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Sensitivity of wildlife to spatial patterns of recreationist behavior: A critical assessment of minimum approaching distances and buffer areas for grassland birds

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Abstract

A major goal of protected area management is to promote coexistence between wildlife and people and managers may restrict human activity by creating buffer zones. There are a number of assumptions implicit in establishing buffer zones that are typically based on how animals respond to approaching humans. Conventional wisdom suggests that animals will be more sensitive to directly approaching humans than humans approaching tangentially. Visibility and detectability are important factors influencing a species' response to an approaching threat. Grasslands are an ideal system to study the different approach types because visibility is similar in all directions. We focused on five species of birds, four of them endemic, in the high Pampa de Achala mountain grassland of Argentina to study the effects of direct and tangential approaches on disturbance, and to evaluate five methods typically used to estimate buffer areas considering their sensitivity to the type of approach and their ability to estimate areas large enough to ensure the protection of the target species. We found that, contrary to conventional wisdom, four out of the five species showed greater flight initiation distance response to tangential rather than direct approaches, and that the minimum approach distance and buffer area estimates for these species varied significantly (in some cases an order of magnitude) between methods. Variability in the estimates between methods could be related to their different assumptions, which are not typically evaluated. More generally, we should be cautious when asserting that a buffer area calculated from direct approaches necessarily eliminates human disturbance.

Keywords: Birds; Buffer areas; Buffer zones; Endemic species; Human disturbance; Recreational activities; Threatened habitat

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1. Introduction

Managers concerned with trying to maintain species diversity within protected areas create buffer areas, areas where human activity is restricted, to reduce human disturbance on wildlife (e.g., Madsen et al., 1998). Typically, buffer areas are estimated with a formula based on empirical estimates of the distance at which humans disturb animals (e.g., Rodríguez-Prieto and Fernández-Juricic, 2005). A fundamental assumption when creating buffer areas is that direct approaches are more disturbing than tangential approaches. This is an important assumption because people walking along a trail approach animals both directly and tangentially.

Evidence is, however, equivocal on the effect of direct and tangential approaches. Some studies have found that direct approaches are more disturbing (animals fled at greater distances, Burger and Gochfeld, 1981, 1990; Cooper, 1997a,b; Cooper et al., 2003); while others

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found that tangential approaches are more disturbing under some circumstances (Bulova, 1994; Cooper et al., 2003). It is essential to have a fundamental understanding of how animals react to the spatial movement of humans because riskier human approaches could reduce the area available for foraging, and eventually habitat use if the levels of human visitation are high (Miller et al., 1998; Fernández-Juricic, 2000; Papouchis et al., 2001; Enggist-Düblin and Ingold, 2003). This effect could become particularly pronounced in open habitats (e.g., Finney et al., 2005), where high visibility could increase the distance at which threats are detected (Whittingham et al., 2004).

There are two general steps used to develop buffer areas (Knight and Skagen, 1988; Knight and Temple, 1995; Richardson and Miller, 1997). Managers first estimate the distance at which humans should be separated from wildlife (minimum approaching distance), and then the areas where humans should not encroach to avoid displacing wildlife (buffer areas). Different methods have been proposed to calculate minimum approaching distances and buffer areas (e.g., Anthony et al., 1995; Fox and Madsen, 1997; Rodgers and Smith, 1995); however, little consideration has been devoted to evaluate their performance quantitatively. Such assessment is necessary, because recommendations for setting aside areas for wildlife protection could vary greatly depending upon the method chosen. For instance, if animals are more sensitive to tangential approaches, then estimating buffer areas with direct approaches (as has been usually the case) could underestimate the area necessary for birds to make use of breeding and/or foraging resources.

Our goals were (1) to assess the effects of tangential and direct approaches on birds from the high Pampa de Achala mountain grassland, an area with a high proportion of endemic plant and animal taxa (Nores, 1995; Cabido et al., 2003), and (2) to critically evaluate methods to estimate buffer areas by assessing their assumptions, their sensitivity to direct and tangential approaches, and the degree of variability in their estimates. We used five grassland bird species as models for our study; four of which are endemic.

2. Methods

2.1. Study area and species

Pampa de Achala (31°34′ S, 64°50′ W) is a dissected plateau (50,000 ha), located in the upper portion of the Córdoba mountains (1800–2300 m) in Argentina. Temperatures range from 5 to 11.4 °C annually, and precipitation (about 840 mm) is concentrated in the warmer months (October–April, Cabido, 1985). The landscape consists of a mosaic of grasslands, granitic outcrops, *Polylepis australis* woodlands, and eroded areas with exposed rock surfaces (Cingolani et al., 2004). In 1997, part of the Pampa de Achala (26,000 ha) was expropriated to create the "Quebrada del Condorito" National Park, while the private lands surrounding the Park were declared National and Provincial Water Reserves (12,000 and 117,000 ha, respectively).

We chose five model species: *Phrygilus unicolor cyaneus* (Plumbeous Sierra-Finch), *Cinclodes comechingonus* (Chestnut-winged Cinclodes), *Geosita rufipennis ottowi* (Rufous-banded Miner), *Sturnella loyca obscura* (long-tailed Meadowlark), and *Vanellus chilensis* (Southern Lapwing). We briefly describe their biology based on Miatello et al. (1999), Dunning (1992), Narosky and Izurieta (1993), and Sergio Salvador (personal communication). *P. unicolor cyaneus* (21.2 g) is endemic at the level of subspecies and a permanent resident inhabiting grasslands and nesting in crevices. They usually forage in pairs or small groups during the breeding season. *C. comechingonus* (29 g) is an endemic species to Argentina that inhabits grasslands and hillsides, and also nests in crevices. *G. rufipennis ottowi* (46.5 g) is a permanent resident and an endemic subspecies. They forage alone or in groups in rocky grasslands and nests in crevices. *S. loyca obscura* (113 g) is a permanent resident and an endemic subspecies, foraging in pairs or small flocks in high altitude rocky grasslands, and nesting in high grasslands. *V. chilensis* (327 g) is a permanent resident that forages in flocks of 3–5 individuals and nests in short grasslands.

2.2. Direct and tangential approaches

We gathered data at the end of the breeding season (January to April). We worked between 0900 and 1900, but not when it was hot in the middle of the day, or when it was raining. We chose areas with little pedestrian traffic (and little use by tourists) so as to not study habituated subjects (e.g., Ikuta and Blumstein, 2003).

After locating animals with binoculars, we began an approach only if the subject did not show any kind of alert behavior towards us. We measured alert distance (AD) following Fernández-Juricic and Schroeder (2003), which we defined as the distance between the observer and the bird at the point where the bird modified its initial behavior in response to the approaching human (namely, by raising its head up from the ground). We measured flight initiation distance (FID), which we defined as the point at which the subject flushed or otherwise moved away from the approaching human. We also measured perpendicular distance (the shortest distance between the bird and the observer's trajectory), which varied from 0 m (direct approaches) to 30 m (tangential approaches, Fig. 1).

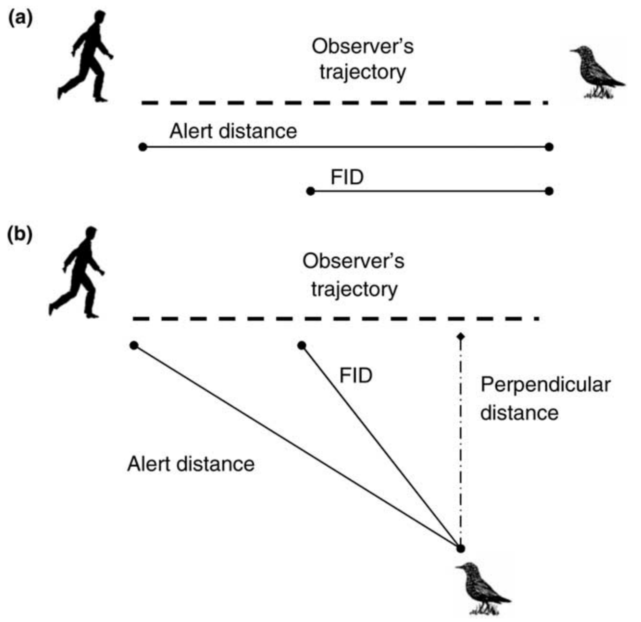

Fig. 1. Schematic representation of (a) direct and (b) tangential approaches. Alert distance is the distance at which animals showed alert behaviors towards the observer's approach; flight initiation distance (FID) is the distance at which the animals flew away from the observer.

A single observer (PV) approached animals with a steady pace (1 step/s – ca. 0.45 m/s) and a linear trajectory, in areas without shrubs or trees visually blocking the pathway between the animals and her, and dropped markers to later measure with a meter tape (±0.05 m) the response variables. Subjects were not marked, but we sampled a different area each sampling day, and we never collected two observations from the same species from contiguous areas.

When flocks were approached, we focused on a single individual chosen before the approach, and recorded the total number of conspecifics in a 10-m radius circular plot. Once the focal bird had fled, we measured some confounding variables that could have affected the variability in FID in 25-m circular plots centered on the focal bird's original position: graminoid grass cover (%), tussock grass cover (%), rock cover (%), shrub cover (%), temperature, and perching height if the bird was perching on a rock or in a shrub. Cover variables were visually estimated following Cingolani et al. (2003). We did not measure grass height because grasses in our study area consisted mostly of very homogeneous graminoid grasses (5–9 cm tall) with few tussock grasses (40–60 cm tall).

2.3. Minimum approaching distances and buffer areas

We used five methods to estimate minimum approaching distances (MAD) and buffer areas for each species and for each type of approach. One method (M1) uses the same formula but two different parameters (AD and FID) for estimation. We describe each method and summarize their assumptions.

Method 1 (M1), based on Stalmaster and Newman (1978), McGarigal et al. (1991), Anthony et al. (1995), Swarthout and Steidl (2001). We plotted the cumulative percentage of individuals fleeing against AD and FID to determine the point at which 95% of the individuals became alert ($M1_{AD}$) and flushed ($M1_{FID}$), which can be considered estimates of MAD. By taking minimum approaching distances as the radius of a circle, buffer areas for individual species are calculated as $\pi * MAD_{AD}^2$ ($M1_{alert}$), and $\pi * MAD_{FID}^2$ ($M1_{FID}$).

Method 2 (M2), based on Fox and Madsen (1997): $MAD = 3\overline{FID}$, where $\overline{FID}$ is the mean FID. Buffer areas are calculated as $\pi * (1.5\overline{FID})^2$.

Method 3 (M3), based on Rodgers and Smith (1995, 1997), Rodgers and Schwikert (2002). $MAD = (\overline{FID} + 1.6495SD) + \overline{AD}$, where $\overline{FID}$ is the mean FID, SD is the standard deviation of $\overline{FID}$, and $\overline{AD}$ is the mean AD. Buffer areas are calculated as $\pi * MAD^2$.

Method 4 (M4), based on Fernández-Juricic et al. (2001). $MAD = \overline{AD}$, where $\overline{AD}$ is the mean AD. MAD is taken as the radius of a circle, so that buffer areas can be estimated as $\pi * MAD^2$.

Method 5 (M5), based on Vos et al. (1985). Minimum approaching distances correspond to the maximum FID recorded + $\overline{AD}$, where $\overline{AD}$ is the mean AD. Buffer areas are estimated as $\pi * MAD^2$.

Only Fox and Madsen (1997) reported the assumptions of their method to calculate buffer areas. We summarize assumptions for each method in Table 1. Three assumptions are shared among methods: (a) the probabilities of fleeing/becoming alert from disturbance are equal in all directions at any given moment, (b) habitat quality is homogeneous throughout the system, and (c) an individual's use of the buffer area is constant and equal to the carrying capacity of the system. All methods estimate buffer areas as having a circular shape. All methods yield estimates of minimum approaching distances and buffer areas without measures of variability (SE or SD).

2.4. Statistical analyses

We first assessed the effects of the confounding factors (number of conspecifics, temperature, graminoid grass cover, tussock grass cover, rock cover, and shrub cover) on FID with a multiple regression. When a factor was significant, we included that factor in the final model assessing the effects of type of approach.

We studied the effects of type of approach on FID, after accounting for the effects of covariates, with general linear models. Considerable variation in FID is typically explained by the distance at which observers begin their experimental approach (Blumstein, 2003), which is

Table 1
Assumptions of methods to estimate minimum approaching distances and buffer areas based on the explanations provided in the papers, the parameters involved in the estimation of minimum approaching distances and buffer areas, and mathematical properties of the formulas

	M1	M2	M3	M4	M5
Probabilities of detecting disturbance are equal in all directions at any given moment	X		X	X	X
Probabilities of fleeing from disturbance are equal in all directions at any given moment	X	X	X		X
FID/AD does not vary with time	X	X	X	X	X
Habitat quality is homogeneous throughout the system	X	X	X	X	X
Bird use of the buffer area is constant and equal to the carrying capacity of the system	X	X	X	X	X
Type of approach does not influence the probabilities of detecting disturbance	X		X	X	X
Type of approach does not influence the probabilities of fleeing from disturbance	X	X	X		X
Variability in AD does not affect estimates of MAD			X	X	X
Variability in FID does not affect estimates of MAD		X			X
AD is a more conservative indicator of tolerance than FID, because it includes an area (the difference between AD and FID) in which birds may adapt their reaction to the behavior of visitors	X		X	X	X
Animals are not negatively affected by disturbance after its detection; they are only affected after they flee from the patch		X			

X = method contains the assumption. See text for details.

highly correlated with alert distance (Blumstein et al., in press). Therefore, we included alert distance as a covariate in all models (see also Fernández-Juricic et al., 2001; Fernández-Juricic and Schroeder, 2003). A second covariate that we included was height above ground, because perching height may influence the decision for some species to flee from humans (Fernández-Juricic et al., 2004a; Blumstein et al., 2004).

General linear models were forced through the origin because if a bird first became alert at distance of 0 m, it must have a FID of nothing greater than 0 m. However, when forced through the origin, the main effect of these models cannot be easily interpreted (Geist et al., in press), so we focused on the interactions between alert distance and type of approach, and between alert distance and other confounding factors. In this case, a significant variable would change the slope of the relationship between alert distance and FID, and these variations will be illustrated in our figures.

Sample size per species and type of approach varied from 15 to 22. Since our design was not balanced, we ran our GLMs with an over-parameterized models, which are robust to unbalanced designs as well as designs with missing cells (Searle, 1987; Searle et al., 1992). All variables were checked for normality and homogeneity of variance.

We calculated minimum approaching distances and buffer areas based on the aforementioned formulas and evaluated quantitatively two attributes of Methods 1–5. First, we analyzed their sensitivity to differences between tangential and direct approaches. Specifically, we wished to know if higher FID with one type of approach would result in larger minimum approach distances and buffer areas compared to the other type of approach. Second, we assessed how conservative methods were when we estimated the minimum approach distances and buffer areas. For this, we followed the precautionary principle and assumed that larger estimates will increase the area available for these species to forage, breed and roost and reduce the degree of human disturbance. Thus, we calculated for each method a performance index, which we defined as: [(ranking of the estimate across all species and types of approach) + (number of times the method correctly estimated the direction of the difference between tangential and direct approaches based on FID)*12]/120. The rank estimates indicate the degree of conservatism in the estimation of distances and areas, such that higher ranks in the estimation suggest more conservative methods. For a given method, there were five species and two types of approaches (10 different estimates), and each rank for each combination of species and method could vary from 1 (lowest estimate) to 6 (highest estimate). Thus, rank estimates could vary from 10 (if a method produced the lowest estimates in the five species and both approach types) to 60 (if a method produced the highest estimates in the five species and both approach types). The second part of the formula (number of times the method correctly estimated the direction of the difference between tangential and direct approaches based on FID) could vary from 0 to 5, so that a particular method could classify correctly the direction of the difference between approach types in 0 species or in the 5 species studied, respectively. So, to make this part of the formula proportional to the first part, we multiplied it by 12, so that the values would vary between 0 and 60. Finally, we divided the two parts of the formula by 120, which is the highest combination of values possible for a given method, to rescale the index between 0 and 1. Higher values of the performance index indicate more sensitivity and conservatism.

3. Results

3.1. Species-specific responses to human approaches

We conducted a total of 103 direct approaches and 84 tangential approaches to the five studied species. We present results for each species.

3.1.1. P. unicolor cyaneus

None of the confounding factors (vegetation cover, number of conspecifics, and temperature) affected FID (model including all factors, $F_{6,35} = 1.34$, $P = 0.263$, $R^2 = 0.18$). The type of approach in relation to alert distance affected FID (interaction, $F_{1,36} = 207.42$, $P < 0.001$): at the same alert distance, individuals approached tangentially moved away from the observer sooner compared to those approached directly (Fig. 2(a)). Controlling for alert distance, perching height also affected FID significantly (interaction, $F_{1,36} = 96.03$, $P < 0.001$): individuals perching on higher rocks had smaller FIDs. The final model explained 75.6% of the variability in FID.

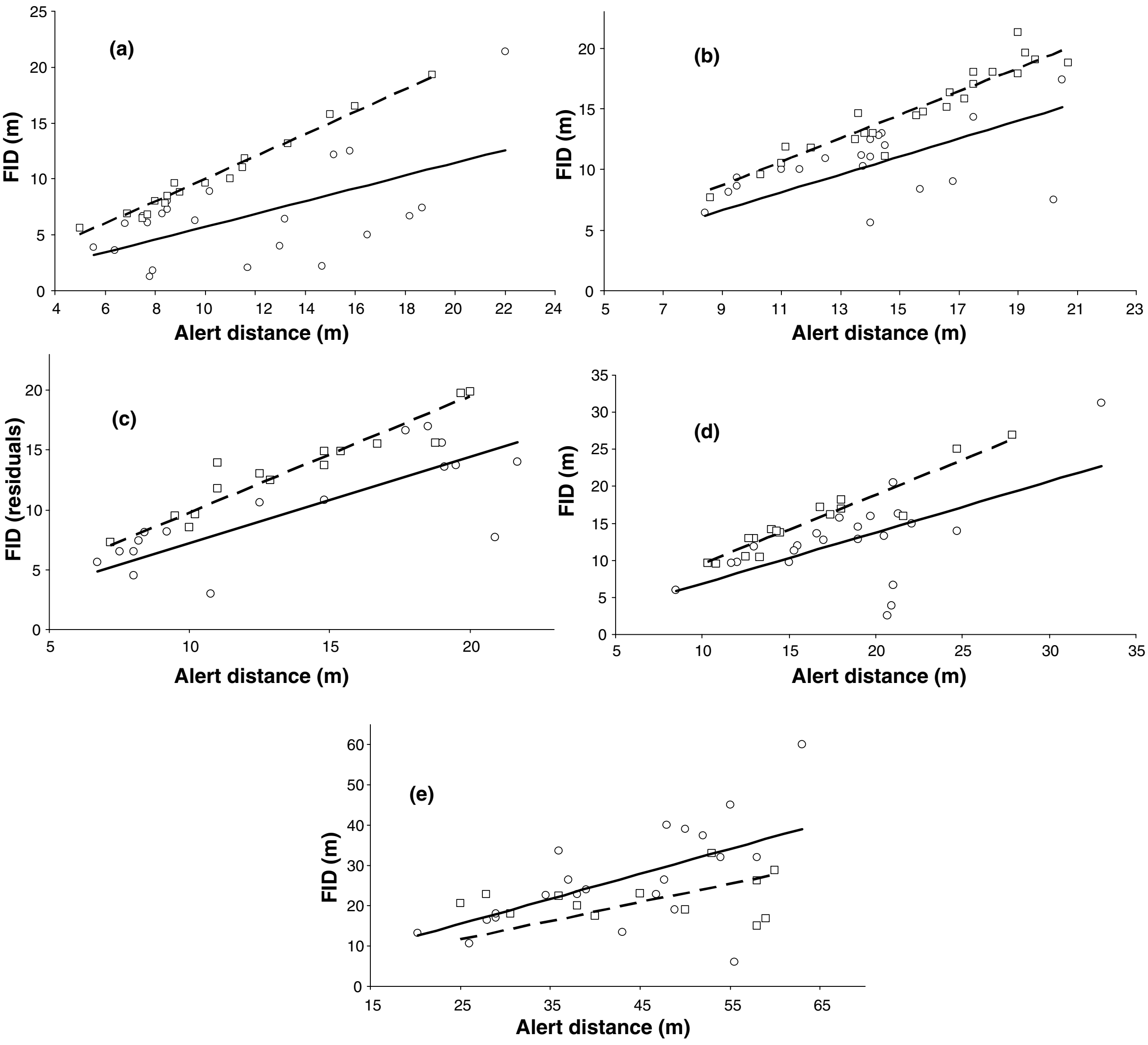

Fig. 2. Effects of approach type (direct, continuous line; tangential, dotted line) on flight initiation distance of five high latitude grassland birds ((a) *Phrygilus unicolor cyaneus*; (b) *Cinclodes comechingonus*; (c) *Geosita rufipennis ottowi*; (d) *Sturnella loyca obscura*; (e) *Vanellus chilensis*), controlling for alert distance.

3.1.2. *C. comechingonus*

Neither vegetation cover, number of conspecifics, nor temperature affected FID (model including all factors, $F_{6,42} = 0.29$, $P = 0.939$, $R^2 = 0.04$). However, FID differed depending on the type of approach in relation to alert distance (interaction, $F_{1,40} = 34.38$, $P < 0.001$): individuals increased FID with tangential approaches (Fig. 2(b)). FID was not affected by perching height, controlling for the variation in alert distance (interaction, $F_{1,40} = 3.68$, $P = 0.062$). The model explained 75.3% of the variability in FID.

3.1.3. *G. rufipennis ottowi*

Graminoid grass cover positively affected FID ($F_{1,36} = 4.90$, $P = 0.033$, $R^2 = 0.12$), but the other factors were not selected by the model. We then included this significant confounding factor in the final model. FID varied with the type of approach, controlling for alert distance (interaction, $F_{1,\ 28} = 23.82$, $P < 0.001$): FID was greater with tangential approaches (Fig. 2(c)). After controlling for the effects of alert distance, perching height did not influence FID (interaction, $F_{1,28} = 1.69$, $P = 0.205$), but graminoid grass cover did (interaction, $F_{1,\ 28} = 5.12$, $P = 0.032$). This model accounted for 76.6% of the variability in FID.

3.1.4. *S. loyca obscura*

Neither vegetation cover, number of conspecifics, nor temperature influenced FID (model including all factors, $F_{6,44} = 0.44$, $P = 0.849$, $R^2 = 0.05$). FID differed depending on the type of approach in relation to alert distance (interaction, $F_{1,35} = 16.70$, $P < 0.001$);

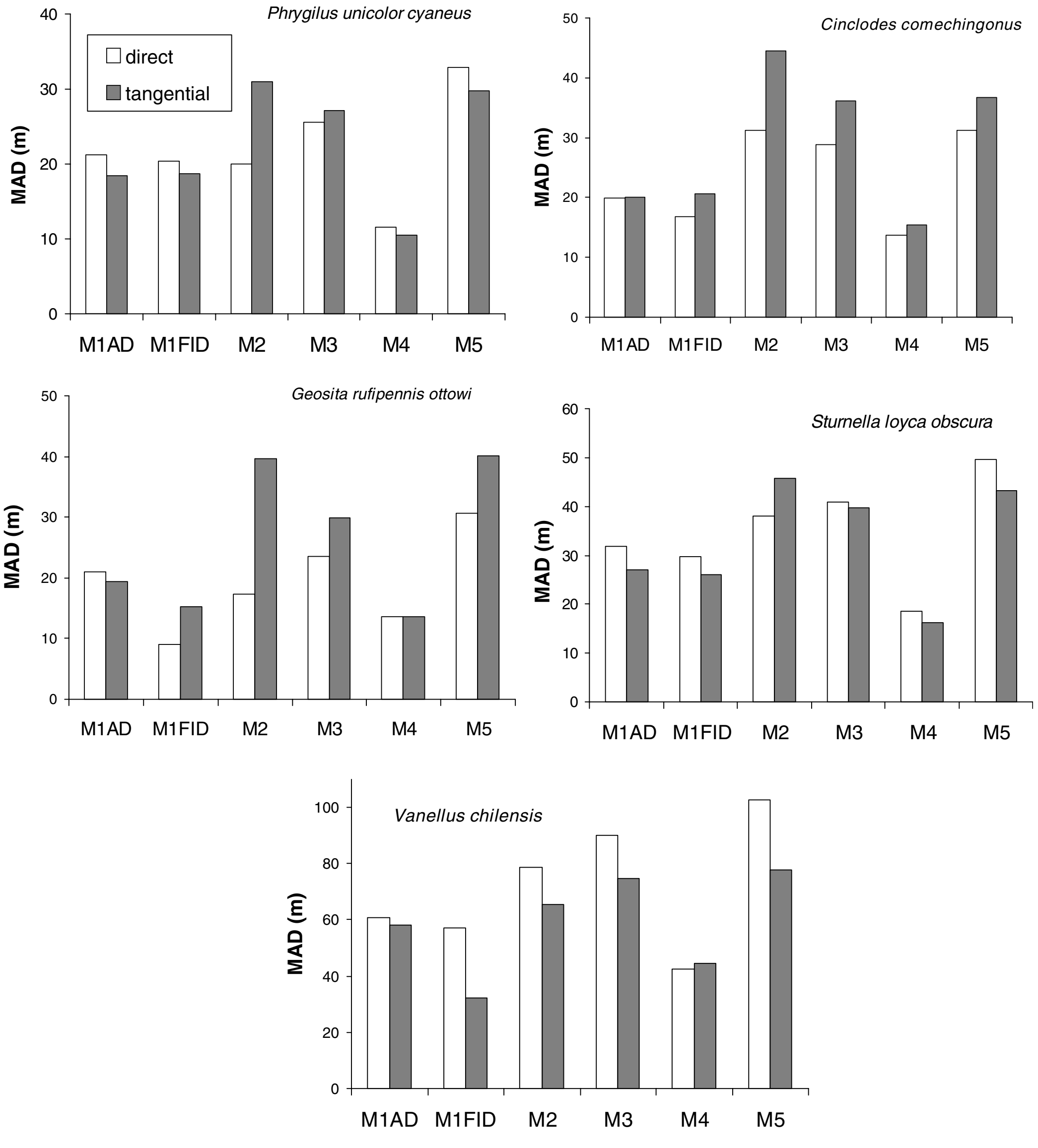

Fig. 3. A comparison of five methods to estimate minimum approaching distance (MAD). For each species, the MAD was estimated based on data collected from direct and tangential approaches.

specifically, at the same alert distance, individuals approached tangentially moved away from the observer sooner compared to those approached directly (Fig. 2(d)). Perching height, after controlling for alert distance, affected significantly FID (interaction, $F_{1,35} = 5.47$, $P = 0.025$): individuals perching on higher rocks showed lower FID. The final model explained 62.7% of the variability in FID.

3.1.5. *V. chilensis*

Neither vegetation cover, number of conspecifics, nor temperature affected FID (model including all factors, $F_{6,30} = 1.24$, $P = 0.312$, $R^2 = 0.19$). FID varied with the type of approach, but in this species, at the same alert distance, individuals approached directly moved away from the observer sooner compared to those approached tangentially (interaction, $F_{1,\ 32} = 4.97$, $P = 0.033$, Fig. 2(e)). Perching height, controlling for alert distance, did not influence FID (interaction, $F_{1,32} = 1.48$, $P = 0.231$). The model accounted for 45.8% of the variability in FID.

3.2. Estimation of minimum approaching distances and buffer areas

The methods studied produced remarkably different estimates of minimum approaching distances and buffer areas (Figs. 3 and 4).

Only Method 2 maintained the direction of the difference in FID between tangential and direct approaches for both minimum approaching distances and buffer areas in all five species. The least sensitive methods to the difference between tangential and direct approaches in FID were $M1_{AD}$, $M1_{FID}$, and M4, because they only

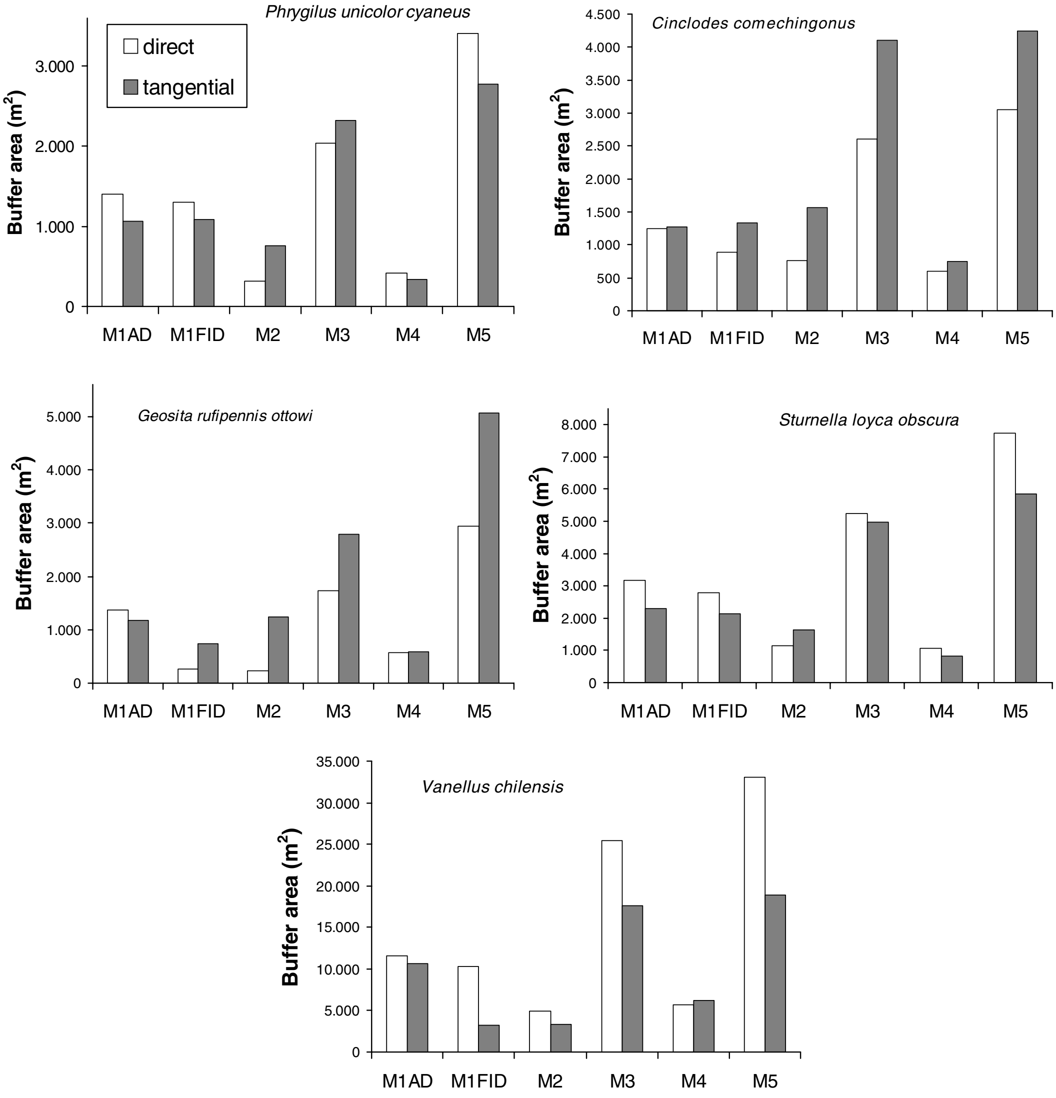

Fig. 4. A comparison of five methods to estimate buffer areas. For each species, the buffer area was estimated based on data collected from direct and tangential approaches.

maintained the same direction of the variation between tangential and direct approaches in only two of the species.

Method 4 was the least conservative method to estimate minimum approach distance, because it estimated the smallest distances 8 out of 10 times; whereas Method 5 was the most conservative, because it estimated the largest distances 6 out of 10 times. Similar results were found for buffer areas: Method 4 was the least conservative method (smallest buffer areas 6 out of 10 times), and Method 5 was the most conservative (with largest buffer area estimates for all the species and for both types of approaches).

For minimum approaching distances, we estimated the following index values to show overall performance: Method 2 = 0.88, Method 3 = 0.78, Method 5 = 0.77, Method $1_{\mathrm{AD}} = 0.45$, Method $1_{\mathrm{FID}} = 0.36$, Method 4 = 0.30. For buffer areas, index values were estimated as: Method 3 = 0.82, Method 5 = 0.80, Method 2 = 0.68, Method $1_{\mathrm{AD}} = 0.50$, Method $1_{\mathrm{FID}} = 0.43$, Method 4 = 0.33. Therefore, Methods 2 and 3 were the most sensitive and conservative methods for the estimation of minimum approaching distances and buffer areas, respectively.

4. Discussion

Our results may not be generalizable to other habitat types, but we conclude that: (a) the open high latitude grassland birds studied are sensitive to tangential and direct approaches, although responses are species-specific, (b) four out of the five species showed greater FID to tangential rather than direct approaches, (c) vegetation structure does not appear to play a major role in affecting FID in this type of habitat, (d) for two of the five species, perching height seems to be involved in the process of deciding when to flee, (e) minimum approaching distance and buffer area estimates for these species varied considerably between methods, and (f) some methods showed greater sensitivity to approach types and produced more conservative estimates.

All studied species reacted to the type of human approach. One species, *V. chilensis*, showed greater FID when approached directly, which suggests that the magnitude of the risk increases when humans walk towards them, as has been found before in other bird species (Burger and Gochfeld, 1981). However, our novel result is that the other four species (*P. unicolor cyaneus*, *C. comechingonus*, *G. rufipennis ottowi*, and *S. loyca obscura*) increased their FID with tangential approaches, which is the exact opposite of a common assumption in human disturbance studies; namely, that wildlife are more sensitive to direct approaches. A similar result was previously reported for two lizard species (Bulova, 1994).

This increase in FID with tangential approaches could be affected by detection probabilities (Bulova, 1994). In tangential approaches, the rate of approach is slower than in direct approaches. A bird may need more time detecting a threat that is moving at a slower rate than one that is moving at a higher rate of approach, particularly if the bird's attention is not towards the threat while it approaches (Dukas and Kamil, 2000, 2001). A recent study (Cooper et al., 2003) supports this explanation: whiptail lizards *Cnemidophorus murinus* fled later when approached tangentially and rapidly, but sooner when approached tangentially and slowly, which might have increased the chances of detection. Reduced detectability could also be affected by species-specific differences in visual fields: some bird species have more difficulty detecting approaching threats than others because the extent of their peripheral vision is more limited (Fernández-Juricic et al., 2004b). Alternatively, if birds are flushing soon after detecting a threat to avoid the higher costs of later flight, then we would expect that a tangential approach represents an even lower risk situation because individuals may assume that the predator has not detected them. In this case, the costs of flushing sooner in response to tangential approaches may be lower than those associated with a direct approach because it is less likely that a predator has focused on the prey if it is approaching it tangentially.

The open high latitude grassland species studied are not greatly affected by potentially confounding variables, such as vegetation structure, number of conspecifics, and temperature, probably because of the low variability in these confounding factors. Only one species (*G. rufipennis ottowi*) delayed its responses when the percentage of graminoid grass cover increased; probably because a higher amount of food availability increased the benefits of staying longer in these areas. Furthermore, perching height, a relevant factor affecting the fleeing decision process in some forest birds (Blumstein et al., 2004; Fernández-Juricic et al., 2004a), only influenced two of the species studied here (*P. unicolor cyaneus* and *S. loyca obscura*). Both species delayed flushing when perched higher, which could be explained by a reduction in risk and the greater chances of a successful escape due to higher visibility (Blumstein et al., 2004; Fernández-Juricic et al., 2004a). The fact that relatively few measured factors affected FID makes open grassland birds good models to study further the sensitivity of wildlife to spatial patterns of recreationist movement in protected areas, which in other systems (namely, riparian and forested habitats) could be highly biased by vegetation structure.

4.1. Conservation implications

The reduced tolerance of some species to tangential approaches has implications for the estimation of buffer areas that are designed to increase the presence or abundance of species of conservation interest, such as the endemic birds studied here. However, the following management recommendations can only be applied to the studied species, because the magnitude of the difference between tangential and direct approaches may be low compared to other species. It is not highly likely that these species were affected by habituation because of the relatively low levels of human visitation to this protected area. However, in Pampa de Achala, the network of pathways is not clearly established, which makes visitors wander around without spatial restrictions. It is possible that by establishing and enforcing the use of pathways, birds will habituate to predictable patterns of human movement (e.g., Miller et al., 2001; Taylor and Knight, 2003). However, this may be difficult to achieve in developing countries with reduced budgets for natural area management. Under these conditions, we believe that concentrating the spatial extent of the visit, rather than designing a complex network of pathways, will reduce the effects of disturbance. Setting small areas for tourist use may reduce the attractiveness of a protected area, but this could be minimized by wildlife viewing areas close to artificially created foraging patches, or by establishing viewing areas delimited by fences which have been shown to reduce disturbance on birds (Ikuta and Blumstein, 2003).

Buffer areas provide spatial estimates of the requirements of species based on different empirically derived indicators of tolerance (e.g., AD, FID). Although we identified a robust method for the estimation of buffer areas in this system (Method 3), its applicability, as well as that of the other methods, is somewhat limited. The assumptions of all methods are difficult to meet, and rarely tested. Some examples follow.

(a) Buffer areas based on only FID do not control for the effects of detection distances (or its proxy, alert distance). This may underestimate the effects of disturbance. For instance, some methods estimated greater buffer areas for direct approaches despite the fact that FID was greater for tangential approaches.
(b) The probabilities of detecting disturbance and fleeing from disturbance are equal in all directions at any given moment; that is, all disturbances within the range of a buffer area are detected. This may not be the case giving the shape of the visual fields of different bird species, where higher detection probabilities occur at the periphery of the individual field of view (Fernández-Juricic et al., 2004b). This may affect the chances of detection and later escape (Olden et al., 2004).
(c) Many methods take into consideration the variability in FID, but not that in AD. This may underestimate the size of areas that need spatial protection.
(d) Buffer areas assume that tolerance indicators do not change in time. Some studies have shown that FID varies with the time of the year (e.g., Fox and Madsen, 1997; Rodgers and Smith, 1997). This is not a problem in cases where buffer areas are established to protect animals during a focused breeding season (e.g., Lafferty, 2001), but might be a problem if the goal is to reduce human disturbance throughout the year.
(e) Buffer areas are sometimes used as an index for a buffer zone around a single bird at a single point. This index may be useful for solitary nesting birds dispersed over a large area where the perimeters of the buffer areas do not overlap (a condition that may apply to a few of our studied species). But, when the perimeters of the buffer areas overlap (namely, birds moving between resource patches, birds foraging in groups, etc.), minimum approaching distances may be more useful management tools because they could be used to outline a boundary around irregular foraging or breeding resources used by many individuals simultaneously.
(f) Some methods to estimate minimum approaching distances and buffer areas are based on the mean value of AD or FID instead of calculating the upper percentile estimate of these parameters, which can lead to biases when the data are not normally distributed.

Overall, we consider that the estimation of distances or areas to reduce human disturbance may be a useful tool for conservation under some circumstances, but its estimation based only on flight initiation distance or alert distance may be too simplistic. Before calculating a buffer area, managers must evaluate the assumptions and applicability of a given method. If assumptions are met, then some methods may provide reliable estimates. If assumptions are not met, estimating and applying buffer areas may under or overestimate the access to protected areas, which could enhance human disturbance or curtail tourism. More realistic methods to estimate buffer areas to be applied to the population level remain to be developed.

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