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Do variations in scanning behavior affect tolerance to human disturbance?

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Abstract

Tolerance to human disturbance can be estimated as the distance at which animals become noticeably alert to humans. Although this alert distance has been studied before, no consideration has been devoted to the relationship between vigilance behavior and the probabilities of detecting pedestrians. Our goal was to test whether and how differences in scanning behavior of two model species (spot-winged pigeon and eared dove) would affect the predicted and observed probabilities of detection of pedestrian approaches in two conditions: individuals foraging alone and in flocks. Overall, we found differences between species and between foraging conditions, but no interaction effects. Spot-winged pigeons and individuals foraging alone spent more time scanning, with longer scanning bout duration, than eared doves and individuals foraging in groups, respectively. Spot-winged pigeons showed greater alert distances (observed detection probabilities) than eared doves, and so did solitary individuals as compared to individuals foraging in groups. Greater scanning time may have increased predicted and observed detection probabilities of spot-winged pigeons. Expected probabilities of detection of pedestrian approaches were higher for group than for solitary foraging conditions, contrary to observed alert distances, probably due to a lack of collective detection in flocks. Our results suggest that vigilance behavior can affect the distance at which birds detect human disturbance and the estimation of tolerance. This behavioral effect could have implications in management scenarios (e.g. determining buffer areas), as similar levels of human visitation to protected areas may exert different effects according to the probabilities of detecting visitors within the detection windows of different species.

Keywords: Birds; Buffer areas; Social foraging; Tourism; Vigilance; Wildlife

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1. Introduction

Conservation biologists and wildlife managers have successfully used predation theory (Ydenberg and Dill, 1986; Lima, 1998) to study the effects of human disturbance on wildlife (e.g. Gill et al., 1996; Fox and Madsen, 1997; Fernández-Juricic and Tellería, 2000). The risk-disturbance hypothesis (Frid and Dill, 2002) synthesizes this behavioral approach to understand and predict the responses of individuals and populations to disturbance on the grounds that wildlife react to humans as if they were potential predators (Knight and Temple, 1995; Whittaker and Knight, 1998). Thus, animals trade off the avoidance of disturbance by humans against activities that may increase fitness, such as foraging, mating, and parental care (Frid and Dill, 2002). Although this behavioral approach may have some limitations when predicting long-term population trends (Gill et al., 2001), it has proved quite useful in assessing the local impacts of different outdoor recreational activities, and the management strategies that may promote coexistence between ecotourism and wildlife in areas of conservation interest (see reviews in Knight and Gutzwiller, 1995).

Many studies underscore the importance of understanding how animals perceive and tolerate humans (e.g. Whittaker and Knight, 1998; Ikuta and Blumstein, in press). Although predator detection has been assessed from different perspectives (Lima, 2002), little empirical consideration has been devoted to how animals monitor and detect tourists. This requires behavioral analyses that can be incorporated into broader conceptual frameworks (e.g. risk-disturbance hypothesis, Frid and Dill, 2002) to better predict wildlife responses to humans under different circumstances.

Flight distance (the distance between animals and people where animals take flight from a foraging or breeding patch in response to that disturbance) has often been employed as an indicator of bird tolerance to visitors (Rodgers and Smith, 1995; Fernández-Juricic et al., 2001a; Blumstein et al., in press), and as the underlying basis to implement buffer zones (areas without disturbance) within protected areas (van der Meer, 1985; Anthony et al., 1995; Fox and Madsen, 1997; Swarthout and Steidl, 2001). Recently, alert distance (the distance between animals and people where animals first become noticeably alert to the disturbance, Ward et al., 1994; Vos et al., 1985; Grubb et al., 1992) has been used as a better parameter to estimate buffer zones because it includes a portion (the difference between alert and flight distance) in which birds may adapt their reaction to the behavior of visitors (Rodgers and Smith, 1995; Camp et al., 1997; Fernández-Juricic et al., 2001b, 2002). After detecting a tourist and before fleeing from a patch, animals may also be negatively affected because they increase the proportion of time spent monitoring pedestrians and reduce foraging activity as a result (Fernández-Juricic and Tellería, 2000).

Alert distances have been studied without regard as to how animals monitor humans, implicitly assuming that individuals have similar patterns of vigilance behavior in different environmental and social conditions (e.g. Fernández-Juricic et al., 2001b). However, variations in vigilance behavior may over- or under-estimate the observed variation in tolerance. For instance, it can be expected that individuals that spent a greater proportion of their foraging time scanning would detect humans sooner, and as a result exhibit greater alert distances, than individuals with a lower proportion of time spent in vigilance. Similarly, individuals with inter-scan intervals (e.g. feeding bouts) longer than the duration of the approaching disturbance (e.g. pedestrians) may have lower probabilities of detection (Hart and Lendrem, 1984; Pöysä, 1987), and consequently shorter alert distances. These effects could be intensified if individuals forage in groups: pedestrians may be detected earlier due to collective vigilance, which increases detection probabilities (Knight and Cole, 1995), thereby increasing alert distances (Fernández-Juricic et al., 2001b). Such behavioral effects are worth considering since they may affect the areas in which animals detect and are affected by tourists and the calculation and later implementation of buffer zones.

Our goal was to assess how variations in the vigilance behavior of two bird species would affect the predicted and observed probabilities of detection of pedestrian approaches in two conditions: individuals foraging alone and in flocks. First, we characterized scanning behavior (scanning rate, proportion of time spent scanning, and scanning bout length) in each species and foraging condition. Second, we analyzed scanning patterns (distribution of inter-scan intervals) and calculated the predicted probabilities of pedestrian detection (following Hart and Lendrem, 1984). Third, we assessed the effects of species and foraging conditions on the observed probabilities of pedestrian detection by means of alert distances. We also evaluated differences in flight distances to better understand the relationship between different indicators of tolerance to humans.

2. Methods

2.1. Study approach, site and species

We conducted all our measurements in one large wooded park (Sarmiento park), located in the city of Cordoba, Argentina. The area comprised 50 ha of high deciduous and coniferous tree cover (mainly *Platanus acertifolia*, *Eucaliptus* sp., *Pinus* sp., *Cupressus* sp., and *Chorisia* sp.). Shrubs were scarce and scattered, whereas grass was maintained short through frequent mowing. This habitat structure allowed us to reduce the bias due to obstruction effects when the observer approached focal individuals (see below). Visitors to this natural recreational area moved through several pathways and sometimes through areas without pathways, which often caused disruption of foraging individuals. Pedestrian traffic was high during weekends, but low during weekdays. Urban parks are good natural laboratories to study human–wildlife interactions because ecological processes in urbanized areas are similar to those in other natural habitats (reviewed in Fernández-Juricic and Jokimäki, 2001).

We used two model species: spot-winged pigeons (*Columba maculosa*) and eared doves (*Zenaida auriculata*). We chose species within the same family (Columbidae) to diminish possible confounding phylogenetic variation in (a) motor patterns (e.g. moving, scanning, etc.) that may increase the difficulty of estimating alert distances, and (b) visual systems that may affect scanning behavior (Guillemain et al., 2002). Several other avian species inhabit the Sarmiento park; however, we did not use species of conservation interest (e.g. threatened) due to ethical reasons. We acknowledged that our goal is not to generalize how scanning behavior may affect alert distance in different species, but to assess whether the behavioral process of detecting human disturbance follows the predictions of theoretical models of predation. Therefore, this is not a study of population differences in tolerance, as done before (e.g. Fernández-Juricic et al., 2001a; Ikuta and Blumstein, in press), but a behavioral analysis that has implications for conceptual frameworks of the effects of human disturbance on wildlife (e.g. Whittaker and Knight, 1998; Frid and Dill, 2002).

Spot-winged pigeons and eared doves are generalists and usually find plenty of food in this park; therefore, food availability was not considered a limiting factor. However, these species are not tolerant of humans, like rock doves (*Columba livia*), and flee from them if approached. Spot-winged pigeons (308.5 g) have greater body mass than eared doves (130.9 g) (Salvador, 1988; Haro, personal communication). Spot-winged pigeons have bluish grey coloration with white triangular spots on the tips of wing feathers, giving them the "spotted" effect; whereas eared doves have a duller olive brown coloration with black markings on wings (del Hoyo et al., 1997). Such differences in coloration made spot-winged pigeons more conspicuous in the habitat in which the study was conducted (Nores and Torres, personal communication). Several known predators of both species were also detected in the Sarmiento park, mainly cats, dogs, Chimango caracara (*Milvago chimango*), and Crested caracara (*Polyborus plancus*).

We concentrated our sampling from September to December 2001 to reduce temporal variations in scanning behavior due to differences in predation risk (Suhonen, 1993), on weekdays (between 06:00 and 10:30 a.m.), and when no pedestrian was present in a radius of at least 100 m of the focal individual. We totaled 154 observation hours, on sunny or cloudy days, but never when raining or in windy conditions. To reduce inter-observer variability, one author (NS, hereafter "the observer") gathered all the data after 1 month of training. Training was conducted in a protected area 30 km away form the Sarmiento park to avoid conditioning birds. The Sarmiento park was visited three times per week, with 1 day interval between visits.

2.2. Scanning and tolerance behavior

We first studied the scanning behavior of both species in two foraging conditions: individuals foraging alone and in flocks. The study was not designed to analyze the continuous variation in scanning behavior in relation to flock size; therefore, we lumped data from individuals in differently sized flocks into the group foraging category. Nevertheless, we assessed how the variability in flock size affected the response variables.

We divided the study area in quadrants and randomly selected the patches to be sampled during each day. After sampling a focal individual in a specific sector, we moved to another quadrant (with at least two quadrants in-between) in order to avoid sampling the same individuals. Upon encountering a flock in the selected patch, the observer chose the focal individual at random before starting the behavioral observations. Sampling was done from fixed observation points that were out of sight of focal individuals. If a focal bird detected the observer, the quadrant was temporarily abandoned. Although double sampling might have occurred during the study, we considered it infrequent due to our sampling scheme. Samples lasted 2–3 min in order to have a snapshot of the scanning and foraging behavior under fixed social conditions (see also Fernández-Juricic and Tellería, 2000), as different individuals joined and left the flock frequently. We gathered 30 samples per species (2 levels) and foraging condition (2 levels), totaling 120 samples. Feeding and scanning were treated as mutually exclusive activities (Desportes et al., 1991). We recorded the number and duration of foraging and scanning events, and calculated scanning rate (number of head-up's per min), proportion of time spent scanning, duration of scanning bout(s), and number and duration(s) of inter-scan intervals (feeding bouts). Although some of these variables are inter-dependent, we conducted statistical analyses on all of them in order to achieve quantitative measurements of the effects of species and foraging conditions along several scanning dimensions, which would help interpret the results. All measurements were tape-recorded and later analyzed with the event-recording program Jwatcher 0.9 (Blumstein et al., 2000).

After characterizing scanning behavior, we took another series of measurements to estimate alert and flight distances of both species in two conditions: individuals foraging alone and in flocks. We began approaching the birds at 100 m with a steady pace (1 step per second). The approach was linear and continuous with no obstacles preventing the observer and bird from seeing each other. A marker was dropped when the focal individual became alert (see below) and when it flushed. Afterwards, the observer measured alert and flight distances with a meter tape (±0.05 m). We took 30 samples (120 in total) in each of the four conditions from randomly selected quadrants. Similar sample sizes have been used before to assess tolerance to human disturbance (Fernández-Juricic et al., 2001b, 2002). The observer never collected two observations from the same species consecutively or from contiguous quadrants to avoid autocorrelation of data. When approaching a flock, the observer focused on a single individual within the group chosen randomly before the approach, and recorded the number of conspecifics. Similar clothing was used to circumvent differential reaction (Gutzwiller and Marcum, 1997).

Alert distances are usually measured as the distance at which birds start showing alert behaviors towards pedestrians (lifting and moving the head as if scanning, Grubb et al., 1992; Swarthout and Steidl, 2001; Fernández-Juricic et al., 2001b). However, such estimates might be affected by the pattern of random scanning in birds (Bednekoff and Lima, 1998), since there exists the possibility that the usual vigilance behavior to spot for potential predators can be given to an approaching observer, particularly if the observer is not within detection distance. Therefore, we performed a study to confirm whether previously published procedures to estimate alert distance were good indicators of pedestrian detection. We measured scanning rate and scanning bout duration in two conditions: with and without human presence within 10 m. We found that the best indicator of pedestrian monitoring was an increase in scanning bout duration in both species. Taking into account 95% confidence intervals, we determined threshold values that would suggest that these species were monitoring pedestrians (controlling for flock size) when the duration of scans were longer than 5.1 s for spot-winged pigeons and 3 s for eared doves. We then performed another series of measurements of alert distances with the two methods on the same individuals: first distance at which individuals exhibit alert behaviors (method *a*), and distance at which scanning bout duration reached the estimated thresholds (method *b*). Estimations of alert distance did not differ significantly between both procedures (*t*-test for dependent samples; spot-winged pigeons, method $a = 43.4 \pm 9.9$, method $b = 40.2 \pm 8.7$, $t_9 = 1.38$, $P = 0.201$; eared doves, method $a = 18.9 \pm 5.6$, method $b = 21.4 \pm 13.7$, $t_9 = 1.69$, $P = 0.124$). We then decided to measure alert distances with the procedure employed in previous studies (method *a*) because it was easier to carry out in field conditions. We assumed that the behaviors denoting detection of a disturbance were the same in solitary and flock foraging conditions, as found elsewhere (e.g. Powell, 1974).

We considered covariates that might have an effect on scanning behavior and the responses to pedestrian approaches. After recording scanning and tolerance behaviors, the observer immediately recorded temperature, tree cover (%), mean tree height (*m*), and number of stems $<$10 to $>$50 cm distance at breast height (dbh) in 25 m circular plots (Fernández-Juricic et al., 2001b). Cover variables were visually estimated following Prodon and Lebreton (1981).

2.3. Statistical analyses

Some response variables were transformed with logarithmic and arcsine transformations to meet normality: scan rate, proportion of time spent scanning, scan bout duration, and alert and flight distances. The effects of species (spot-winged pigeon, eared dove) and foraging conditions (solitary individuals and individuals in flocks) on scanning rate, proportion of time scanning, scanning bout duration, alert distance, and flight distance were modeled with general linear models (ANCOVA analysis). Species and condition were entered as independent fixed factors. Temperature, tree cover, tree height, and number of stems were included as covariates to control for possible confounding factors.

To determine the predicted probabilities of pedestrian detection, we first analyzed the distribution of inter-scan intervals, which may be as important in detecting potential predators as overt scans (Lendrem, 1984). The rationale of Hart and Lendrem's (1984) model is based on the relationship between predator approach time and the duration of inter-scan intervals. If brief, it takes a predator a certain time z to catch the prey after breaking cover. If the duration of inter-scan intervals d is longer than z, then the probabilities of predator detection are low, and the chances of being caught are high (Hart and Lendrem, 1984). Higher probabilities of predator detection are associated with $d < z$. Although visitors to natural areas do not cause direct mortality to birds, a similar argument can be applied to scenarios in which humans interact with wildlife to predict the probabilities of detection of pedestrians on the grounds that birds tend to avoid humans (Knight and Temple, 1995). Hart and Lendrem's (1984) model was previously used in empirical studies to estimate the probabilities of detection of aerial predators (Pöysä, 1987) and of scroungers (Thompson and Lendrem, 1985). We assumed that pedestrians in our study area approached birds at random, that individuals scanned at random, that individuals could detect pedestrians when looking up only and when pedestrians were within their sight. For solitary individuals, the probability of detecting an approach lasting z is:

$$G(z) = \sum_{i=1}^{x} g(d_i) + \sum_{i=x+1}^{c} \frac{z}{d_i} g(d_i) \quad (1)$$

where $g(d_i)$ is calculated with the following expression:

$$g(d_i) = \frac{d_i f(d_i)}{\sum_{i=1}^{c} d_i f(d_i)} \quad (2)$$

d_i is the frequency distribution of inter-scan intervals among classes $i = 1, 2$, etc. The denominator of this expression is the sum of the products of the intervals and their frequencies (see details in Hart and Lendrem, 1984). We used one data point per individual in each condition.

For individuals foraging in flocks, the probability that one individual detects a pedestrian that begins the approach when all heads are down is:

$$H(z) = 1 - (1 - G(z))^n \tag{3}$$

where n is flock size, and $G(z)$ is calculated as in (1). In this formula, we used median flock size of each species to estimate n. $H(z)$ yields the probability of detecting pedestrian approaches when no flock member is scanning. However, when one or more flock members are scanning the approach will always be detected. The overall detection probability will then be:

$$P(z) = p_{\mathrm{s}} + (1 - p_{\mathrm{s}})H(z) \tag{4}$$

where p_{s} is the sum of time each flock member has its head up minus the time that all flock members have their heads up simultaneously.

The Kolmogorov–Smirnov two-sample test was used to test differences in the distribution of inter-scan intervals between and within species and foraging conditions. We plotted the expected probabilities of pedestrian detection as a function of approach time for the different conditions following Pöysä (1987). All statistical analyses were conducted with Statistica, version 6.1 (StatSoft, 2003).

3. Results

3.1. Flock size

In this section, we report the relationships between flock size and the response variables used in this study considering the data gathered in the group foraging category (>1 individuals).

In the scanning behavior dataset, flock size did not differ between species (ANOVA, $F_{1,58} = 0.77$, $P = 0.382$, spot-winged pigeons, 5.67 ± 4.69; eared doves, 6.73 ± 4.68). Spot-winged pigeon flock sizes ranged from 2 to 20 individuals, but 93% of the observations were concentrated on the range 2–11 individuals. Scan rate (Pearson product moment correlation, $r = -0.31$, $P = 0.096$) and scan bout duration ($r = -0.33$, $P = 0.079$) were not significantly affected by flock size. The proportion of time spent scanning did decrease with flock size ($r = -0.38$, $P < 0.05$); however, such relationship turned to be non-significant ($r = 0.004$, $P = 0.982$) if the two samples recorded in flocks of 20 individuals were not considered. As for eared doves, flock size varied between 2 and 20 individuals. No variation in scan rate ($r = -0.27$, $P = 0.151$), proportion of time spent scanning ($r = -0.18$, $P = 0.338$), and scan bout duration ($r = 0.001$, $P = 0.997$) was found in relation to flock size. In both species, inter-scan interval duration was not affected by flock size (spot-winged pigeons, $r = 0.29$, $P = 0.112$; eared doves, $r = 0.26$, $P = 0.163$).

In the alert and flight distances dataset, we did not find significant differences in flock size between species (ANOVA, $F_{1,58} = 0.04$, $P = 0.843$, spot-winged pigeons, 5.10 ± 3.05; eared doves, 5.27 ± 3.43). Flock sizes of spot-winged pigeons varied between 2 and 13 individuals, and those of eared doves, between 2 and 16 individuals. However, the size of foraging groups did not affect alert distances (spot-winged pigeons, $r = -0.26$, $P = 0.151$;

eared doves, $r = -0.29$, $P = 0.112$) and flight distances (spot-winged pigeons, $r = 0.07$, $P = 0.702$; eared doves, $r = -0.02$, $P = 0.931$) of either species.

Finally, we found no differences in flock size between flocks approached to study scanning behavior and those approached to assess alert and flight distances (one-way ANOVA, spot-winged pigeons, $F_{1,58} = 0.31$, $P = 0.581$; eared doves, $F_{1,58} = 1.91$, $P = 0.172$).

3.2. Scanning behavior

Scanning rate varied between species and foraging conditions ($R^2 = 0.33$, $F_{7,112} = 7.72$, $P < 0.001$), with eared doves performing more scans per unit time than spot-winged pigeons ($F_{1,112} = 4.05$, $P < 0.05$, Fig. 1a), and solitary individuals more than individuals in flocks ($F_{1,112} = 19.16$, $P < 0.001$, Fig. 1a). No interaction effect was detected between species and condition ($F_{1,112} = 2.95$, $P = 0.088$). Spot-winged pigeons spent a greater proportion of time scanning than eared doves, and so did solitary individuals as compared to flocks (overall model, $R^2 = 0.47$, $F_{7,112} = 14.31$, $P < 0.001$; species, $F_{1,112} = 15.62$, $P < 0.001$; condition (solitary versus flocks), $F_{1,112} = 58.63$, $P < 0.001$, Fig. 1b). Similarly, spot-winged pigeons had longer scanning bouts than eared doves (overall model, $R^2 = 0.36$, $F_{7,112} = 9.10$, $P < 0.001$; species, $F_{1,112} = 39.39$, $P < 0.001$, Fig. 1c). Scanning bout duration also increased when individuals foraged alone ($F_{1,112} = 8.05$, $P < 0.01$, Fig. 1c). We found no interaction effects in either the proportion of time scanning ($F_{1,112} = 0.01$, $P = 0.952$) or scanning bout duration ($F_{1,112} = 0.08$, $P = 0.779$). These models explained between 33 and 47% of the variability in vigilance behavior. As for the covariates, scanning rate and the proportion of time scanning were decreased by increasing tree cover, the proportion of time spent scanning and scanning bout length were increased by increasing tree height, and scanning rate was increased by increasing number of stems ($F_{1,112} > 4.77$, $P < 0.05$).

3.3. Distribution of inter-scan intervals and detection probabilities

We contrasted the distribution of inter-scan intervals (median values; spot-winged pigeons: alone, 0.77 s, $n = 30$, in flocks, 2.68 s, $n = 30$; eared doves: alone, 0.99 s, $n = 30$, in flocks, 2.91 s, $n = 30$), and found that there was a significantly higher proportion of long inter-scan intervals in flocks as compared to solitary foraging conditions (Kolmogorov–Smirnov two-sample test, $P < 0.001$). However, the distribution of inter-scan intervals did not differ significantly between species when individuals foraged alone ($P > 0.10$) and in flocks ($P > 0.10$).

The expected probabilities of detection showed different patterns depending on the approach time. Approach times of less than 1 s were more likely to be detected by solitary individuals (Fig. 2), because individual foraging in groups had longer inter-scan intervals. However, such approach times are unrealistic for human approaches (e.g. tourists, birdwatchers, etc.). When approach times were longer than 1 s, the probabilities of detection were lower for solitary individuals of both species (Fig. 2). The expected probabilities of pedestrian detection of spot-winged pigeons were higher than those of eared doves mainly when foraging alone, and to a lesser extent when foraging in flocks (Fig. 2).

3.4. Alert and flight distances

Alert distances differed between species, with spot-winged pigeons showing alert behaviors towards pedestrians at greater distances than eared doves (overall model, $R^2 = 0.73$, $F_{7,112} = 7.72$, $P < 0.001$; species, $F_{1,112} = 197.32$, $P < 0.001$, Fig. 3a). Solitary indi-

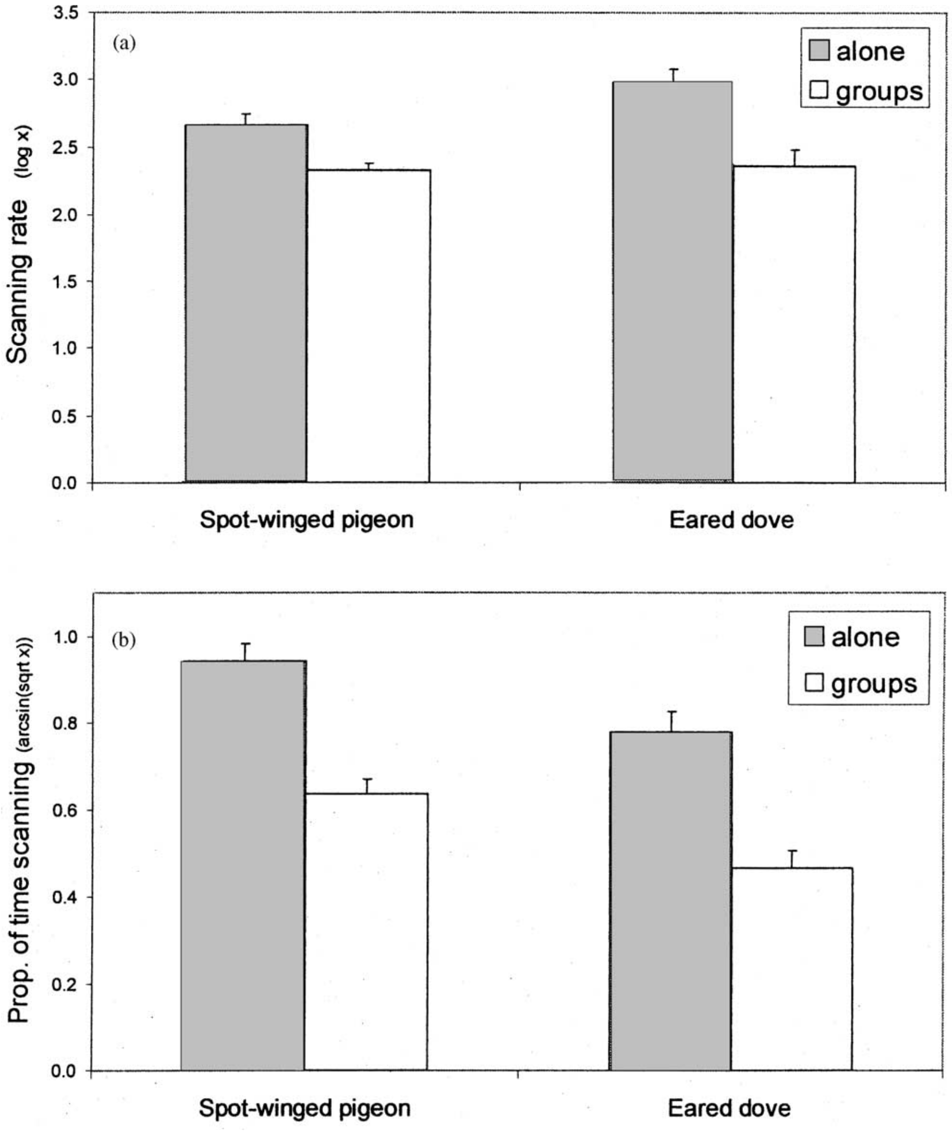

Fig. 1. Variations in: (a) scanning rate; (b) proportion of time spent scanning; and (c) scanning bout duration of two species (spot-winged pigeon and eared dove) in two conditions (alone and in groups). All differences between species and conditions were significant. Shown are means (±S.E.).

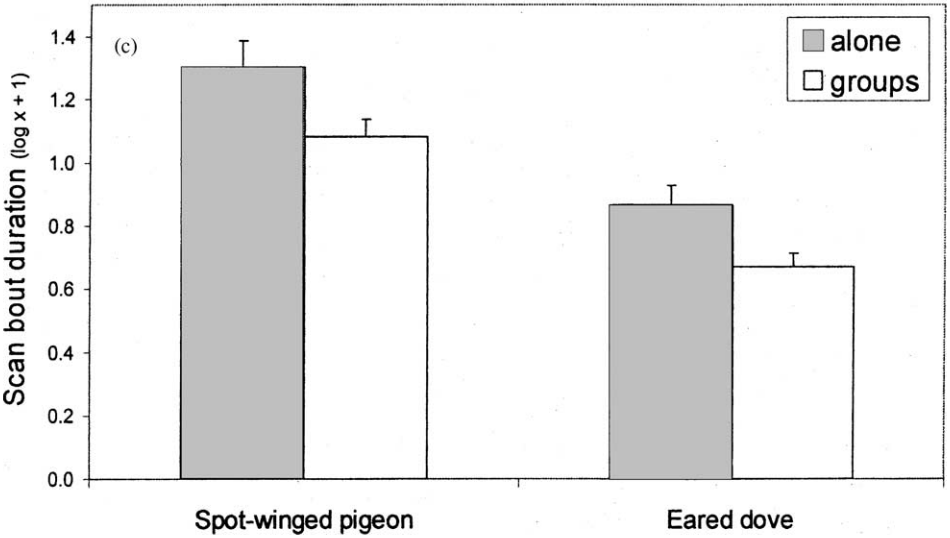

Fig. 1. (*Continued*).

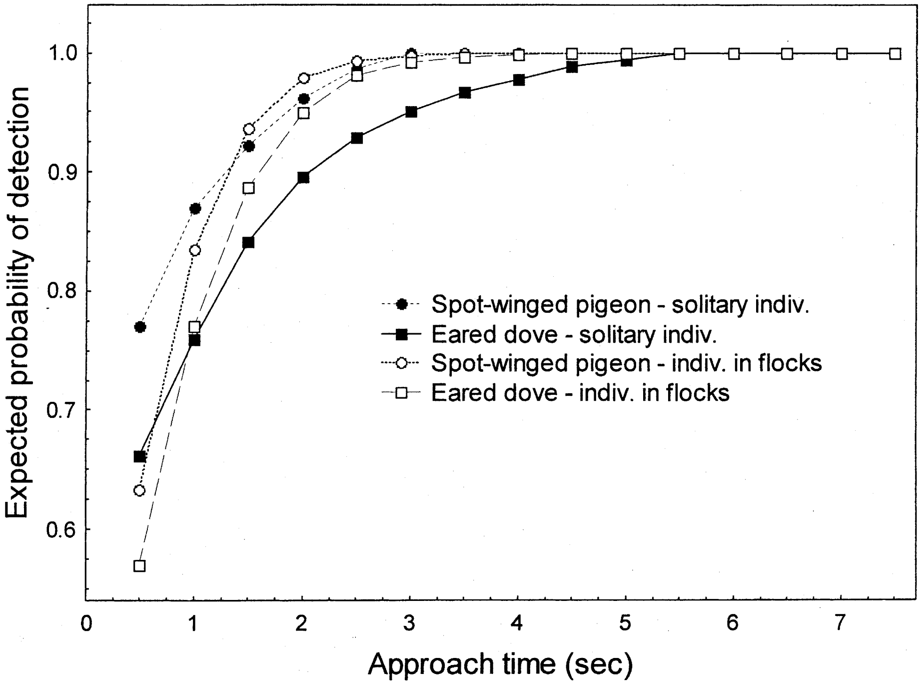

Fig. 2. Expected probabilities of detection of spot-winged pigeons and eared doves foraging alone and in flocks in relation to the approach time of pedestrians.

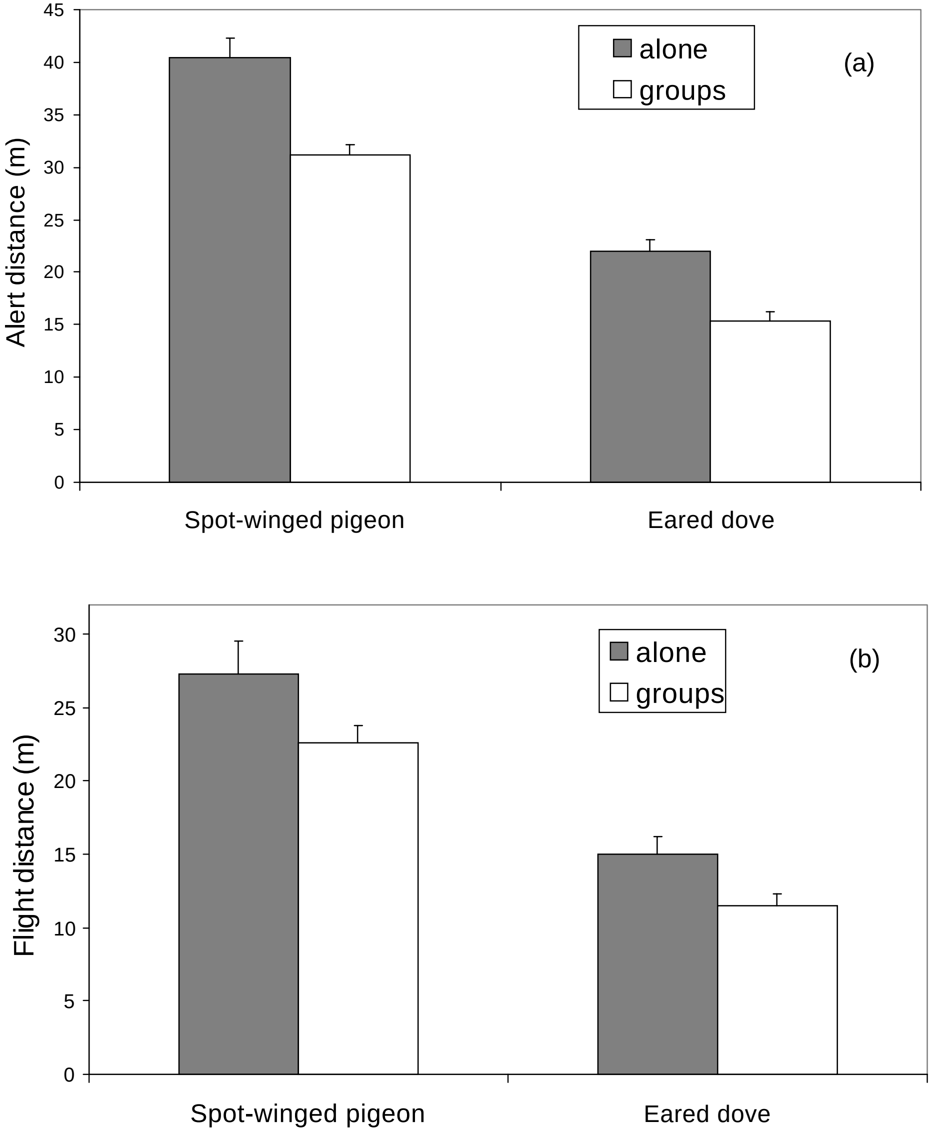

Fig. 3. Variation in: (a) alert distance; and (b) flight initiation distance between two species (spot-winged pigeon and eared dove) in two conditions (alone and in groups). Statistical analyses were performed with log-transformed data, but untransformed data are presented here for illustrative purposes. All differences between species and conditions were significant. Shown are means (±S.E.).

viduals of both species also showed greater alert distances ($F_{1,112} = 45.57$, $P < 0.001$, Fig. 3a); however, there was no interaction between species and condition ($F_{1,112} = 1.75$, $P = 0.187$). Moreover, alert distances decreased with tree height and number of stems ($F_{1,112} > 5.32$, $P < 0.05$). Variations in flight distances yielded similar results, with spot-winged pigeons flushing sooner than eared doves (overall model, $R^2 = 0.50$, $F_{7,112} = 16.17$, $P < 0.001$; species, $F_{1,112} = 69.43$, $P < 0.001$, Fig. 3b). Likewise, solitary individuals had higher flight distances than individuals foraging in flocks ($F_{1,112} = 7.54$, $P < 0.01$, Fig. 3b). There was no interaction between species and condition ($F_{1,112} = 0.46$, $P = 0.499$). Covariates also affected flight distances, which decreased with increasing tree height and number of stems ($F_{1,112} > 5.07$, $P < 0.05$). Models accounted for 50–73% of the observed variability.

4. Discussion

Previous studies have shown that variations in the configuration of the visual fields of different species affect their scanning patterns (e.g. Guillemain et al., 2002). Our result suggests that variations of scanning behavior of phylogenetically similar species may affect their probabilities of detecting pedestrians in different foraging scenarios. Spot-winged pigeons and eared doves differed in the way they allocated their time to foraging and scanning activities. Spot-winged pigeons spent more time scanning, with longer scanning bout duration, which reduced their scanning rates in relation to eared doves. Such variations could be related to different strategies to cope with predation/disturbance risk in the same habitat. An increased proportion of time spent scanning could be related to higher perceived predation risk (Lima and Dill, 1990), with longer scan bout duration facilitating the monitoring of larger visual ranges (Desportes et al., 1991). One factor that may account for the relative increased risk of predation is the slightly more conspicuous coloration of spot-winged pigeons in this woodland habitat. Even under the unprofitable prey hypothesis, which posits that conspicuous species would experience lower predation risk (Götmark and Unger, 1994), the scanning behavior of species with contrasting coloration is expected to increase in order to detect and evade predators more effectively (Baker and Parker, 1979). Another source of increasing risk for spot-winged pigeons may be their larger body mass in relation to eared doves, as some avian predators usually prefer larger prey species (Zalewski, 1994, Creswell, 1995, but see Sodhi and Oliphant, 1993). However, these explanations remain speculative and require further testing. In contrast, eared doves seem to compensate for the less time spent scanning by increasing scanning rate, particularly in solitary conditions.

The observed probabilities of detection, based on alert distances, showed that spot-winged pigeons detected pedestrians earlier than eared doves when foraging alone and in groups. This is in accordance with the increased allocation of time to scanning, and with the expected probabilities of pedestrian detection based on the distribution of inter-scan intervals. Consequently, individuals with longer scanning bouts and an increasing proportion of short inter-scan intervals may have higher chances of detecting pedestrians.

An alternative, but not mutually exclusive, explanation is that inter-specific differences in detection may have to do with differences in the distance at which species can detect objects (Fernández-Juricic et al., 2001b), which would be ultimately affected by the larger body mass of spot-winged pigeons. Larger species have greater visual acuity (Brooke et al., 1999; Kiltie, 2000), which would enable them to detect human approaches at greater distances.

The effect of foraging condition was independent of variations in scanning between species, suggesting that both species showed the same behavioral adjustments from foraging alone to foraging in flocks. The lower level of security during solitary foraging likely triggered an increasing proportion of time spent scanning, longer scanning bout duration, greater scanning rate, and shorter inter-scan intervals, as has been shown by theoretical and empirical studies on predation risk (e.g. Elgar, 1989; Lima and Dill, 1990; McNamara and Houston, 1992; Roberts, 1996). This corroborates that some theoretical models of predation can be used to predict more specific responses of wildlife to humans (see also Frid and Dill, 2002).

Nevertheless, we found an unexpected result: observed probabilities of detection (alert distances) were higher for solitary individuals than for individuals in flocks, contrary to the expected probabilities of detection (approach times >1 s) and early empirical evidence (Powell, 1974, Kenward, 1978). Theory predicts that individuals in groups would increase the proportion of longer inter-scan intervals (Hart and Lendrem, 1984) and decrease scanning bout duration (McNamara and Houston, 1992); both predictions being supported by our data. For these behavioral adjustments to be effective, information about the detection of a given disturbance should be transmitted evenly and quickly among flock mates (Bednekoff and Lima, 1998), ultimately improving levels of detection. However, in spot-winged pigeons and eared doves, information transmission appears not to be so effective, as shorter alert distances are in accordance with the lower proportion of time spent scanning in groups. This partly supports the view that individuals do not pay attention to the level of vigilance of conspecifics (Lima and Zollner, 1996, Beauchamp, 2002), and that the main benefits of group living for these species may lie in the dilution of risk (Roberts, 1996). Thus, these species have lower chances of detecting tourists walking by when foraging in flocks, which would allow closer approaches of pedestrians to foraging areas that favor group aggregation (e.g. patches with higher food availability).

Flight distances showed a similar response pattern to alert distances: spot-winged pigeons and individuals foraging alone fled sooner than eared doves and individuals in flocks, respectively. However, the reasons accounting for these responses may be different. Body mass may have affected inter-specific decisions as to when to flee: smaller species (e.g. eared dove) flee later from disturbance because they have greater ratios of surface area to body weight, which would increase energy expenditure from unnecessary flights (Holmes et al., 1993). The greater flight distance of solitary individuals may have to do with the greater risks of being singled-out and disturbed as compared to when foraging in flocks, where such risks are diluted by conspecifics (Roberts, 1996). Similar results have been found in other avian species (e.g. Burger and Gochfeld, 1991; Holmes et al., 1993; Fernández-Juricic et al., 2001a, 2002). Consequently, when proposing management recommendations several behavioral responses to human disturbance should be considered. For instance, ecotourists may be concentrated in areas with low chances of detection by wildlife; namely, high habitat heterogeneity disrupting human visual profiles, vegetation blocking human approaches, etc. Wildlife viewing areas can be designed specifically to meet such requirements (Camp et al., 1997). But, when pedestrians move closer to areas that are within flight distance, buffer zones should be considered because wildlife are likely to leave profitable foraging areas. This two-tiered approach should be further tested, but it could potentially improve coexistence between wildlife and tourism.

Although our results cannot be generalized to other species and habitats, they underscore the existence of a behavioral strategy (greater scanning behavior increases the chances of detecting tourists) that could be incorporated into the conceptual framework of the risk-disturbance hypothesis (Frid and Dill, 2002) in order to generate new predictions on wildlife responses to human disturbance. For instance, it would be important to define the detection windows (areas in which the probabilities of detecting pedestrians are higher) of species of conservation interest based on their scanning patterns and detection distances in different habitat types. If detection windows differ inter-specifically (e.g. increasing with species body mass), and if scanning behavior is affected by social and physical factors (Lazarus and Symonds, 1992), responses to tourists would depend not only on the context of the encounter (Steidl and Anthony, 1996) but also on the vigilance behavior in that context, which would affect the chances of visually detecting pedestrians. Therefore, similar levels of human visitation to protected areas may exert different effects according to the detection windows of different species.

5. Conclusions

Vigilance behavior can affect the distance at which birds detect human disturbance. Individuals with longer scanning bouts and a greater proportion of short inter-scan intervals had higher chances of detecting tourists. This type of scanning behavior was found mainly in individuals foraging alone rather than in flocks. This calls for considering variation in scanning behavior when assessing inter-specific responses to ecotourists in order to develop better indicators of tolerance.

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