

## Avian responses to tourism in the biogeographically isolated high Córdoba Mountains, Argentina

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**Abstract** Species do not respond identically to the presence of humans, and this may have consequences at higher-levels of ecological organization. We established bird transects on and off recreational trails in the high Córdoba Mountains of Argentina, a biogeographic island characterized by high levels of endemism, to examine the effect of human visitation at three different levels: (a) community (avian species richness and diversity), (b) guild (relative density of carnivores, granivores, insectivores, and omnivores), and (c) population (relative density of individual bird species). Human presence in the high Córdoba Mountains decreased avian species richness and diversity, and reduced insectivorous relative density, but we did not detect significant effects on granivores, omnivores, and carnivores. At the population level, 6 of 28 species were negatively affected by human visitation; four of these species are of conservation concern. Our results show negative responses to recreationists at multiple levels (e.g., reductions in density, displacement of species from highly visited areas), which may be related to spatial and temporal access to suitable resources, physical disturbance or species-specific tolerance thresholds. Our study area had lower levels of human visitation relative to other protected areas in

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the Northern Hemisphere, which raises the issue of whether this kind of biogeographically isolated habitat may be too fragile to sustain increasing levels of tourism.

**Keywords** Endemic species · Guild · Human disturbance · Mountainous ecosystem · Recreational activities · South America

## Introduction

Conventional wisdom suggests that the impact of tourism is localized because tourists often prefer to visit areas close to established facilities (Priskin 2003), and consequently wildlife further away may be minimally affected. This is an important management paradigm that might be challenged in the future as the number of tourists visiting natural areas worldwide is expected to double by 2020 (Christ et al. 2003), which raises concerns about the large scale environmental impacts of recreational activities (e.g., development of infrastructure, disease transmission, invasion of non-native species, reduced habitat quality, etc.). Importantly, tourism has become profitable for developing countries, energizing local economies and, in some countries, generating revenues for the conservation of protected areas (Sekercioglu 2002; Christ et al. 2003; but see Kiss 2004). For instance, tourism is contributing between 3% and 25% of the Gross Domestic Product of developing nations worldwide (Diaz Benevides and Perez-Ducy 2001). Therefore, managers face the challenge of finding strategies that would promote coexistence between humans and wildlife. Ultimately, the goal is to increase the chances of wildlife viewing without eroding ecological integrity in protected areas (Blumstein et al. 2005).

Previous studies have shown that the effects of tourists on wildlife may trigger short-term behavioral responses (Frid and Dill 2002), modify predation risk assessment (Webb and Blumstein 2005), reduce breeding performance (Beale and Monaghan 2004a; Müllner et al. 2004), influence habitat selection (Gill et al. 1996; Gutzwiller and Anderson 1999) and population abundance (van der Zande et al. 1984; Miller et al. 1998), and modify community structure (Skagen et al. 1991; Gutzwiller 1995; Fernández-Juricic 2002). Most of these studies have been conducted in the Northern Hemisphere, which has experienced a higher volume of recreationists than areas in the Southern Hemisphere. However, tourism has increased sharply in the Southern Hemisphere recently, particularly within biodiversity hotspots (Christ et al. 2003). Thus, to increase our ability to predict the large-scale and long-term effects of tourism and to devise proper management strategies, it is necessary to assess population and community responses to recreationists in threatened ecosystems in parts of the world without a long history of human visitation.

We studied the effects of human visitation on birds inhabiting a biogeographically isolated area in South America (high Córdoba Mountains, Argentina), with many plant and animal endemic species (Cabido et al. 1998; 2003). Our goal was to assess the effects of recreationists in areas with low (off-trails) and high (on-trails) levels of visitation at different ecological levels: (a) community (avian species richness and diversity), (b) guild (relative density of carnivores, granivores, insectivores, and omnivores), and (c) population (relative density of individual bird species).

Some of the mechanisms proposed to explain wildlife responses to recreationists predict that higher frequencies of human visitation reduce the spatial and temporal

access to foraging and breeding resources, which could eventually lead to reductions in species occurrence and density if disturbance is prevalent in space and time (Gill et al. 1996; Fernández-Juricic 2002; Frid and Dill 2002; Fernández-Juricic et al. 2003). Therefore, we predicted a decrease in species richness, species diversity, relative density of guilds and individual species in highly visited areas controlling for differences between study sites, habitat structure, and altitude.

## Methods

### Study area

The high Córdoba Mountains (1,500 to 2,800 m) are almost 1,000 m higher than the surrounding mountain systems in central Argentina, and their altitude and weather make their ecological conditions different from surrounding habitats (Luti et al. 1979; Cabido et al. 1998). Vegetation consists of a mosaic of tussock grasslands, lawns, granite outcrops, eroded areas with exposed rock surfaces and low densities of *Polylepis australis* woodlands and shrublands (Cingolani et al. 2004). Mean precipitation is 854 mm, which is concentrated between October and March (Renison et al. 2002). The climate is temperate with cold winters, and the mean annual temperature is 8°C (Cabido 1985). Forty one endemic plant and animal taxa are found in this area (Cabido et al. 2003), including 12 endemic sub-species of birds (Nores 1995; Miatello et al. 1999).

In 1997, part of the high Córdoba Mountains (26,000 ha above 1,500 m.a.s.l.) was expropriated to create the Quebrada del Condorito National Park, while the private lands surrounding the Park were declared National (12,000 ha) and Provincial (117,000 ha) Water Reserves. Because the high Córdoba Mountains are relatively close to several big cities, and because hiking and climbing began increasing in Argentina in the 1990's, tourists visit the area year round, and generally hike and use tents or mountain lodges to overnight.

We selected three sites which are the most widely visited in the high Córdoba Mountains: (a) Champaquí mountain (S 31° 59'; W 64° 49') with an un-maintained trail of 14.0 km that usually varies in width from 0.8 m to 2 m, but may reach a width of 30–40 m in areas where there is no clear trail; (b) Quebrada del Condorito National Park (S 31° 37'; W 64° 42') with a trail of 7.8 km which is well maintained and usually varies in width from 0.8 to 1.5 m; and (c) Los Gigantes (S 31° 24'; W 64° 47') with an un-maintained trail of 10.8 km with similar characteristics to the Champaquí mountain trail (National Parks Administration, pers. comm; personal observations). For the sake of simplicity, hereafter we will call these areas Champaquí, Condorito, and Gigantes, respectively. Visitor rates to the Champaquí trail vary between 6,000 and 12,000 visitors per year, mostly trekking groups that may use horses for cargo and occasionally motorcycles. Eight local families also use the trail (mainly on horseback). Visitors to the Condorito trail vary between 3,000 and 4,000 per year, mostly trekking and some bicycles. No horses or motorcycles are allowed in the trail and there is no use by local inhabitants. In the Gigantes trail, visitation rates vary between 3,000 and 6,000 per year, mostly trekking. In a few areas, there is also some occasional use by motorcycles and vehicles, but the steep terrain precludes motorized vehicles in the rest of trail. Around five local families use the trail (mainly on horseback), but there is no horse use by visitors. Hunting is illegal in all the Córdoba Mountains.

## General sampling procedures

Using a Geographic Information System (GIS) with vegetation, erosion, topography, human settlements, and trails layers at a pixel size of  $30 \times 30$  m (Cingolani et al. 2004), we selected 21 pairs of locations for transects. The number of locations for transects in each study site was determined according to the availability of straight trail sections and the possibility of obtaining appropriate off-trail transects (see below). As a result, the pairs of transects differed among study sites (Champaquí,  $n=10$ ; Condorito,  $n=6$ ; Gigantes,  $n=5$ ). No more transects could be established in the study areas without relaxing our transect selection criteria.

From each pair, one transect was placed on a trail used by tourists (on-trail) and the other transect was placed on an area with similar topography, vegetation, natural rock outcrops, and rock exposed by erosion but without tourist use (off-trail). The criteria for determining habitat similarity for each pair of transects was based on the GIS thematic layers. After locating sectors with trails that were fairly straight for at least 600 m and that were at least 300 m from each other (average distance between the closest ends of transects was  $1,145 \pm 1,129$  m), we chose off-trail transects that were more than 200 m away from on-trail transects but with similar proportion of habitat composition (see also Results), altitude, slope orientation, and aspect, and as a result were presumably influenced by similar potential confounding factors. All transects were selected in areas with no human settlements or camping areas near them. Livestock is the main determinant of vegetation types in the High Córdoba Mountains (Cingolani et al. 2003). As our vegetation types were similar on and off trails, long term grazing pressure can be assumed to be approximately equal.

In a preliminary study, we estimated that in the habitat with the least visibility (sparse *Polylepis* woodland and shrubland), detection probabilities started dropping substantially 30 m away from the centre of the transect. Thus, we established transects that were 60 m wide and 600 m long (3.6 ha).

Bird surveys were conducted between December 2002 and March 2003, which encompassed the breeding and post-breeding seasons, because bird species richness (Ordano 1996) and the frequency of human visitation (National Parks Administration, pers. comm.) are at the highest levels during this period, which would increase the chances of human–wildlife interactions. We surveyed birds between 0800 and 1200 and 1530 and 1930 because those were the periods with the highest bird activity. Adult and fledgling individuals were counted during surveys. Pairs of on- and off-trail transects were surveyed consecutively on a given day (but each pair visited in random order between surveys). We visited each transect three times to obtain better estimates of species presence and abundance between areas with low and high visitation. All surveys were conducted by only one person (LH) during favorable weather conditions to avoid inter-observer bias.

In each transect, we recorded the identity and abundance of all individuals seen or heard within 30 m at each side of the center of the transect. We included in the analyses individuals that were only using the transects (e.g., discarded observations with individuals flying high). The observer was trained to visually estimate the 30 m with <10% error prior to beginning the surveys. Vegetation is mainly composed of short grassing lawns, many flat rocky areas, and tussock grasslands where bird detection was relatively easy. Potential small biases in detection probability between habitats should not affect our on and off-trail comparisons due to the similarity in habitat composition between pairs of transects. Since four species of the genus

*Anthus* (*A. correndera*, *A. furcatus*, *A. hellmayri* and *A. lutescens*) were difficult to distinguish, we lumped all individuals in one category (*Anthus sp.*).

We could not get density estimates following distance sampling (Buckland et al. 2001), because the studied species had relatively low abundances (Ordano 1996), and the assumptions of this method could not be met. Consequently, we developed a relative index of density by averaging the number of individuals detected on each transect over the three visits and dividing that by the area of each transect (3.6 ha). This index can only be used for comparisons between the conditions studied, but not to make inferences about the absolute density of the species. The relative density index was expressed as number of individuals per 10 ha.

We used the vegetation map in the GIS (Cingolani et al. 2004) to determine habitat composition in each transect. In a  $90 \times 600$  m area including a transect, we counted the number of pixels of each of seven distinct habitat types (*Polylepis* woodland and shrubland, thick tussock grassland with hydromorphic lawn, thin tussock grassland, lawn, outcrop with tussock grassland, natural rock outcrop mixed with exposed rock, and rock exposed by erosion, Appendix 1, as described by Cingolani et al. 2004). We also calculated the average altitude of each transect. These variables were included in the statistical analyses to control for variations in habitat composition between transects.

### Statistical analyses

We used a nested ANOVA to check whether habitat composition would vary between on- and off-trail transects *within* and among study sites.

From our surveys, we calculated the following dependent variables in each transect: species richness (mean number of species detected per transect), species diversity (Shannon diversity index), relative density of carnivores, granivores, insectivores, and omnivores, and relative density of individual species. In the statistical analyses, we only included species present in at least five transects (following Fernández-Juricic 2002). We analyzed these dependent variables with General Linear Models (GLM), including the following categorical factors: visitation frequency (2 levels, on- and off-trail transects), study area (three levels, Champaquí, Condorito and Gigantes), and the interaction between visitation frequency and study area. We also included the following covariates (all continuous): transect altitude and habitat composition (number of pixels of seven different habitat types, see Appendix 1). The results of step-wise selection procedures could be misleading with unbalanced designs (in our case, different number of transects per study site), but such effect could be minimized by running full models. We included all variables in the analyses, but for the sake of clarity in the presentation we reported only the main factors (frequency of visitation and study area), their interaction, and the significant covariates. All other factors not reported were non-significant ( $P > 0.05$ ). We also ran the same models for species richness, species diversity, and guild relative density but excluding the species that were significantly affected by visitation frequency (see Results) to determine if the community and guild level patterns were consistent or relied on the effects of individual species.

The effects of human disturbance may become noticeable only at certain densities. For instance, Reijnen and Foppen (1995) found that the negative effects of road noise were intensified when the density of breeding birds was lower. Using a logistic regression, we assessed whether the probabilities of finding a significant

effect of human visitation could be affected by the relative densities of each species.

We checked the normality and homoscedasticity of our data before and after running the analyses. We log-transformed some variables (see Results) to meet assumptions of linear models. Throughout, we reported untransformed means  $\pm$  SE.

## Results

We recorded a total of 45 bird species in a total of 151.2 ha (considering the four species from the genus *Anthus* as one species, Appendix 2). The mean relative density of all recorded species was  $22.55 \pm 3.14$  individuals per 10 ha.

Habitat composition varied among some study sites (*Polylepis* woodland and shrubland,  $F_{2, 36}=5.47$ ,  $P=0.008$ ; thick tussock grassland with hydromorphic lawn,  $F_{2, 36}=14.23$ ,  $P<0.001$ ; outcrop with exposed rock,  $F_{2,36}=7.02$ ,  $P=0.002$ ; the other relationships were non-significant,  $F_{2, 36} > 3.25$ ,  $P > 0.05$ ). However, there were no differences in habitat composition between on- and off-trail transects within each study site ( $F_{3,36}$  varied between 0.04 and 0.87,  $P > 0.05$ ).

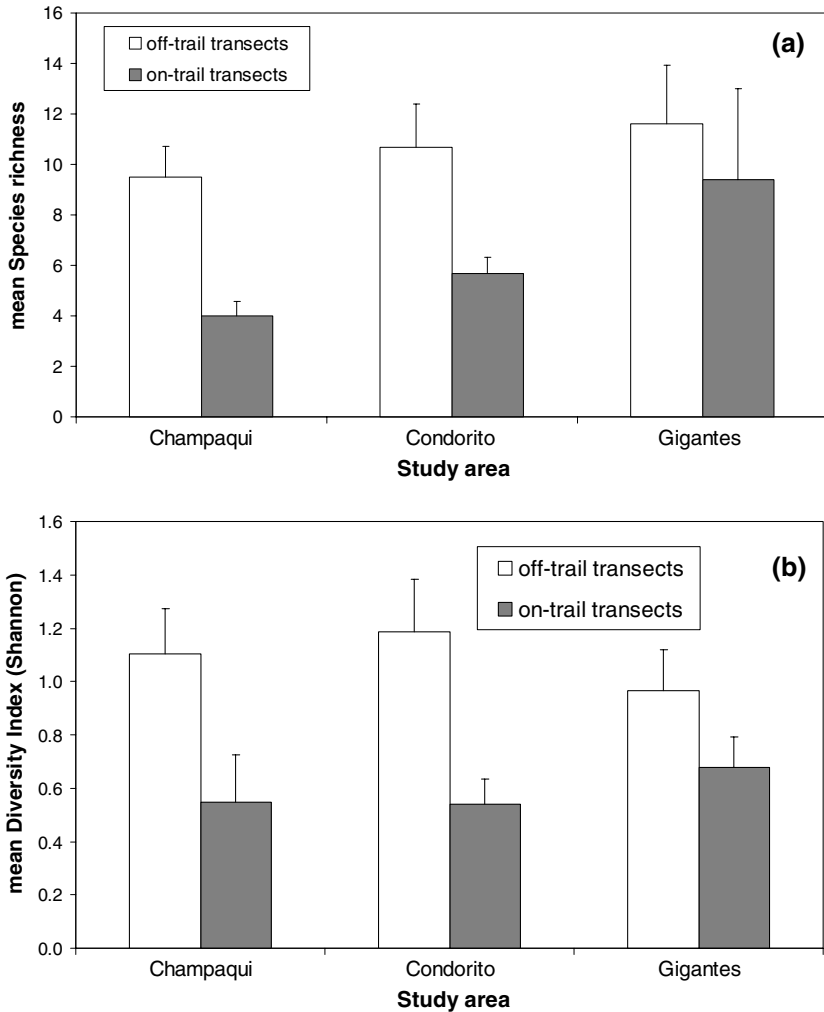
### Community level

Species richness was lower in on-trail transects compared to off-trail transects (Fig. 1a). Species richness also varied among study sites (Fig. 1a). The interaction between study area and visitation frequency was not significant (Table 1). Only three covariates were significant (Table 1): species richness was positively affected by altitude and the amount of lawn, and negatively by the amount of rock exposed by erosion. A similar result was found without considering the species that were affected by human disturbance (see Population level section): species richness was lower in on-trail than in off-trail transects, with variations among study sites and similar effects of the covariates (Table 1).

Species diversity (Shannon index) was lower in on-trail relative to off-trail transects, but no variation was found among sites (Table 1, Fig. 1b). The study site vs. visitation frequency interactions were not significant; however, species diversity was positively associated with the amount of lawn and with altitude (Table 1). Species diversity calculated without considering the species affected by visitation frequency (see Population level section) was also lower in on-trail relative to off-trail transects, but it varied among study sites (Table 1), and was positively associated with *Polylepis* woodland and shrubland and altitude, and negatively with rock exposed by erosion (Table 1).

### Guild level

At the guild level, we found lower carnivorous relative density in on-trail relative to off-trail transects (Table 2, Fig. 2a). Study area and study area vs. visitation frequency interaction did not affect carnivorous relative density (Table 2), nor did any of the other covariates ( $P > 0.05$ ). However, when we ran another model with carnivorous relative density excluding the two carnivorous species that were affected by human visitation (see Population level section), we found no significant effect of



**Fig. 1** Species richness **(a)** and species diversity **(b)** in areas with low (off-trail) and high (on-trail) levels of human visitation in the high Córdoba Mountains

the frequency of visitation (off-trail transects =  $1.808 \pm 0.431$  individuals/10 ha, on-trail transects =  $0.749 \pm 0.244$  individuals/10 ha) and the other factors (Table 2).

Granivorous relative density did not differ between visitation frequencies (off-trail transects =  $5.776 \pm 1.735$  individuals/10 ha, on-trail transects =  $6.041 \pm 2.917$  individuals/10 ha), but it did vary among study sites (Table 2, Champaqui =  $3.702 \pm 1.508$  individuals/10 ha, Condorito =  $2.701 \pm 0.907$  individuals/10 ha, Gigantes =  $14.167 \pm 5.746$  individuals/10 ha). Granivorous relative density was also positively affected by altitude, and negatively by the amount of rock exposed by erosion (Table 2).

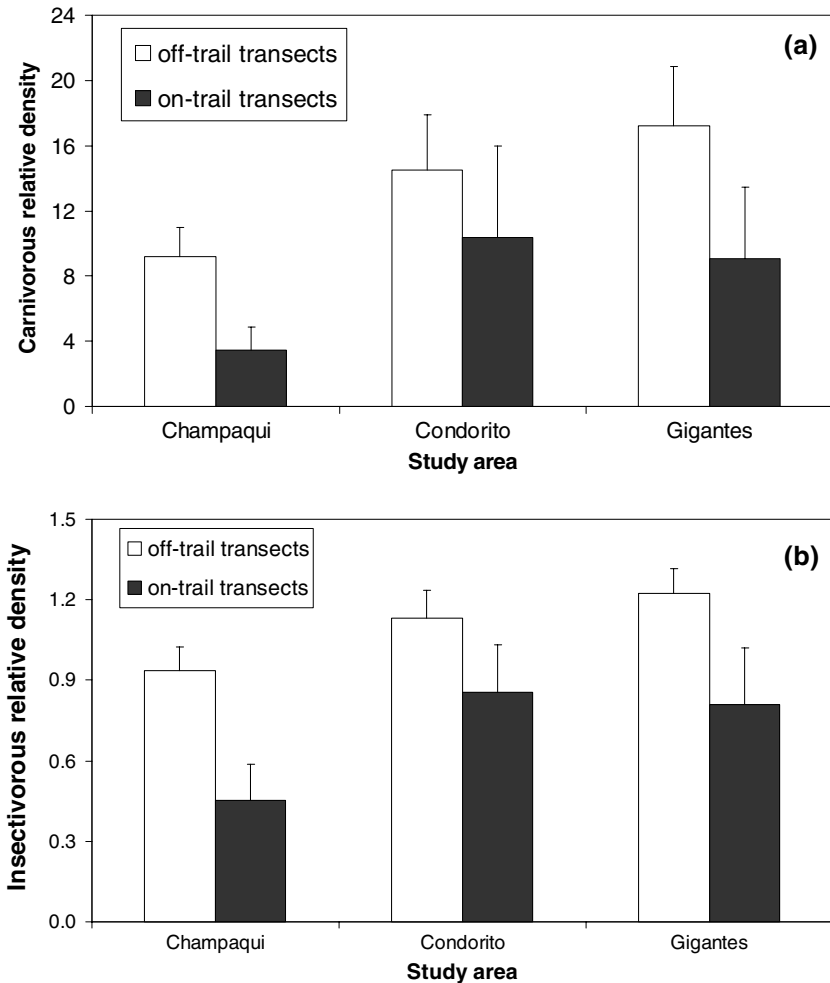
Insectivorous relative density was lower in on-trail transects relative to off-trail transects and varied among study sites (Table 2, Fig. 2b). The study site vs. visitation frequency interaction was not significant (Table 2), but insectivorous relative density

**Table 1** Results from general linear models explaining variation in species richness and diversity as a function of human visitation, study area, and habitat-related characteristics

Dependent factor	Independent factors	F	d.f.	P	
Species richness $R^2 = 0.71$	Intercept	0.05	1, 28	0.758	
	Visitation frequency (VF)	13.33	1, 28	<b>0.001</b>	
	Study area (SA)	6.41	2, 28	<b>0.005</b>	
	VF × SA	0.40	2, 28	0.675	
	Rock exposed by erosion (-)	9.53	1, 28	<b>0.005</b>	
	Lawn (+)	4.25	1, 28	<b>0.048</b>	
	Altitude (+)	14.91	1, 28	<b>&lt;0.001</b>	
	Intercept	2.68	1, 28	0.551	
	Visitation frequency (VF)	5.09	1, 28	<b>0.032</b>	
	Study area (SA)	8.40	2, 28	<b>0.001</b>	
Species richness without species affected by VF $R^2 = 0.69$	VF × SA	0.28	2, 28	0.757	
	Rock exposed by erosion (-)	8.82	1, 28	<b>0.006</b>	
	Lawn (+)	5.38	1, 28	<b>0.027</b>	
	Altitude (+)	18.04	1, 28	<b>&lt;0.001</b>	
	Intercept	0.58	1, 28	0.451	
	Visitation frequency (VF)	8.18	1, 28	<b>0.007</b>	
	Study area (SA)	0.28	2, 28	0.756	
	VF × SA	0.89	2, 28	0.423	
	Lawn (+)	5.77	1, 28	<b>0.023</b>	
	Altitude (+)	4.21	1, 28	<b>0.049</b>	
Species diversity $R^2 = 0.51$	Intercept	0.01	1, 28	0.952	
	Visitation frequency (VF)	4.33	1, 28	<b>0.046</b>	
	Study area (SA)	8.27	2, 28	<b>0.002</b>	
	VF × SA	0.34	2, 28	0.711	
	Rock exposed by erosion (-)	7.53	1, 28	<b>0.010</b>	
	<i>Polytepis</i> woodland and shrubland (+)	4.89	1, 28	<b>0.035</b>	
	Altitude (+)	12.99	1, 28	<b>0.001</b>	
	Species diversity without species affected by VF $R^2 = 0.61$	Intercept	0.01	1, 28	0.952
		Visitation frequency (VF)	4.33	1, 28	<b>0.046</b>
		Study area (SA)	8.27	2, 28	<b>0.002</b>
VF × SA		0.34	2, 28	0.711	
Rock exposed by erosion (-)		7.53	1, 28	<b>0.010</b>	
<i>Polytepis</i> woodland and shrubland (+)		4.89	1, 28	<b>0.035</b>	
Altitude (+)		12.99	1, 28	<b>0.001</b>	

Shown are covariates with  $P < 0.05$ . Significant  $P$ -values are marked in bold





**Fig. 2** Relative density (individuals/10 ha) of **(a)** carnivores and **(b)** insectivores in areas with low (off-trail) and high (on-trail) levels of human visitation in the high Córdoba Mountains

was positively associated with altitude and the amount of lawn (Table 2). Insectivorous relative density without considering the species affected by human visitation (see Population level section) was also lower in on-trail ( $9.082 \pm 1.658$  individuals/10 ha) transects compared to off-trail ( $5.996 \pm 2.013$  individuals/10 ha), and differed among study sites (Champaqui =  $3.889 \pm 1.219$  individuals/10 ha, Condorito =  $10.802 \pm 3.126$  individuals/10 ha, Gigantes =  $10.925 \pm 2.559$  individuals/10 ha) (Table 2). Three covariates were positively associated with this insectivorous relative density: altitude, and the amount of lawn and thin tussock grassland (Table 2).

Omnivorous relative density did not differ between on-trail ( $5.996 \pm 1.576$  individuals/10 ha) and off-trail ( $4.629 \pm 1.643$  individuals/10 ha) transects, and was not affected by any of the other studied factors (Table 2). Similar results were found with omnivorous relative density without considering the species affected by human

**Table 2** Results from general linear models explaining variation in the relative density of carnivorous, granivorous, insectivorous, and omnivorous foraging guilds as a function of human visitation, study area, and habitat-related characteristics

Dependent factor	Independent factors	F	d.f.	P
Carnivorous relative density $R^2 = 0.46$	Intercept	0.36	1, 28	0.552
	Visitation frequency (VF)	5.56	1, 28	<b>0.025</b>
	Study area (SA)	1.30	2, 28	0.287
	VF $\times$ SA	1.69	2, 28	0.201
Carnivorous relative density without species affected by VF $R^2 = 0.03$	Intercept	0.10	1, 28	0.749
	Visitation frequency (VF)	2.18	1, 28	0.151
	Study area (SA)	1.37	2, 28	0.269
	VF $\times$ SA	0.53	2, 28	0.589
Granivorous relative density $R^2 = 0.65$	Intercept	0.54	1, 28	0.467
	Visitation frequency (VF)	0.17	1, 28	0.682
	Study area (SA)	6.47	2, 28	<b>0.005</b>
	VF $\times$ SA	1.29	2, 28	0.289
	Rock exposed by erosion (-)	5.59	1, 28	<b>0.025</b>
	Altitude (+)	11.07	1, 28	<b>0.002</b>
log Insectivorous relative density $R^2=0.65$	Intercept	0.48	1, 28	<b>0.490</b>
	Visitation frequency (VF)	14.21	1, 28	<b>&lt;0.001</b>
	Study area (SA)	4.10	2, 28	<b>0.027</b>
	VF $\times$ SA	0.01	2, 28	<b>0.996</b>
	Lawn (+)	11.72	1, 28	<b>0.002</b>
	Altitude (+)	4.36	1, 28	<b>0.045</b>
log Insectivorous relative density without species affected by VF $R^2=0.66$	Intercept	2.03	1, 28	<b>0.164</b>
	Visitation frequency (VF)	5.96	1, 28	<b>0.021</b>
	Study area (SA)	8.71	2, 28	<b>0.001</b>
	VF $\times$ SA	0.05	2, 28	<b>0.952</b>
	Lawn (+)	10.29	1, 28	<b>0.003</b>
	Thin tussock grassland (+)	4.97	1, 28	<b>0.034</b>
	Altitude (+)	7.54	1, 28	<b>0.010</b>
Omnivorous relative density $R^2=0.04$	Intercept	1.97	1, 28	<b>0.171</b>
	Frequency of visitation (FV)	0.06	1, 28	<b>0.801</b>
	Study area (SA)	0.92	2, 28	<b>0.413</b>
	FV $\times$ SA	1.86	2, 28	<b>0.174</b>
Omnivorous relative density without species affected by VF $R^2=0.02$	Intercept	1.42	1, 28	<b>0.244</b>
	Visitation frequency (VF)	0.28	1, 28	<b>0.603</b>
	Study area (SA)	0.62	2, 28	<b>0.547</b>
	VF $\times$ SA	1.85	2, 28	<b>0.174</b>

Shown are covariates with  $P < 0.05$ . Significant  $P$ -values are marked in bold

visitation (see Population level section): no differences between on-trail ( $4.629 \pm 1.571$  individuals/10 ha) and off-trail ( $3.791 \pm 1.617$  individuals/10 ha) transects, and no effect of the other studied factors (Table 2).

### Population level

We modeled the effects of visitation frequency on 28 of the 45 species recorded, and found that the relative densities were lower in on-trail transects in 6 species (three insectivores: *Anthus* sp., *Asthenes modesta cordobae*, *Asthenes sclateri sclateri*; two carnivores: *Buteo albicaudatus*, *Falco sparverius*; and one omnivore: *Turdus chiguanco*, Table 3, Fig. 3). Two of these species are endemic (*Asthenes modesta cordobae*, *Asthenes sclateri sclateri*, Appendix 2), and two are declining (*Buteo albicaudatus*, *Turdus chiguanco*, Appendix 2).

**Table 3** Results from general linear models explaining variation in the relative density of individual species in relation to human visitation frequency, altitude, and habitat-related characteristics

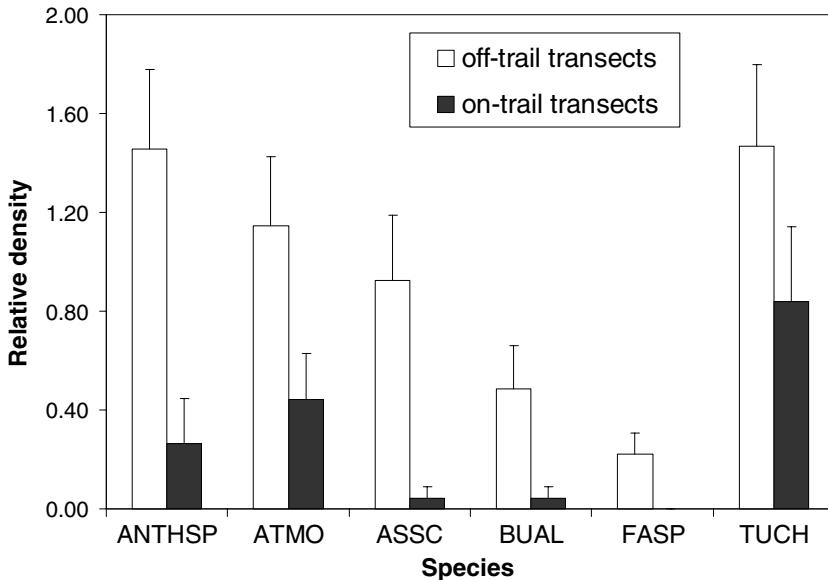
Species	Model <i>R</i> <sup>2</sup>	VF	SA	FV × SS	Altitude	PWS	RP	OER	OTG			
AEAN	0.47	0.44	4.94**	0.80								
AGMO	0.06	0.08	0.36	0.01								
ANTHSP	0.51	7.20*	0.07	1.66								
ATMO	0.56	4.33*	0.63	0.75	(+)	6.26*						
ASSC	0.51	11.16**	0.57	0.57								
BOAY	0.09	0.05	0.51	0.53								
BUAL	0.58	5.23*	0.16	3.20		(+)	5.43*					
BUPO	0.52	0.01	2.01	0.02		(-)	5.72*					
CAMA	0.63	0.05	1.20	5.92*	(+)	5.11*	(-)	4.24*				
CAIN	0.54	0.23	1.46	1.34	(+)	5.55*	(-)	6.37*				
CAAU	0.02	0.23	1.74	1.08								
CICO	0.15	0.02	0.52	2.11								
CIFU	0.56	1.06	1.06	2.77	(+)	15.89**	(-)	4.29*				
CIOR	0.55	1.15	6.26**	0.91	(+)	5.82*						
CIPL	0.60	0.05	0.37	1.09				(-)	5.09*			
FASP	0.24	4.51*	0.13	0.06								
MURU	0.50	1.11	0.68	0.80	(+)	11.89**						
NOCY	0.43	0.28	0.91	1.35								
NOMA	0.35	0.26	0.24	1.76	(-)	6.17**						
PHUN	0.60	0.25	4.34*	0.54	(+)	11.72***	(+)	6.28*				
POPL	0.09	2.09	0.09	0.52								
SASP	0.52	0.01	2.39	0.46	(+)	4.56*						
STLO	0.43	0.04	3.39*	1.08								
TRAE	0.02	0.38	0.18	1.91								
TUCH	0.61	4.19*	4.29*	0.45								
VACH	0.01	0.64	0.47	0.64								
VUGR	0.04	0.53	1.60	0.18								
ZOCA	0.63	1.71	9.05**	0.09	(+)	4.88*	(-)	9.55**	(-)	13.61***	(+)	4.87*

Shown for each factor are the direction of the relationship (+, positive; -, negative), the *F*-values and *P*-values when significant. Study area and its interaction with visitation frequency had 2, 28 degrees of freedom; the remainder of the factors had 1, 28 degrees of freedom. All densities were log-transformed, but MURU, TRAE, and STLO. Shown are covariates with *P*<0.05

\*, *P*<0.05; \*\*, *P*<0.01; \*\*\*, *P*<0.001; VF, visitation frequency; SA, study area; PWS, *Polylepis* woodland/shrubland; RP, rock exposed by erosion; outcrop with exposed rock, OER; outcrop with tussock grassland, OTG; AEAN, *Aeronautes andecolus*; AGMO, *Agriornis montana fumosus*; ANTHSP, *Anthus* sp.; ATMO, *Asthenes modesta Córdobae*; ASSC, *Asthenes sclateri sclateri*; BOAY, *Bolborhynchus aymara*; BUAL, *Buteo albicaudatus*; BUPO, *Buteo polyosoma*; CAMA, *Carduelis magellanica*; CAIN, *Catamenia inornata*; CAAU, *Cathartes aura*; CICO, *Cinclodes comechingonus*; CIFU, *Cinclodes fuscus*; CIOR, *Cinclodes olrogi*; CIPL, *Cistothorus platensis*; FASP, *Falco sparverius*; MURU, *Muscisaxicola rufivertex achalensis*; NOCY, *Nothiochelidon cyanoleuca*; NOMA, *Nothura maculosa*; PHUN, *Phrygilus unicolor cyaneus*; POPL, *Polyborus plancus*; SASP, *Sappho sparganura*; STLO, *Sturnella loica obscura*; TRAE, *Troglodytes aedon*; TUCH, *Turdus chiguanco*; VACH, *Vanellus chilensis*; VUGR, *Vultur gryphus*; ZOCA, *Zonotrichia capensis*

There was no relationship between the probability of finding a significant visitation frequency effect and the relative density of the studied species (logistic regression,  $\chi^2=0.005$ , d.f. = 1, *P*=0.938).

We found a significant interaction between visitation frequency and study area for *Carduelis magellanica* (Table 3). This granivore was not affected by visitation frequency in Champaqui (off-trail transects = 0.012 ± 0.056 individuals/10 ha, on-trail transects = 0.024 ± 0.056 individuals/10 ha), but its relative density was lower in on-trail transects in Condorito (off-trail transects = 0.261 ± 0.091 individuals/10 ha,



**Fig. 3** Relative densities (individuals/10 ha) of *Anthus* sp. (ANTHSP), *Asthenes modesta cordobae* (ATMO), *Asthenes sclateri* (ASSC), *Buteo albicaudatus* (BUAL), *Falco sparverius* (FASP); *Turdus chiguanco* (TUCH) in areas with low (off-trail) and high (on-trail) human visitation in the high Córdoba Mountains

on-trail transects =  $0.021 \pm 0.081$  individuals/10 ha), and higher in on-trail transects in Gigantes (off-trail transects =  $0.018 \pm 0.072$  individuals/10 ha, on-trail transects =  $0.214 \pm 0.083$  individuals/10 ha).

We also found that the relative density of six species (two insectivores, two granivores, two omnivores) varied among study sites (Table 3). Altitude significantly affected ten species (four insectivores, four granivores, two omnivores, Table 3), which in all cases but one (*Nothura maculosa*) increased their relative densities at higher altitudes. The amount of different habitat types affected several species in different ways (Table 3): *Polylepis* woodland and shrubland, four species (two granivores, one granivore, one carnivore), rock exposed by erosion, four species (three granivores, one insectivore); outcrop with exposed rock, one insectivore species; and outcrop with tussock grassland, one granivore species.

## Discussion

Our findings suggest that human disturbance may be involved in the responses found at different levels (community, guild, population). Six species, four of them of conservation concern, had lower densities in areas with relatively high levels of human visitation in the high Córdoba Mountains. Two of the four guilds studied had lower densities in areas with high visitation levels (carnivores and insectivores); although, the effects on carnivores were apparently caused by two abundant species negatively affected by visitors. Finally, species richness was lower in highly visited areas, even when the six species sensitive to disturbance were not considered. We compare these results with previous studies and suggest some mechanisms involved in these responses.

Like ours, some studies found a decrease in the occurrence of species associated with recreational activities in different habitat types (Hammit and Cole 1987; Miller et al. 1998; Riffell et al. 1996; Fernández-Juricic 2002). The displacement of species from highly visited areas has been suggested to be the result of reductions in habitat quality (e.g., Gill et al. 1996; Fernández-Juricic 2002; Frid and Dill 2002; Fernández-Juricic et al. 2003). Physical disturbance may decrease habitat structural complexity (Miller et al. 1998; Laiolo 2003) and/or affect the spatial and temporal patterns of resource exploitation due to the presence of pedestrians (Soulé et al. 1992; Fernández-Juricic 2000). We found that habitat composition was not significantly different between off- and on-trail areas; this suggests that a reduction in the proportion of suitable habitat available to birds may be underlying human–wildlife interactions in this habitat. However, future studies should rule out physical effects of disturbance (namely, soil compaction, soil erosion, and increase in trail width and depth; Deluca et al. 1998; McDougall and Wright 2004; Roovers et al. 2004) and explore this mechanism experimentally (Fernández-Juricic et al. 2003) before reaching definite conclusions.

Taking aside the effects of recreational activities on single species, only the insectivorous guild consistently had lower relative densities in highly visited areas. Similar effects on insectivores were also found in other studies conducted in urbanized landscapes (Chuan Lim and Sodhi 2004; but see Fernández-Juricic 2002). The decrease in the density of insectivores with higher human disturbance has been usually associated with food limitation (Canaday 1996; Laiolo 2003; Chuan Lim and Sodhi 2004) rather than low tolerance levels (Fernández-Juricic 2002). The composition of insect communities can indeed change at habitat edges associated with human disturbance (Webb et al. 1984; Shure and Phillips 1991; Suarez et al. 1998; Bolger et al. 2000; Kitahara et al. 2000), in some cases with invasive species being more abundant near human-induced edges and native species farther from those edges (Webb 1989). If bird insectivores rely mainly on native insects, variations in insect community composition with recreationists might potentially affect food availability; a possibility that deserves further study in the high Córdoba Mountains.

We found that 21.4% of the species whose abundance could be modeled decreased their densities in highly visited areas. However, the proportion of species affected by recreational activities was lower than in other studies, which reported negative effects in 53–92% of species (van der Zande and Vos 1984; Fernández-Juricic 2002; van der Zande et al. 1984; Miller et al. 1998). The low proportion of species affected by recreationists may have to do with the reduced levels of human visitation to the high Córdoba Mountains (3,000–12,000 visitors per year) relative to other areas (60,000 visitors per year in Laiolo 2003; 3,500,000 visitors per year in Miller et al. 1998; > 5,000,000 visitors per year in Fernández-Juricic 2002) or with species-specific differences in tolerance to disturbance (Blumstein et al. 2003). Alternatively, the low proportion of species affected could be related to behavioral adjustments to disturbance (Frid and Dill 2002). For instance, Forsman et al. (1998) found in boreal forests that territories tended to be more clumped when animals were exposed to an artificial predator during the breeding season. Territorial species in the High Córdoba Mountains could reduce the perceived risk imposed by the presence of visitors by reducing inter-specific neighbor distances; a strategy that might not be profitable at the intra-specific level due to competition effects (Pulliam and Caraco 1984). If behavioral responses like this are enough to reduce human

disturbance, population level effects might not be noticeable (see also, Gill et al. 2001; Beale and Monaghan 2004b).

### Conservation implications

Understanding human–wildlife interactions in this kind of environment provides an opportunity to assess how the spread of recreational activities might affect species with limited geographic distribution, which has become a top-priority for conservation biology (Soulé et al. 2001). Despite the low number of species negatively affected by recreationists, two of them are endemic and two are in decline. Furthermore, our relatively low number of transects suggest that more species could be decreasing due to tourism, but could not be detected with our samples. In threatened ecosystems, species of high conservation concern could be the first ones to be influenced by tourism, and raises the issue of whether or not biogeographic islands may be too fragile to support tourism. Given the geographic isolation of the high Córdoba Mountains, alternative habitats may not be available for these species, which could affect their persistence. Besides ecological loss, the decreased abundance of these species might also reduce wildlife-viewing opportunities and the economic benefits for local communities.

What strategies could then promote coexistence? First, small-scale manipulative studies to determine sustainable levels of human visitation must be conducted (e.g., Rodríguez-Prieto and Fernández-Juricic 2005). Second, visitation should be limited to few trails rather than expanding the area visitors can access, because the mere presence of visitors could reduce the access to suitable habitat for some species and guilds. Third, in areas with high visitation levels, increasing protective cover (e.g., *Polylepis* woodland) might also reduce negative impacts of human disturbance.

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## Appendix 1

**Table 4** Brief description of the different habitat types identified in the study areas in the high Córdoba Mountains (based on Cingolani et al. 2004)

Habitat types	Description
<i>Polylepis</i> woodland and shrubland	Dominated by <i>Polylepis</i> woodland/shrubland, with shrubby grassland and rock outcrop, but low total rock cover. Generally occurred below 2000 m on steep slopes in mid to low topographic positions, but was also found on flat sites in ravine bottoms or in gentle slopes. Erosion and grazing pressure were present

**Table 4** continued

Habitat types	Description
Thick tussock grassland with hydromorphic lawn	Generally located in low, flat, sometimes flooded positions. Some stands lack the hydromorphic lawn type, being mostly covered by <i>Poa</i> grassland. Proportion of active erosion edges was relatively high, but restricted to the margins of water courses. Grazing pressure was variable
Thin tussock grassland	Dominated by <i>Deyeuxia/Festuca</i> tussocks. Generally found on gentle slopes and flat summits at all altitudes, although the dominant species shifted with altitude. Below 1,900 m <i>Festuca</i> dominated at all topographic positions, being gradually replaced by <i>Deyeuxia</i> as altitude increased, up to 2,300 m where this species dominated at all topographic positions. Erosion activity was low, and livestock pressure intermediate
Lawn	Largely dominated by <i>Alchemilla-Carex</i> lawn, with some patches of other types. Rock exposed by erosion was generally found at the bottom of concavities which get flooded in the rainy season. Located at sites with less than a 10% slope, usually at high altitudes. Erosion was more active, and grazing pressure more intense, than in tussock grasslands
Outcrop with tussock grassland	A mixture of natural outcrops, exceptionally reaching 120 m tall, and tussock grasslands, together with small patches of other types, including <i>Polylepis</i> woodlands or shrublands. Mainly located on mid and upper steep slopes. Erosion activity was intermediate, and grazing pressure low
Outcrop with exposed rock	Dominated by rock, with small vegetation patches. Found at similar topographic positions than outcrop with tussock grassland, although at somewhat higher altitudes in more exposed and northerly sites. Activity of erosion and grazing pressure were high
Rock exposed by erosion	Its bare rock cover was higher than 80%, most of which was exposed due to erosion. Generally located in flat sites with high erosion activity. The grazing pressure on the few remaining vegetation patches was very intense

## Appendix 2

**Table 5** List of all recorded species, emphasizing their conservation status and degree of endemism (based on Miatello et al. 1999)

Common name	Scientific name	Guild	Conservation status (degree of endemism)
Andean swift	<i>Aeronautes andecolus</i>	Insectivorous	Unknown
Black-bellied shrike-Tyrant	<i>Agriornis montana fumosus</i>	Insectivorous	Unknown (subendemic)
Tufted tit-Tyrant	<i>Anairetes parulus</i>	Insectivorous	Unknown
“ <i>Anthus sp.</i> ”*		Insectivorous	Unknown
Cordilleran Canastero	<i>Asthenes modesta cordobae</i>	Insectivorous	Unknown (subendemic)
Córdoba Canastero	<i>Asthenes sclateri sclateri</i>	Insectivorous	Unknown (subendemic)
Gray-hooded Parakeet	<i>Bolborhynchus aymara</i>	Granivorous	Declining/ CITES II
White-tailed Hawk	<i>Buteo albicaudatus</i>	Carnivorous	Declining
Red-backed Hawk	<i>Buteo polyosoma</i>	Carnivorous	Declining
Swainson’s Hawk	<i>Buteo swainsoni</i>	Carnivorous	Unknown
Hooded Siskin	<i>Carduelis magellanica</i>	Granivorous	Unknown
Band-tailed Seedeater	<i>Catamenia analis</i>	Granivorous	Declining

**Table 5** continued

Common name	Scientific name	Guild	Conservation status (degree of endemism)
Plain-colored Seedeater	<i>Catamenia inornata cordobensis</i>	Granivorous	Declining (subendemic)
Turkey Vulture	<i>Cathartes aura</i>	Carnivorous	Unknown
White-winged Cinclodes	<i>Cinclodes atacamensis</i>	Insectivorous	Unknown (subendemic)
Chestnut-winged Cinclodes	<i>Cinclodes comechingonus</i>	Insectivorous	Abundant
Bar-winged Cinclodes	<i>Cinclodes fuscus</i>	Insectivorous	Abundant
Olrog's Cinclodes	<i>Cinclodes olrogi</i>	Insectivorous	Abundant (endemic)
Cinereous Harrier	<i>Circus cinereus</i>	Carnivorous	Unknown
Grass Wren	<i>Cistothorus platensis</i>	Insectivorous	Abundant
Field Flicker	<i>Colaptes campestris</i>	Insectivorous	Abundant
Golden-breasted Woodpecker	<i>Colaptes melanolaimus</i>	Insectivorous	Abundant
Black Vulture	<i>Coragyps atratus</i>	Carnivorous	Unknown
Peregrine Falcon	<i>Falco peregrinus</i>	Carnivorous	Declining
American Kestrel	<i>Falco sparverius</i>	Carnivorous	Unknown
Common Snipe	<i>Gallinago gallinago</i>	Insectivorous	Declining
Common Miner	<i>Geositta cunicularia contrerasi</i>	Insectivorous	Unknown (subendemic)
Rufous-banded Miner	<i>Geositta rufipennis otowi</i>	Insectivorous	Unknown (subendemic)
Black-chested Buzzard-Eagle	<i>Geranoaetus melanoleucus</i>	Carnivorous	Declining
Spectacled Tyrant	<i>Hymenops perspicillata</i>	Insectivorous	Unknown
Brown-capped Tit-Spinetail	<i>Leptasthenura fuliginiceps</i>	Insectivorous	Declining
Rufous-naped Ground-Tyrant	<i>Muscisaxicola rufivertex achalensis</i>	Insectivorous	Declining (subendemic)
Blue-and-White Swallow	<i>Nothiochelidon cyanoleuca</i>	Insectivorous	Abundant
Spotted Tinamou	<i>Nothura maculosa</i>	Omnivorous	Abundant
Band-tailed Sierra-Finch	<i>Phrygilus alaudinus</i>	Granivorous	Unknown
Ash-breasted Sierra-Finch	<i>Phrygilus plebejus naroskyi</i>	Granivorous	Unknown (subendemic)
Plumbeous Sierra-Finch	<i>Phrygilus unicolor cyaneus</i>	Granivorous	Abundant (subendemic)
Crested Caracara	<i>Polyborus plancus</i>	Carnivorous	Abundant
Red-tailed Comet	<i>Sappho sparganura</i>	Omnivorous	Declining/ CITES II
Long-tailed Meadowlark	<i>Sturnella loica obscura</i>	Omnivorous	Abundant (subendemic)
House Wren	<i>Troglodytes aedon</i>	Insectivorous	Abundant
Chiguanco Thrush	<i>Turdus chiguanco</i>	Omnivorous	declining
Southern Lapwing	<i>Vanellus chilensis</i>	Insectivorous	Abundant
Andean Condor	<i>Vultur gryphus</i>	Carnivorous	Declining/ CITES I
Rufous-collared Sparrow	<i>Zonotrichia capensis</i>	Granivorous	Abundant

\**Anthus sp.*'' includes the following species: *A. correndera*, *A. furcatus*, *A. hellmayri* and *A. lutescens*

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