Available online at www.sciencedirect.com
SCIENCE DIRECT®

Biological Conservation 117 (2004) 407–416

BIOLOGICAL CONSERVATION

www.elsevier.com/locate/biocon

Spatial and temporal responses of forest birds to human approaches in a protected area and implications for two management strategies

Esteban Fernández-Juricic[a,*], Raul Vaca[b], Natalia Schroeder[b]

[a]Department of Ecology, Evolution and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St. Paul, MN 55108, USA
[b]Museo de Zoología, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Av. Velez Sarsfield 299, 5000, Córdoba, Argentina

Received 1 August 2002; received in revised form 12 January 2003; accepted 18 February 2003

Abstract

Little is known about the responses of forest birds, other than raptors, to human disturbance despite their being highly sensitive to habitat disruption. We tested five hypotheses about the spatial and temporal interactions between recreationists and wildlife by using five South American birds as model species. We measured two components of flight distance, horizontal (distance between a visitor and the base of a perching tree) and vertical (distance between the base of a tree and the perch), and estimated the third diagonal component (distance between a visitor and the perch). We found that (a) the relationships between horizontal and vertical components of flight distance were negative (rufus-collared sparrow, golden-billed saltator, chiguanco thrush), positive (spot-winged pigeon), and neutral (bay-winged cowbird), suggesting that different components are used as clues to the proximity of people when birds vacated the perching tree; (b) the distance to the nearest pathway correlated positively with flight distance components of two species (bay-winged cowbird and spot-winged pigeon); and (c) physical structure of the vegetation affected differently flight distances of all species. Interspecific comparisons showed that (d) all flight distance components increased linearly with body size, and (e) species differed in landing distances but not in response duration: large-bodied species tended to land farther than smaller-bodied ones. By implementing buffer zones (areas without access to visitors), spatial restrictions would conflict with recreational activities. We recommend re-distributing (but not restricting) human visitation by varying the number of visitors and area of visitation according to the spatial requirements of differently sized species.

Keywords: Argentina; Buffer zones; Flush response; Human disturbance; Mountain woodland; Park design; Protected area

1. Introduction

Unrestricted access to protected areas may decrease their ecological value due to humans disturbing individuals, populations, and communities (reviewed in Hockin et al., 1992; Knight and Gutzwiller, 1995; Hill et al., 1997; Carney and Sydeman, 1999; Gill and Sutherland, 2001). To predict the long-term and large-scale consequences of human disturbance, population level studies may be necessary (Gill et al., 2001). Nevertheless, to solve short-term and local-scale human–wildlife conflicts (e.g., seasonal high levels of human visitation to protected areas), behavioral studies of the response to visitors are useful (e.g., Anthony et al., 1995; Blumstein et al., 2002). This behavioral approach provides the baseline information on wildlife tolerance levels to set up management strategies that could improve human–wildlife coexistence (Rodgers and Smith, 1995, 1997).

One of the strategies put forward to reduce human disturbance is the creation of buffer zones that restrict access to specified areas and specified periods of time (Richardson and Miller, 1997). However, such restrictions may create conflicts of interests (Steidl and Anthony, 1996); for instance, by reducing visitation levels in areas where visitors are a source of income for local people. An alternative strategy to buffer zones is to manage the frequency of human visitation in relation to

---

* Corresponding author. Present address: Department of Biological Sciences, California State University Long Beach, Peterson Hall, 1–109, 1250 Bellflower Blvd., Long Beach, CA 90840, USA.
E-mail addresses: efernand@csulb.edu (E. Fernández-Juricic).

0006-3207/$ - see front matter © 2003 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2003.02.001

the frequency of resource use by wildlife (Fernández-Juricic and Telleria, 2000; Fernández-Juricic, 2000; Fernández-Juricic et al., 2003). Re-distributing (but not restricting) pedestrian rates (number of people per unit time per unit area) may allow animals to meet their breeding and feeding requirements without significantly reducing the temporal and spatial availability of resources (Fernández-Juricic, 2000; Fernández-Juricic et al., 2003).

Before recommending specific management strategies it is necessary to understand the spatial and temporal interactions between humans and wildlife (Keller, 1989; Whittaker and Knight, 1998). Since individuals do not usually flee as soon as they detect visitors (Fernández-Juricic et al., 2002), it is important to assess the distance at which they are displaced from foraging or breeding patches (Klein et al., 1995; Rodgers and Smith, 1995; Gutzwiller and Anderson, 1999). Such distances are usually known as flight distances, and have been thoroughly studied in birds foraging or nesting on the ground (Burger and Gochfeld, 1991; Rodgers and Smith, 1997; Lord et al., 2001). However, comparatively little empirical evidence exists as to interspecific variations in flight distances in species that spend part of the day perching in trees (but see Holmes et al., 1993; Gutzwiller et al., 1998), and the spatial and temporal responses after fleeing from human approaches. Understanding such responses is relevant because forest birds are usually highly sensitive to secondary fragmentation effects (Soulé et al., 1992), whereby certain factors, such as visitors to protected areas, can increase the spatial and temporal heterogeneity in habitat quality within forest fragments.

Flight distances of perching birds are more complex than those of birds foraging on the ground (Fig. 1), with horizontal (X, the distance between the visitor and the base of a tree), vertical (Y, the distance between the base of a tree and the perch), and diagonal (Z, the straight line distance between the visitor and the perch) components. Theoretically, the three components are mathematically related [$Z = \sqrt{(Y^2 + X^2)}$, Fig. 1]. Previous studies have considered the vertical component (Y) as an independent factor affecting flight distances (Holmes et al., 1993; Swarthout and Steidl, 2001). However, if birds detect visitors, move within the canopy, and then vacate the tree, the vertical component can be considered another level of decision making in the flushing response. We therefore take a different approach and consider the vertical component as a dependent variable by assuming that the difference between detection and flight distances within the perching tree > 0 (Fernández-Juricic et al., 2001a, 2002). If flushing decisions of forest birds rely on these components, important implications for management can be derived since various habitat types within a protected area can have different perceived risk of disturbance according to vegetation structure (Knight and Cole, 1991; Holmes et al., 1993; Steidl and Anthony, 1996; Swarthout and Steidl, 2001).

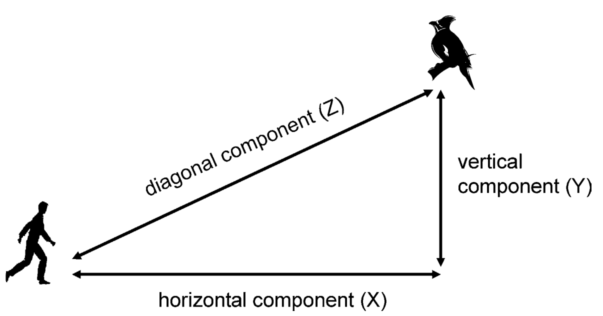

Fig. 1. Schematic representation of the three components of flight distance as a pedestrian approaches a perching bird. We assumed that individuals vacated the tree after detecting the observer and moving within the canopy.

Our general purpose was to test some hypotheses about the spatial and temporal interactions between visitors and individuals perching in trees by using five South American birds as model species. First, we assessed the relationships between the horizontal (X) and vertical (Y) components of flight distances to ascertain their role in the behavioral response to people. Three predictions were tested: (a) X and Y are negatively correlated (Z is kept constant with variations in X and Y), suggesting that birds perceive less risk as they perch higher (Knight and Fitzner, 1985; Datta and Pal, 1993); (b) X and Y are positively correlated (Z increases proportionally with variations in X and Y), implying that birds detect people from farther away, and consequently flee sooner as they perch higher (Swarthout and Steidl, 2001); and (c) X and Y are not correlated (Z varies independently from variations in X and Y), indicating that birds use the three distance components differently in human–wildlife encounters. Second, we determined the relationship between distance to pathways and the three components of flight distance, expecting that the proximity to sources of frequent disturbance, such as walking paths, would decrease tolerance to people (increasing flight distances), as found elsewhere (Steidl and Anthony, 1996; Fernández-Juricic and Telleria, 2000; but see Miller et al., 2001). Third, we assessed how habitat structure surrounding the perching tree affected the three components of flight distance, which would be affected by the obstructive or protective properties of vegetation for each species (Lazarus and Symonds, 1992; Knight and Temple, 1995). Fourth, we evaluated interspecific differences in flight distance components controlling for habitat structure. Following previous findings (Cooke, 1980; Burger and Gochfeld, 1991; Skagen et al., 1991; Holmes et al., 1993; Fernández-Juricic et al., 2001b), we expected flight distances to increase with species body size. Fifth, we analyzed interspecific variations in landing distance (the distance individuals moved from their perching tree until they stopped fleeing from the disturbance) and time to resume predisturbance activities; variables not usually considered in human disturbance studies (but see Swarthout and Steidl, 2001). We expected that the spatial and temporal displacement from perching trees would be greater for larger species due to less tolerance levels (Fernández-Juricic et al., 2002). Finally, we determined threshold distances and minimum approaching areas for each species (areas beyond which humans should not approach to minimize the risk of disturbance) and discussed two management strategies: setting aside areas without access to visitors or areas with low frequency of human disturbance.

2. Methods

2.1. Study area and species

The study was conducted in La Quebrada Reserve (31° 14′ S, 64° 20′ W), Córdoba, Argentina during winter–autumn 2000. The annual rainfall was 750 mm, and the mean temperature, 13.1 °C. This reserve is aimed at protecting the biodiversity of three main habitat types: mountain woodland (457 ha), mountain shrubland (429 ha), and mountain grassland (2611 ha) (Briguera, in press). This study was carried out in the mountain woodland, with a mix of deciduous (*Acacia* sp., *Rupectia apetala*, *Celtis tala*) and perennial (*Lithraea ternifolia*, *Fagara coco*, *Schinus fasciculatus*, *Condalia buxiflora*) species (Bertran de Solis, 1986). Three major walking paths covered most of the Reserve, which were used by recreationists, particularly during weekends. Landowners and farmers used an extensive network of smaller paths. La Quebrada Reserve was a good model to study human wildlife interactions since it received about 80,000 people annually, with approximately 2000 visitors per weekend (E. Medina, G. Bronstein, and A. Acuña, Provincial Park Service, personal communication).

We selected five bird species (rufus-collared sparrow, *Zonotrichia capensis*; bay-winged cowbird, *Molothrus badius*; golden-billed saltator, *Saltator aurantiirostris*; chiguanco thrush, *Turdus chiguanco*; and spot-winged pigeon, *Columba maculosa*) that spent part of their daily activities perching in trees. Any of these species exhibited synanthropic behaviors. What follows is a brief account of their foraging habits and conservation status in the province of Córdoba (based on Zotta, 1936; Ridgely and Tudor, 1989; Fjeldsa and Krabbe, 1990; Haro and Gutierrez, 1992; Yzurieta, 1995).

- *Rufus-collared sparrow*: it generally forages on the ground (seeds and occasionally insects), and perches in trees and bushes to rest, sing, or look for food. Populations are stable and widespread across the province.
- *Golden-billed saltator*: it usually feeds on fruits in trees and bushes, but sometimes on seeds on the ground. Populations are dwindling owing to extraction of adults for pets and high nest predation in rural areas.
- *Bay-winged cowbird*: it is an omnivorous species (mainly insects and seeds), breeding in wooded patches but foraging in adjacent pastures or areas with tall grasses. Populations are stable due to its ability to colonize different types of habitats.
- *Chiguanco trush*: it forages in trees (insects and fruits) and on the ground (insects). It also uses perches to sing. Although widespread, populations are declining because of the extraction of individuals for pets.
- *Spot-winged pigeon*: it feeds on seeds on the ground and spends a considerable amount of time perching in trees, resting, preening, and singing. Populations are increasing due to the expansion of agricultural areas.

During our approaches, the five species were usually roosting, and the rufus-collared sparrow and the golden-billed saltator sometimes were also foraging. We took body sizes from published (Fiora, 1933; Salvador, 1988, 1990) and unpublished sources (G. Haro, National University of Córdoba, personal communication). In a preliminary study, we confirmed that these species moved within the canopy after detecting approaching pedestrians and before fleeing.

2.2. Flight distances

Data were gathered between 08:00 and 12:00, and between 15:00 and 18:00 to avoid high midday temperatures, which can affect responses to humans (Fernández-Juricic et al., 2002). We totaled 307 observation hours, on sunny or cloudy days, but never when raining or in windy conditions. Ambient temperatures varied from 5 to 32 °C, but these hourly variations did not affect the components of flight distance measured (Pearson product moment correlation; rufus-collared sparrow, X, $r=-0.18$, $P=0.25$, Y, $r=0.24$, $P=0.13$; golden-billed saltator, X, $r=-0.23$, $P=0.16$, Y, $r=0.04$, $P=0.82$; bay-winged cowbird, X, $r=-0.27$, $P=0.09$, Y, $r=0.01$, $P=0.93$; chiguanco thrush, X, $r=-0.11$, $P=0.53$, Y, $r=-0.05$, $P=0.79$; spot-winged pigeon, X, $r=$- 0.10, $P=0.52$, Y, $r=-0.22$, $P=0.17$). Two observers (R.V. and N.S.) gathered all the data after being trained (in a different location) for one month in recording variables to reduce inter-observer variability. The Reserve was visited randomly during weekdays (twice per week), with at least a 1-day interval between visits. We sampled only twice during weekends because of high levels of human visitation that reduced the sectors of the Reserve available for sampling.

Flight distance was defined as the distance between an approaching pedestrian and a bird at which the latter flushed. Of the three components of flight distance, we measured two (horizontal and vertical), and calculated the third with the Pythagorean theorem (Fig. 1). After locating birds with binoculars, we began approaching them at 75–90 m with a steady pace (1 step/s) and a linear trajectory. Observers approached birds wearing similar clothing to circumvent differential reaction (Gutzwiller and Marcum, 1997). All birds approached were perching in trees >1.5 m in height. We recorded the horizontal and vertical components when the bird vacated the tree; that is, after it detected the approaching human and moved within the canopy. When the bird flushed, we dropped a marker attached to a meter tape to measure the horizontal component (± 0.05 m) up to the base of the tree where the bird was perching. We then measured the vertical component (Y) as the distance (± 0.05 m) between the base of the tree and the vacated perch. In a preliminary study, we determined sample sizes with $\alpha = 0.05$ and $\beta = 0.05$ (40 observations per species). We did not mark individuals, but recorded responses to our approaches from randomly selected locations to reduce the likelihood of sampling the same individual. Observers never collected two observations from the same species from contiguous areas to avoid affecting responses between approaches. Measuring flight distances from unmarked individuals of the same population has been done before to determine threshold distances (Anthony et al., 1995; Steidl and Anthony, 1996; Swarthout and Steidl, 2001).

When the observer approached a group of birds, s/he focused on a single individual within the group chosen before the approach, but recorded the number of conspecifics and heterospecifics perching in the same tree. Once the focal individual flew away, we also recorded its landing distance (within or beyond a 25-m circular radius) and response duration (time in seconds from flight response to resumption of pre-disturbance activity). Pre-disturbance activity was determined before initiating the approach (roosting or foraging). When the individual detected the observer, its scanning (based on head position) and movement behavior (within the tree) increased substantially before fleeing and after landing in a different tree. We recorded the amount of time it took the bird to resume foraging or roosting activity after vacating the original perching tree. We also measured the distance from the perching tree to the nearest walking path (m). Observers then walked to the base of the perching tree, from which the following variables were recorded in 25-m circular plots centered on the tree: shrub cover (%), cover of trees with foliage (%), cover of trees without foliage (%), mean shrub height (m), mean tree height (m), number of stems <10, 10–30, 30–50, and >50 cm dbh. Cover variables were visually estimated following Prodon and Lebreton's scales (1981).

2.3. Statistical analyses

We transformed the following variables using logarithmic and arcsine transformations to meet statistical assumptions of normality: horizontal, vertical, and diagonal components of flight distance, shrub cover (%), cover of trees with foliage (%), cover of trees without foliage (%), number of stems <10, 30–50, and >50 cm dbh. We used Pearson product moment correlations to relate the horizontal (X) and vertical (Y) components of flight distance, and distance to walking path and the three components of flight distance (X, Y, and Z).

Group size can affect flight distances by decreasing tolerance to pedestrians (Knight and Cole, 1995). Through multiple stepwise regressions, we found that only the horizontal component (X) of rufus-collared sparrows ($F_{1,\ 38} = 10.09$, $R^2 = 0.18$, $P < 0.001$) and the vertical component (Y) of spot-winged pigeons ($F_{1,\ 38} = 6.81$, $R^2 = 0.13$, $P < 0.05$) significantly correlated with number of conspecifics; all other relationships were not significant ($P > 0.05$). Furthermore, number of heterospecifics perching in the same tree did not affect flight distance components of any species ($P > 0.05$). Our purpose was not to study the effects of group size; however, we controlled for its potential influence on the different components before analyzing habitat structure effects and interspecific differences in flight distances (see below).

In assessing the influence of habitat structure on the three components of flight distance, we performed multiple regressions with forward stepwise selection procedures to identify the most significant factors (Nicholls, 1989). For rufus-collared sparrows and spot-winged pigeons, the dependent variables were the residuals of the relationship between flight distance and number of conspecifics, as explained above. To analyze whether the three components of flight distance varied among species, we employed an ANCOVA, including those physical factors, along with group size, significantly affecting the different components as covariates. With a polynomial linear model using planned comparisons, we examined whether the three components followed a linear increase with body size. Differences between levels of a factor were assessed with Tukey HSD tests. Interspecific variations in landing distance categories were analyzed with a Chi-square contingency test. Finally, we used an unbalanced ANOVA to test for interspecific differences in time to resume predisturbance activity, because the number of observations in which individuals remained in the observer's sight (within a 25-m circular plot) varied among species (see below). Therefore, this is the only test including less than 40 observations per species (sample sizes, rufus-collared sparrow = 24, bay-winged cowbird = 22, golden-billed saltator = 21, chiguanco thrush = 15). We did not include the spot-winged pigeon in this analysis due to the low number of observations.

We plotted the cumulative percentage of individuals fleeing against the horizontal and vertical components of flight distances to determine frequencies over distances for each species (Anthony et al., 1995). We reported the point at which 95% of the individuals flushed, which can be considered a reliable estimate of threshold distance (McGarigal et al., 1991). By taking threshold distances (TD) as the radius of a circle, minimum approaching areas for individual species (the area around an individual that if encroached by a pedestrian would cause a flushing response) were calculated as $\Pi{*}TD^2$ (Fox and Madsen, 1997). It has been suggested that estimating minimum approaching areas based on direct approaches to birds may overprotect wildlife and unnecessarily restrict recreational activities, because individuals usually have greater responses to direct than to tangential approaches (Taylor and Knight, Colorado State University, unpublished data). However, in La Quebrada Reserve, visitors sometimes leave walking paths to picnic or camp; hence, our estimates of minimum approaching areas should be more realistic.

3. Results

3.1. Horizontal and vertical components of flight distance

Horizontal and vertical components were negatively correlated in three species: rufus-collared sparrow ($r = -0.34$, $P = 0.03$), golden-billed saltator ($r = -0.29$, $P = 0.03$), and chiguanco thrush ($r = -0.31$, $P = 0.04$). The correlation between components was positive for spot-winged pigeons ($r = 0.25$, $P = 0.04$), whereas there was no significant correlation for bay-winged cowbirds ($r = 0.001$, $P = 0.97$).

3.2. Proximity to walking path

Distance to the nearest walking path did not affect any of the components of flight distance in most of the species (r varied between -0.23 and 0.07, $P > 0.05$). However, the vertical component of bay-winged cowbird flight distance was positively correlated with distance to walking path ($r = 0.40$, $P < 0.01$). A positive correlation was also found for the horizontal ($r = 0.31$, $P < 0.04$) and diagonal ($r = 0.31$, $P < 0.05$) components of spot-winged pigeon flight distance.

3.3. Habitat structure effects

- *Rufus-collared sparrow*. After correcting for the effects of group size, horizontal and diagonal components of flight distance were negatively correlated with mean tree height (Table 1). Number of stems > 50 cm dbh was positively associated to the horizontal component (Table 1). No model could be fitted for the vertical component.
- *Golden-billed saltator*. The vertical component of flight distance correlated positively with mean shrub height (Table 1) whereas both horizontal and diagonal components were not affected by any habitat structure factor.
- *Bay-winged cowbird*. Number of stems < 10 cm dbh were negatively associated with the horizontal and diagonal components of flight distance (Table 1). No habitat structure factor affected the vertical component.
- *Chiguanco thrush*. Two factors affected flight distances of this species: shrub cover correlated negatively with horizontal and diagonal components, and mean shrub height correlated positively with the vertical component (Table 1).
- *Spot-winged pigeon*. Only the vertical component was affected by habitat structure (after controlling for group size), with a negative correlation with percentage cover of trees with vegetation, and with mean tree height (Table 1).

3.4. Interspecific differences in flight distances

We found interspecific differences in the three components of flight distances, after controlling for the effects of habitat structure and group size. The horizontal component increased linearly with body size ($F_{1,\ 188} = 148.4$, $P < 0.001$, Fig. 2a). Post-hoc comparisons confirmed that all species differed from one another (Tukey test, $P < 0.02$), except for the contrasts between rufus-collared sparrow and golden-billed saltator (Tukey test, $P = 0.069$), and bay-winged cowbird and golden-billed saltator (Tukey test, $P = 0.779$). The vertical component also showed a significant linear increase with body size ($F_{1,\ 188} = 23.13$, $P < 0.001$, Fig. 2b), but the effect resulted only from greater flight distances of spot-winged pigeons in relation to the other species (Tukey tests, $P < 0.05$). The contrasts between other species were not significant (Tukey test, $P > 0.05$). Finally, the diagonal component increased linearly with body size as well ($F_{1,\ 188} = 154.6$, $P < 0.001$, Fig. 2c). All contrasts between pairs of species were significant (Tukey tests, $P < 0.05$) but one: between golden-billed saltator and bay-winged cowbird (Tukey test, $P = 0.851$).

3.5. Landing distance and response duration

We found interspecific differences in landing distance after individuals flushed from human approaches ($\chi^2 = 26.81$, $P < 0.001$, Table 2). These differences were mainly determined by rufus-collared sparrows and

Table 1
Effects of habitat structure on the three components of flight distances for five bird species perching in trees at La Quebrada Reserve (Cordoba, Argentina)[a]

Species[b]	Horizontal component (X)	Vertical component (Y)	Diagonal component (Z)
RcS	X_c[c] $= 1.29 - 0.27$ MTH $+ 0.33$ N50, $F_{2,\,37} = 6.01$, $R^2 = 0.24$,**	No model fitted[d]	Z_c[c] $= 0.83 - 0.17$ MTH, $F_{1,\,38} = 5.58$, $R^2 = 0.13$,*
GbS	No model fitted	$Y = -0.02 + 1.75$ MSH, $F_{1,\,38} = 4.30$, $R^2 = 0.10$,*	No model fitted
BwC	$X = 2.84 - 0.01$ N10, $F_{1,\,38} = 5.68$, $R^2 = 0.13$,*	No model fitted	$Z = 2.87 - 0.02$ N10, $F_{1,\,38} = 5.21$, $R^2 = 0.12$,*
ChT	$X = 3.59 - 0.25$ SHC, $F_{1,\,38} = 6.90$, $R^2 = 0.15$,*	$Y = 0.29 + 0.25$ MSH, $F_{1,\,38} = 7.64$, $R^2 = 0.17$,**	$Z = 3.54 - 0.21$ SHC, $F_{1,\,38} = 6.06$, $R^2 = 0.13$,*
SwP	No model fitted	Y_c[c] $= -5.74 - 1.52$ TWFC $- 8.56$ MTH, $F_{2,\,37} = 6.88$, $R^2 = 0.27$,**	No model fitted

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

[a] Shrub cover (SHC); percentage cover of trees with foliage (TWFC); percentage cover of trees without foliage (TWOFC); mean tree height (MTH); mean shrub height (MSH); number of stems < 10 cm dbh (N10); number of stems > 50 cm dbh (N50).

[b] RcS, rufus-collared sparrow; GbS, golden-billed saltator; BwC, bay-winged cowbird; CHT, chiguanco thrush; SwP, spot-winged pigeon.

[c] X_c, Y_c, and Z_c, components corrected for group size effects.

[d] The contribution of all factors to R^2 was less than 1%.

golden-billed saltators that landed in substrates within 25 m of the fleeing point, and spot-winged pigeon that usually landed farther (Table 2). Response duration did not differ among species ($F_{3,\,84} = 0.54$, $P = 0.656$; rufus-collared sparrow, 38 ± 105 s; golden-billed saltator, 31 ± 29 s; bay-winged cowbird, 21 ± 10 s; chiguanco thrush, 44 ± 62 s).

3.6. Threshold distances and minimum approaching areas

Horizontal 95% threshold distances for individual species were estimated as: rufus-collared sparrow, 17.5 m; golden-billed saltator, 20 m; bay-winged cowbird, 25 m; chiguanco thrush, 40 m; and spot-winged pigeon, 45 m. As for vertical threshold distances, little variation was found between four of the five species: rufus-collared sparrow, 5 m; bay-winged cowbird and chiguanco thrush, 7 m; golden-billed saltator, 8 m; and spot-winged pigeon, 13 m. Minimum approaching areas were estimated for these species in the mountain woodland of La Quebrada reserve as: rufus-collared sparrow, 0.09 ha; golden-billed saltator, 0.13 ha; bay-winged cowbird, 0.20 ha; chiguanco thrush, 0.50 ha; and spot-winged pigeon, 0.64 ha.

4. Discussion

Flight distance of species that inhabit forest habitats involves complex relationships between its components. For rufus-collared sparrows, golden-billed saltators, and chiguanco thrushes, the negative correlation between horizontal and vertical components underscores that these species may use the diagonal component as a threshold distance to flee from pedestrians (Fig. 1). Therefore, as individuals perched higher, flight distance decreased, likely because of a reduction in the perceived risk of disturbance, a pattern also found in raptors (Holmes et al., 1993; Steidl and Anthony, 1996). For spot-winged pigeons, the positive correlation between the horizontal and vertical components may be related to an enhanced visibility of the surroundings at higher perches, which has also been reported for Mexican spotted owls *Strix occidentalis lucida* (Swarthout and Steidl, 2001). Finally, no relationship between vertical and horizontal components was found in bay-winged cowbirds, which indicates that the cues individuals use to flee from pedestrians (X, Y, Z) may differ in each encounter. Our level of analysis did not allow us to identify specific cues, but it suggests that there are interspecific differences, as well as intraspecific variability, in the decision-making process affecting the three components of flight distances.

Contrary to our expectations, we found a positive correlation between distance to walking paths and the different components of flight distances of bay-winged cowbirds and spot-winged pigeons. This finding may be related to the predictability of pedestrian movements (Mainini et al., 1989; Whittaker and Knight, 1998; Miller et al., 2001). For instance, the closer to the walking path the observer was, the lower the risk of disturbance since the probabilities that s/he returned to the path would be greater. On the other hand, the farther from the walking path, the higher the chances that the observer intended a closer approach, increasing the risk of an interaction as a result (Miller et al., 2001). Thus, for management measures that regulate the rates of pedestrians moving across pathways to be successful in reducing human disturbance effects, complementary educational programs should encourage visitors not to go off trails.

The relationships found between habitat structure and flight distance components may be related to the

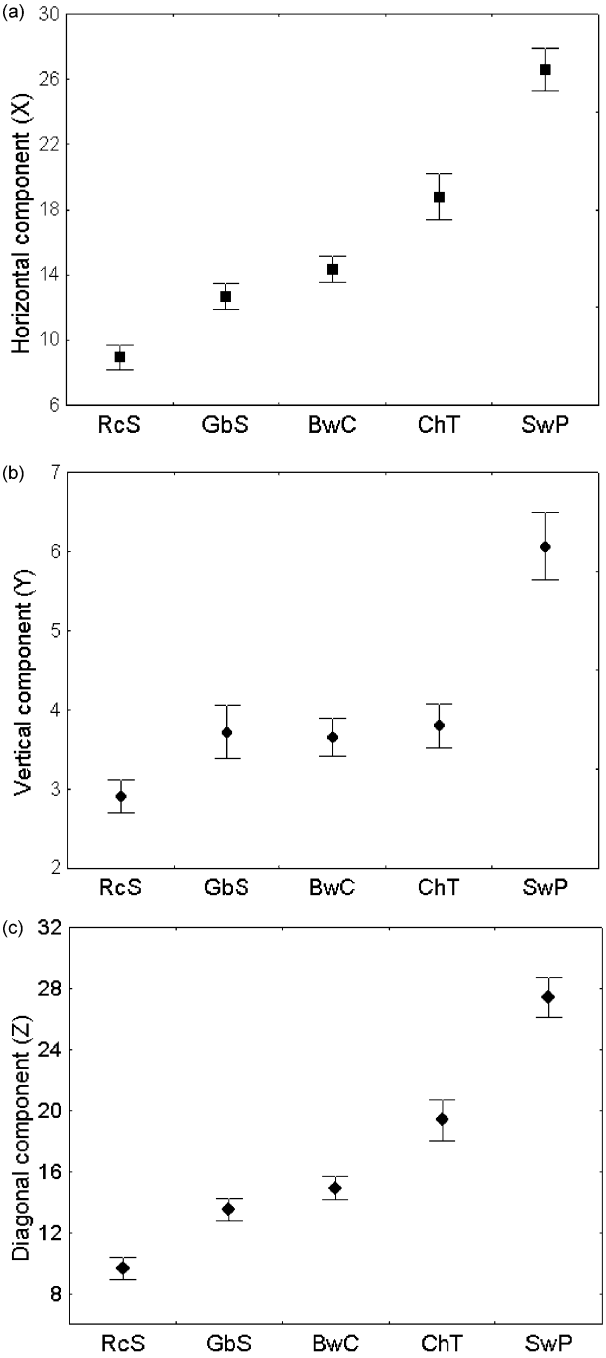

Fig. 2. Differences in the horizontal (a), vertical (b), and diagonal (c) components of flight distance (m) among five bird species with different body sizes: rufus-collared sparrow (RcS, 19.8 g), golden-billed saltator (GbS, 47.3 g), bay-winged cowbird (BwC, 53.3 g), chiguanco trush (ChT, 95.7 g), spot-winged pigeon (SwP, 367.5 g).

protective and obstructive properties of vegetation for different species (Lima et al., 1987; Lima, 1990; Lazarus and Symonds, 1992; Harkin et al., 2000). Any interpretation should be taken with care because we did not manipulate vegetation structure; thus, we can only point out characteristics of the vegetation that would increase the probabilities of individuals being more tolerant of visitors. For instance, tree height is expected to increase the tolerance (due to the negative correlation with flight distance components) of rufus-collared sparrows and spot-winged pigeons, likely because taller trees provide greater availability of refugees. The negative correlation between the vertical component of golden-billed saltators and chiguanco thrushes and mean shrub height may result from the obstructive effects of vegetation. This pattern suggests a hypothesis that requires further testing: whether increasingly taller shrubs may reduce visibility and the ability of the birds to keep track of pedestrian movements. Another factor that would increase tolerance of bay-winged cowbirds (in the horizontal and diagonal components) is the number of thin stems (< 10 cm dbh). One potential explanation may be that thin trees were not as visually obstructive as thick trees, so birds could keep track of the observer's movement as s/he approached the perching tree. Though significant, the effects of the physical structure of the patch surrounding the perching tree explained a relatively low proportion of the variability of flight distances (Table 1), which suggests that other factors were involved during these human–wildlife encounters, such variations in individual behavior, sex, age, etc. Nevertheless, we consider that these relationships provide managers some guidelines to reduce the negative effects of human disturbance by increasing the number of visitors moving along pathways surrounded by vegetation or by increasing the availability of these substrates in highly visited areas.

Interspecific differences in flight distances of species perching in trees have been reported only in raptors (Holmes et al., 1993). Our results point out that small species inhabiting forest habitats might also differ in some components of flight distance, with a negative relationship between tolerance and species body size. The horizontal and diagonal components correlated linearly with species size, whereas the vertical component only showed a significant increase at the upper end of the range. That suggests that species may have a similar response in terms of the vertical component between 20 and 95 g, which might be related to the physical constraints imposed by tree height. That larger species flee sooner from pedestrians is commonplace in ground foragers and ground nesters (Cooke, 1980; Burger and Gochfeld, 1991; Skagen et al., 1991; Fernández-Juricic et al., 2001b). We do not consider that hunting could account for the reduction in tolerance with body size, because there is no past or present evidence of such activity in the reserve.

Interestingly, we found that larger species were not only less tolerant of pedestrians but also more likely to land farther from perching trees. Escape tactics can affect patch selection (Lima, 1993), because the chances of using the same foraging patch decrease as trips to alternative refuges are longer (Kramer and Bonenfant,

Table 2
Interspecific differences in landing distance (within or beyond a 25-m circular plot) from the flushing point[a]

Species	<25 m	>25 m
Rufus-collared sparrow	24 (2.68)	16 (2.03)
Golden-billed saltator	21 (0.84)	19 (0.63)
Bay-winged cowbird	22 (1.34)	18 (1.01)
Chiguanco thrush	15 (0.28)	25 (0.21)
Spot-winged pigeon	4 (10.13)	36 (7.64)

[a] Shown are the number of observations per species and category (cell χ^2 in parentheses indicate cell contributions to the overall relationship).

1997). A recent study showed that after fleeing from pedestrians, large ground foragers landed farther and used higher landing substrates than small species (Fernández-Juricic et al., 2002). Consequently, larger species may be more affected by pedestrians, as they are likely to vacate more frequently foraging or roosting patches (Keller, 1989). This interpretation assumes that flight distances are species-specific traits, which has been corroborated recently even after considering habituation effects (Blumstein et al., 2003). Moreover, since most of our model species also breed in the reserve, the effects of visitors on large species might also affect their breeding behavior and success by reducing the availability of suitable habitats to breed and forage when the amount of human visitation is greater (spring–summer). Therefore, the relationship between the levels of human visitation and the probabilities of using suitable patches, controlling for their availability, during the breeding period needs further testing to evaluate potential negative effects at the population level.

4.1. Conservation implications

Spatial and temporal dimensions of human–wildlife interactions should be considered when managing species that use forest areas and that are bound to interact with tourists frequently. Unlike species that spend most of their time on the ground, forest species need special consideration of horizontal as well as vertical components of their habitat, since both appear to be used in the decision-making process as to when to flee from pedestrians. For instance, the negative correlation between horizontal and vertical components in rufus-collared sparrows, golden-billed saltators, and chiguanco thrushes would permit reductions in horizontal restrictions in areas with higher trees (Holmes et al., 1993).

One management strategy to reduce human disturbance is to set aside areas from visitors (buffer zones) based on minimum approaching areas (Anthony et al., 1995; Rodgers and Smith 1995, 1997; Fox and Madsen, 1997). Based on previous estimates of the density of the five species in the mountain woodland of La Quebrada Reserve (Jacome-Rivera, 1996), we calculated the percentage area of this habitat that would need spatial restriction as (multiplying population size by minimum approaching area, and assuming that populations were large enough to be viable and displacement by tourists would reduce the overall availability of suitable habitat): rufus-collared sparrow, 8.3%; golden-billed saltator, 8.7%; bay-winged cowbird, 21.5%; chiguanco thrush, 95.7%; and spot-winged pigeon, 150%. This suggests that for increasingly large-bodied species restricting access to visitors might not be feasible because 95% of the tourism is concentrated on the mountain woodland and the reserve plays an important educational role (e.g., wildlife viewing). Therefore, we suggest that visitors be re-distributed (not restricted) based on the spatial and temporal responses of differently sized species.

Two management scenarios for the studied species in the La Quebrada Reserve deserve further testing. We assume that (1) the intensity of the responses to people increases with the number of visitors in a group (Burger and Gochfeld, 1991), and that (2) the response to visitors depends upon the frequency of human visitation (number of visitors per unit time per unit area, Fernández-Juricic et al., 2003). If small species are not entirely displaced from foraging/roosting areas and if they resume pre-disturbance activities relatively quickly, we predict that by concentrating the number of visitors in large groups instead of several small groups, individuals would be displaced less frequently by pedestrians, with lower effects to their foraging/roosting activities. On the other hand, if large species detect human approaches earlier (Fernández-Juricic et al., 2001a) and they land farther once displaced (this study and Fernández-Juricic et al., 2002), reducing the spatial extent of the visit by concentrating pedestrians in small areas rather than dispersing them in large areas of the reserve would reduce the frequency of human–wildlife interactions, which would diminish the negative effects of visitors. If there are similar differences in the responses to pedestrians with respect to body size in other habitats, then body size of species of conservation interest may be used as a surrogate to implement these management scenarios and increase the coexistence of wildlife and recreationists.

Acknowledgements

We thank R. Torres, G. Haro, M. Nores, and V. Briguera for their valuable help during different stages of this study, and D.N. Cole and A.R. Taylor for critically reviewing an earlier version of the manuscript. E.F.J. was funded by "la Caixa" Foundation and Consejo Nacional de Investigaciones Cientificas y Tecnicas.

References

Anthony, R.G., Steidl, R.J., McGarigal, K., 1995. Recreation and bald eagles in the Pacific Northwest. In: Knight, R.L., Gutzwiller, K.J. (Eds.), Wildlife and Recreationists: Coexistence through Management and Research. Island Press, Washington, pp. 223–241.

Bertran de Solis, M.A., 1986. Vegetacion. Estructura y composicion de la comunidad de Bosque Serrano. In: Luti, R. (Ed.), Efecto de las actividades humanas sobre los ecosistemas montañosos y de tundra. MAB-UNESCO, Argentina, pp. 97–111.

Blumstein, D.T., Anthony, L.L., Harcourt, R.G., Ross, G., 2003. Testing a key assumption of wildlife buffer zones: is flight initiation distance a species-specific trait? Biological Conservation 110, 97–100.

Briguera, V. Aportes para la planificacion de la Reserva Hidrica La Quebrada (Cordoba, Argentina) en base a la aplicacion de medidas cualitativas y variables de sintesis integradas en un SIG. Boletin de Estudios Geograficos (in press).

Burger, J., Gochfeld, M., 1991. Human distance and birds: tolerance and response distances of resident and migrant species in India. Environmental Conservation 18, 158–165.

Carney, J.M., Sydeman, W.J., 1999. A review of human disturbance effects on nesting colonial waterbirds. Waterbirds 22, 68–79.

Cooke, A.S., 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biological Conservation 18, 85–88.

Datta, T., Pal, B.C., 1993. The effect of human interference on the nesting of the Openbill Stork Anastomus oscitans at the Raignj Wildlife Sactuary, India. Biological Conservation 64, 149–154.

Fernández-Juricic, E., 2000. Local and regional effects of human disturbance in a fragmented landscape. Condor 102, 247–255.

Fernández-Juricic, E., Tellería, J.L., 2000. Effects of human disturbance on Blackbird *Turdus merula* spatial and temporal feeding patterns in urban parks of Madrid, Spain. Bird Study 47, 13–21.

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2001a. Bird tolerance to human disturbance in urban parks of Madrid. Spain. Management implications. In: Marzluff, J.M., Bowman, R., Donnelly, R. (Eds.), Avian Ecology and Conservation in an Urbanizing World. Kluwer Academic, Norwell, MA, pp. 261–275.

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2001b. Alert distance as an alternative measure of bird tolerance to human disturbance. Implications for park design. Environmental Conservation 28, 263–269.

Fernández-Juricic, E., Jimenez, M.D., Lucas, E., 2002. Factors affecting intra- and inter-specific variations in the difference between alert distances and flight distances of birds in forested habitats. Canadian Journal of Zoology 80, 1212–1220.

Fernández-Juricic, E., Sallent, A., Sanz, R., Rodríguez-Prieto, I., 2003. Testing the risk-disturbance hypothesis in a fragmented landscape: nonlinear responses of House Sparrows to humans. Condor 105, 316–326.

Fiora, A., 1933. El peso de las aves. Hornero 5, 353–365.

Fjeldsa, J., Krabbe, N., 1990. Birds of the High Andes. Zoological Museum, University of Copenhagen and Apolo Books, Suendborg.

Fox, A.D., Madsen, J., 1997. Behavioral and distributional effects of hunting disturbance on waterbirds in Europe: implications for refuge design. Journal of Applied Ecology 34, 1–13.

Gill, J.A., Sutherland, W.J., 2001. Predicting the consequences of human disturbance from behavioral decisions. In: Gosling, L.M., Sutherland, W.J. (Eds.), Behavior and Conservation. Cambridge University Press, Cambridge, pp. 51–64.

Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioral responses may not reflect the population consequences of human disturbance. Biological Conservation 97, 265–268.

Gutzwiller, K.J., Anderson, S.H., 1999. Spatial extent of human-intrusion effects on subalpine bird distributions. Condor 101, 378–389.

Gutzwiller, K.J., Marcum, H.A., 1997. Bird reactions to observer clothing color: implications for distance-sampling techniques. Journal of Wildlife Management 61, 935–947.

Gutzwiller, K.J., Marcum, H.A., Harvey, H.B., Roth, J.D., Anderson, S.H., 1998. Bird tolerance to human intrusion in Wyoming montane forests. Condor 100, 519–527.

Harkin, E.L., van Dongen, W.F.D., Herbestein, M.E., Elgar, M.A., 2000. The influence of visual obstructions on the vigilance and escape behavior of house sparrows, *Passer domesticus*. Australian Journal of Zoology 48, 259–263.

Haro, G., Gutierrez, M., 1992. La avifauna de una forestacion de pinos de rio de los Sauces, Córdoba. El Hornero 13, 214–218.

Hill, D., Hockin, D., Price, D., Tucker, P., Morris, R., Treweek, J., 1997. Bird disturbance: improving the quality and utility of disturbance research. Journal of Applied Ecology 34, 275–288.

Hockin, D., Ounsted, M., Gorman, M., Hill, D., Keller, V., Barker, M., 1992. Examination of the effects of disturbance on birds with reference to the role of environmental impact assessments. Journal of Environmental Management 36, 253–286.

Holmes, T., Knight, R.L., Stegall, L., Craig, G.R., 1993. Responses of wintering grassland raptors to human disturbance. Wildlife Society Bulletin 21, 461–468.

Jacome-Rivera, M., 1996. Avifauna de quebradas humedas en la Sierra Chica de Cordoba. Situacion actual y pautas para su manejo. Dissertation, Centro de Zoología Aplicada, Universidad Nacional de Córdoba, Argentina.

Keller, V., 1989. Variations in the response of great crested grebes *Podiceps cristatus* to human disturbance— a sign of adaptation? Biological Conservation 49, 31–45.

Klein, M.L., Humphrey, S.R., Percival, H.F., 1995. Effects of ecotourism on distribution of waterbirds in a wildlife refugee. Conservation Biology 9, 1454–1465.

Knight, R.L., Cole, D.N., 1991. Effects of recreational activity on wildlife in wildlands. Transactions North American Wildlife and Natural Resources Conference 56, 238–247.

Knight, R.L., Cole, D.N., 1995. Factors that influence wildlife responses to recreationists. In: Knight, R.L., Gutzwiller, K.J. (Eds.), Wildlife and Recreationists: Coexistence through Management and Research. Island Press, Washington, USA, pp. 71–79.

Knight, R.L., Gutzwiller, K.J. (Eds.), 1995. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, DC, USA.

Knight, R.L., Fitzner, R.E., 1985. Human disturbance and nest site placement in black-billed magpies. Journal of Field Ornithology 56, 153–157.

Knight, R.L., Temple, S.A., 1995. Wildlife and recreationists: coexistence through management. In: Knight, R.L., Gutzwiller, K.J. (Eds.), Wildlife and Recreationists: Coexistence through Management and Research. Island Press, Washington, pp. 327–333.

Kramer, D.L., Bonenfant, M., 1997. Direction of predator approach and the decision to flee to a refuge. Animal Behaviour 54, 289–295.

Lazarus, J., Symonds, M., 1992. Contrasting effects of protective and obstructive cover on avian vigilance. Animal Behaviour 43, 519–521.

Lima, S.L., 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. Wilson Bulletin 105, 1–47.

Lima, S.L., 1990. Protective cover and the use of space: different strategies in finches. Oikos 58, 151–158.

Lima, S.L., Wiebe, K.L., Dill, L.M., 1987. Protective cover and the use of space by finches: is closer better? Oikos 50, 225–230.

Lord, A., Waas, J.R., Innes, J., Whittingham, M.J., 2001. Effects of human approaches to nests of northern New Zealand dotterels. Biological Conservation 98, 233–240.

Mainini, B., Neuhaus, P., Ingold, P., 1993. Behavior of marmots *Marmota marmota* under the influence of different hiking activities. Biological Conservation 64, 161–164.

McGarigal, K., Anthony, R.G., Isaacs, F.B., 1991. Interactions of humans and bald eagles on the Columbia River estuary. Wildlife Monographs 115.

Miller, S.G., Knight, R.L., Miller, C.K., 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29, 124–132.

Nicholls, A.O., 1989. How to make biological surveys go further with generalised linear models. Biological Conservation 50, 51–75.

Prodon, R., Lebreton, J.D., 1981. Breeding avifauna of a Mediterranean succession: the holm oak and cork oak series in the eastern Pyrenees, 1. Analysis and modelling of the structure gradient. Oikos 37, 21–38.

Richardson, C.T., Miller, C.K., 1997. Recommendations for protecting raptors from human disturbance: a review. Wildlife Society Bulletin 25, 634–638.

Ridgely, R., Tudor, G., 1989. The Birds of South America. Vol 1. The Oscine Passerines. Oxford University Press, Oxford.

Rodgers, J.A., Smith, H.T., 1995. Set-back distances to protect nesting bird colonies from human disturbance in Florida. Conservation Biology 9, 89–99.

Rodgers, J.A., Smith, H.T., 1997. Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. Wildlife Society Bulletin 25, 139–145.

Salvador, S.A., 1988. Datos de peso de aves argentines. Hornero 13, 78–83.

Salvador, S.A., 1990. Datos de peso de aves argentinas. 2. Hornero 13, 169–171.

Skagen, S.K., Knight, R.L., Orians, G.H., 1991. Human disturbance of an avian scavenging guild. Ecological Applications 1, 215–225.

Soulé, M.E., Alberts, A.C., Bolger, D.T., 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63, 39–47.

Steidl, R.J., Anthony, R.G., 1996. Responses of bald eagles to human activity during the summer in interior Alaska. Ecological Applications 6, 482–491.

Swarthout, E.C.H., Steidl, R.J., 2001. Flush responses of Mexican spotted owls to recreationists. Journal Wildlife Management 65, 312–317.

Whittaker, D., Knight, R.L., 1998. Understanding wildlife responses to humans. Wildlife Society Bulletin 26, 312–317.

Yzurieta, D., 1995. Manual de reconocimiento y evaluación ecológica de las aves de CórdobaGobierno de Córdoba, Ministerio de Agricultura, Ganadería y Recursos Renovables. Córdoba, Argentina.

Zotta, A., 1936. Sobre el contenido estomacal de aves argentines. Hornero 6, 261–270.