area – in the present case partly as a consequence of increased tourism (Bertonatti and Corcuera, 2000). According to our findings a strip of at least up to 350 m away from a road is bad habitat for Andean Condors, similar to the distance found for other bird species in Spain (Palomino and Carrascal, 2007). This represents an area of 0.7 km² per kilometre of road. There already exist recommendations for road construction regarding the problems of habitat fragmentation and transformation (van der Zande et al., 1980; Spellerberg, 1998; Reijnen et al., 1995; Caro, 1999; Forman et al., 2003). Although our findings are partly different from previous studies of effects of roads and traffic, our conclusions emphasize previous findings that roads may have severe effects on wildlife. Other current critically endangered vultures (Koenig, 2006) could be suffering from similar risks. These results are important to take into account when planning conservation strategies and the selection of reintroduction areas for endangered species. Our work highlights the importance of taking the little considered big flying birds into account in the land use planning.

In this study we have been able to establish the usefulness of behavioural indicators to study habitat suitability for condors. The study is rather small, but many of the results are still of general relevance. Importantly, this study can serve as a starting point for further, more detailed and quantitative

studies of the effects of anthropogenic disturbance on condors.

The Patagonian steppe and the ecotone between it and the temperate austral forest are ones of the least protected regions in Argentina (Bertonatti and Corcuera, 2000). This allows the creation of highly disturbed places like oil wells, mining industry, or uncontrolled tourism, which in turn generate new roads. Hitherto, roads have not been considered as risks for big flying birds. We propose that the maintenance and protection of large patches of land far from roads is a key strategy for the conservation of the Andean condor and possibly for the California condor and other vultures of the world as well.