Antipredator behavior in blackbirds: habituation complements risk allocation

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Several studies showed that animals allow closer approaches (measured through flight initiation distances, FIDs) by potential predators (e.g., humans) in high–predator density areas, which has been explained by habituation effects. We assessed whether this pattern could be produced by not only habituation but also risk allocation by simulating attacks on blackbirds *Turdus merula* by both usual (pedestrians) and novel (radio-controlled vehicle) potential predators in parks with different levels of human visitation. Individual blackbirds from parks with higher pedestrian rates showed lower FID than individuals from parks with lower pedestrian rates, in response to both usual and novel approaches. Blackbirds adjusted their antipredator behavior to the specific level of pedestrian rate encountered every morning and evening in each park, with higher FID in the period with lower pedestrian rate. Similar responses to usual and novel potential predators among parks and daily variation in antipredator behavior support the risk allocation hypothesis and could not be explained by habituation. However, the rate at which FID was reduced in individuals from low-visited parks to high-visited parks was greater for pedestrian attacks than for novel potential predator attacks, suggesting that habituation is also present in our system and complements the effects of risk allocation. Our results have applied implications: the reduction in FID with increasing human visitation in natural areas is usually attributed to habituation; however, we propose that risk allocation can also reduce antipredator behavior effort to survive in habitats with high levels of recreational activities at the expense of potential physiological costs. *Key words:* antipredator behavior, flight initiation distance, predator density, risk reduction. *[Behav Ecol 20:371–377 (2009)]*

The distance at which prey flees from an approaching predator is termed flight initiation distance (FID) and is a common parameter used to study the processes associated with prey escape decision making because it is related to the costs and benefits of remaining in a patch (Ydenberg and Dill 1986; Cooper and Frederick 2007). Factors like availability of resources, group size, microhabitat characteristics, distance to the refuge, and predator behavior often influence FID during predator–prey interactions (reviewed in Lima and Dill 1990; Stankowich and Blumstein 2005).

Another factor affecting the variability in FID is the density of predators. The relationship between prey FID and predator density has particular ecological relevance because it could affect the outcome of the interactions between prey with multiple predators (Sih et al. 1998) and density-dependent predator processes (Abrams and Matsuda 1997). A recent meta-analysis showed that predator density tends to be negatively associated with FID (Stankowich and Blumstein 2005). This association has been found in reptiles (e.g.,Labra and Leonard 1999; Cooper et al. 2003), birds (e.g., Fernández-Juricic et al. 2001; Ikuta and Blumstein 2003), and mammals (e.g., Louis and Le Berre 2000; Magle et al. 2005). In most of these studies, humans have been used as model predators because human disturbance can cause antipredator responses similar to those elicited by natural predators (Frid and Dill 2002).

Habituation is commonly proposed as the mechanism implicated in the reduction of FID with increasing predator density (Stankowich and Blumstein 2005). Under the habituation hypothesis, animals reduce their responses to the stimuli by a learning process in which the stimuli cease to be regarded as dangerous after repeated exposures to it (Thompson and Spencer 1966; Mirza et al. 2006). In areas with high levels of human visitation, the frequency of exposures to nonthreatening human encounters increases, thereby reducing the perceived risk of predation. Hence, animals would allow humans to approach closer before fleeing in subsequent encounters. However, there are some results that cannot be explained by habituation alone. For instance, Webb and Blumstein (2005) found a negative relationship between FID and predator (human) density in Western gulls (*Larus occidentalis*) sampled in a Californian beach; however, habituation was ruled out because the observed variability in FID (and human disturbance) occurred along a single beach whose area was far shorter than the daily home ranges of the gulls.

Although the role of habituation is commonly accepted in FID studies, alternative mechanisms could produce the same prediction. For instance, the risk allocation hypothesis (Lima and Bednekoff 1999) could account for a negative relationship between FID and predator density because it predicts that animals should decrease their allocation of antipredator effort to increasingly frequent high-risk situations. Otherwise, prey animals would be fleeing so frequently that they would not be able to cope with their resource acquisition needs. Increasing predator density can lead to an increase in the frequency of high-risk situations for prey due to higher probabilities of predator–prey encounters. Nevertheless, one common problem in the studies testing the risk allocation hypothesis is that habituation cannot be ruled out as a competing hypothesis (Hamilton and Heithaus 2001; Pecor and Hazlett 2003; Mirza et al. 2006; but see Sih and McCarthy 2002).

The goal of our study was to test whether the pattern of FID reduction with increasing predator (human) density can be explained by risk allocation, habituation, or a combination of both. We studied antipredator responses of blackbirds (*Turdus merula*) in urban wooded parks that differed in pedestrian rate (i.e., predator density) and in the temporal patterns of daily visitation, using usual (pedestrian) and novel (radio-controlled vehicle) potential predator stimuli. A previous study showed that the pattern of FID reduction with increasing pedestrian rate is present in this system (Fernández-Juricic et al. 2001); however, no empirical test of the underlying mechanisms was conducted. The differences in pedestrian rates between parks and between daily periods within parks allowed us to test the following predictions.

Predictions

Because risk allocation and habituation may not be mutually exclusive, they could be acting simultaneously. First, it is necessary to establish whether risk allocation is involved in the FID–predator density pattern (Figure 1). Second, even if risk allocation is present in our system, it is necessary to determine whether habituation exists and acts in combination with risk allocation (Figure 1).

Under the risk allocation hypothesis, high pedestrian rates create frequent high-risk situations that would make blackbirds reduce their antipredatory effort, which would affect responses to any predation risk situation, whether it is caused by humans or by other predators. On the other hand, habituation can produce a reduction in antipredation effort only toward abundant and sympatric predators because blackbirds cannot be habituated to unfamiliar predators. Thus, if risk allocation is involved in the pattern of FID reduction with predator density among populations, we predict that blackbirds would show higher FID in parks with lower predator density than in parks with higher predator density, in response to both pedestrian approaches and radio-controlled vehicle approaches (novel predator) (Figure 1). However, if habituation is the only mechanism responsible, the FID of individual blackbirds from high–predator density parks would be higher than the FID of blackbirds from low–predator density parks in response to approaches by pedestrians but not by novel predators (Figure 1). Moreover, if risk allocation is an underlying mechanism for the decrease in FID with predator density, we also expect that there would be temporal variation in FID within parks in relation to the temporal variability in park pedestrian rates because under the risk allocation hypothesis blackbirds would need to reduce their FID in order to acquire enough resources in periods with frequent pedestrian disturbance. Hence, in parks with higher pedestrian rate in the evening than in the morning, we predicted that FID would be higher in the morning, whereas, in parks with higher pedestrian rates in the morning than in the evening, FID would be higher in the evening (Figure 1). No temporal variation in FID would be expected in parks with similar pedestrian rates during the day. Habituation cannot explain this specific pattern of temporal variation in FID because blackbirds could not habituate and dishabituate within a few hours.

Finally, if both risk allocation and habituation are present in our system, the FID reduction in high–predator density areas caused by risk allocation could be further pronounced by habituation to pedestrians (e.g., additive effects). This extra reduction in FID would be apparent only on pedestrian approaches, but not on the radio-controlled vehicle approaches, because blackbirds could not be habituated to an unknown predator. Thus, if both mechanisms are present, we would expect an interaction effect between park and type of attacker (Figure 1).

MATERIALS AND METHODS

Study site and species

The study was conducted between June 28 and August 27 2004 in the city of Madrid (40.25°N, 03.43°W), Spain. Four wooded city parks were selected: Capricho (19 ha), Moro (19 ha), Oeste
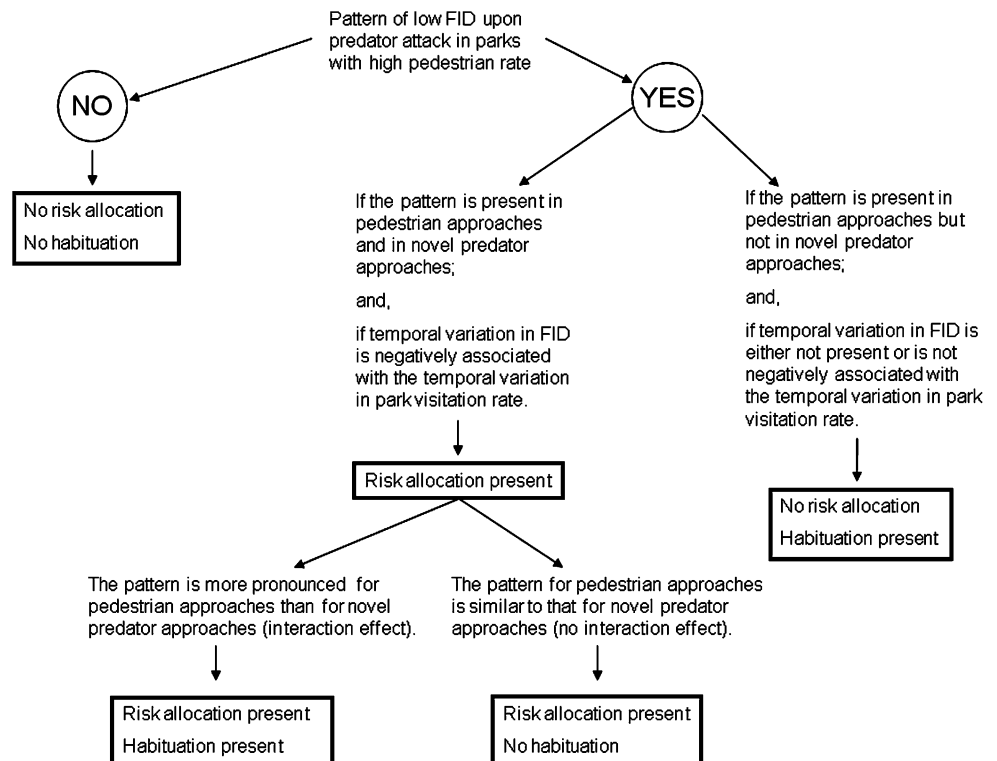

Figure 1
Flowchart showing the predicted responses of blackbirds to usual and novel predator approaches based on 2 mechanisms: habituation and risk allocation. See text for details.

(60 ha), and Retiro (114 ha). We chose these parks because there was enough pedestrian rate variation within (morning vs. evening) and among them to test our predictions (see Results). These parks have lawns, native and exotic shrubs, and high tree cover with a mixture of coniferous and deciduous trees (see description of vegetation structure in Fernández-Juricic 2000). The presence of cats is low and similar among the 4 parks. No radio-controlled vehicle was seen during the study period in any park. Pedestrian rate was considered a proxy of predator density (see also Stankowich and Blumstein 2005).

We used the blackbird (*T. merula*) as a model species because it is relatively abundant in Madrid city parks. Previous studies have used blackbirds to assess the effects of human disturbance because they react to humans as if these were potential predators (e.g., Fernández-Juricic and Tellería 2000; Fernández-Juricic et al. 2002; Blumstein et al. 2004). Moreover, blackbirds can be detected easily because they are ground foragers that frequently use open areas (Greenwood and Harvey 1978).

Sampling procedures

Park visitation rates and vegetation structure

In each park, we measured separately pedestrian rates in the morning and in the evening by recording the number of pedestrians walking within a 50-m-diameter circular plot for a period of 5 min (pedestrian rate). Pedestrian rate samples were conducted during weekdays in those areas of the park where birds were experimentally approached (following Fernández-Juricic et al. 2002). A total of 18 plots in Retiro, 20 plots in Oeste, 18 plots in Moro, and 20 plots in Capricho were used to characterize human disturbance, totaling 4 sampling sessions per park (2 in the morning and 2 in the evening). We found differences between parks and between temporal periods in visitation rates (see Results).

FID variation among parks could be influenced by several factors, such as habitat structure. We measured the following park vegetation structure variables in 50-m-diameter randomly chosen circular plots in the areas of the park where we conducted our approaches (20 plots per each park; these plots were different from those used to assess pedestrian rates): tree cover, shrub cover, mean tree height, mean shrub height, distance to nearest tree, and distance to nearest shrub. Heights were visually estimated; cover measurements were estimated visually following Prodon and Lebreton (1981); and distances were measured in paces and later transformed to meters. These measurements were done to assess between-park differences in habitat structure; however, we also recorded similar parameters in the spots that the Blackbirds used during our approaches (see below).

Flight initiation distance

We gathered FID information during weekdays, between 0830 and 1130 h official time (morning period) and between 1830 and 2130 h official time (evening period). Madrid's summer daylight conditions provide light even after 2130 h. We avoided sampling during windy and rainy days. Two observers (I.R.P. and Y.R.) gathered all the data after a 1-week training period aimed at reducing interobserver variability in behavior and speed while approaching animals, measuring vegetation cover and height, and using paces to measure distances.

We performed experimental approaches to blackbirds foraging on the ground only, but not perching. FID was defined as the distance (in paces and later transformed into meters following Blumstein et al. 2004) between an approaching disturbance (human or radio-controlled vehicle) and a focal blackbird at which the latter ran or flew away as a response to the approaching threat. We also recorded the distance between the blackbird and the approaching disturbance when the approach started (starting distance) to control for its potential confounding effects (Blumstein 2003). All approaches were performed on a direct trajectory, with no vegetation blocking the focal bird and the approaching observer or vehicle. Observers wore dull colors during approaches.

Human approaches were performed by a single observer. Radio-controlled vehicle approaches required 2 observers. The radio-controlled vehicle was an electric New Bright 6-V Black Mongoose black and red car (55 × 30 × 22 cm). After positioning the vehicle and placing a marker in its position to measure starting distance, both observers moved away from the vehicle and situated themselves in hidden positions, maintaining a good line of sight toward the focal blackbird and the path of the vehicle approach. One of the observers drove the vehicle toward the focal blackbird, whereas the other one observed the blackbird in order to alert the driver when the blackbird flushed away. Following this procedure, the driver retained eye contact with the point where the vehicle was when the blackbird flushed away, and he walked to that point (without losing eye contact with it) while the other observer walked to the point where the blackbird initially was, and then starting distance and FID were measured. The observer approached a focal blackbird at a speed of 1 m/s, whereas the radio-controlled vehicle approached at 1.3 m/s. Note that the goal of this study was not to directly compare human versus vehicle responses (see Discussion).

In the few instances in which blackbirds aggregated around a patch, we selected the individual nearest to the observer. However, if this focal blackbird was not the first one to flush, we discarded the observation to minimize the effects of collective detection. For each approach, we recorded the number of conspecifics and also the number of individuals from all bird species (total number of birds) that were around the focal bird within a 10-m radius. In a 25-m-radius circular plot centered on the focal bird, we also recorded for each approach the following: shrub cover (%), tree cover (%), mean shrub height (meters), and mean tree height (meters). Cover variables were estimated following the scales of Prodon and Lebreton (1981). We also measured in paces (later transformed into meters), the distance from the blackbird's initial position to the nearest cover (shrub or tree).

We did not mark individual blackbirds but recorded their responses from randomly selected territories (following Fernández-Juricic and Tellería 2000). We are confident that this procedure allowed us to reduce the likelihood of sampling the same individual more than once because blackbirds are highly territorial, spending most of their time within the boundaries of their nonoverlapping territories (Greenwood and Harvey 1978). We pooled data from both sexes because preliminary analysis did not show sex differences in FID ($F_{1,193} = 0.20$, $P = 0.66$).

Statistical analysis

We log transformed some variables to meet normality and homoscedasticity assumptions in different types of tests: 1) park visitation and vegetation structure analyses (pedestrian rate, tree height, shrub height, distance to the nearest tree from the plot center, and distance to the nearest shrub from the plot center) and 2) FID analysis (FID, starting distance, number of conspecifics, total number of birds, shrub height, tree height, and distance to nearest cover).

We conducted 2 principal component analyses (PCAs) to reduce the number of vegetation variables in the park vegetation structure analysis (percentage of tree cover, percentage of shrub cover, mean tree height, mean shrub height, distance to

nearest tree, and distance to nearest shrub) and in the FID analyses (percentage of shrub cover, percentage of tree cover, mean shrub height, and mean tree height). Following the Kaiser criterion, we selected only those PCA factors with eigenvalues >1.

We used general linear models to analyze the variation in vegetation structure and in pedestrian rates among parks and between periods (morning vs. evening). We used planned comparisons to establish differences between levels of a factor.

In assessing the effects of park and type of attacker on FID, we ran a general linear model with data (both pedestrian and radio-controlled vehicle attacks) gathered exclusively in the evenings to avoid confounding factors associated with temporal variations in FID. A total of 206 observations were used for this test, with a minimum of 20 observations for each type of attacker/park combination. From the set of confounding factors, we excluded those that showed significant correlation coefficients ($r > 0.6$). We eliminated total number of birds; so the final model included categorical (type of attacker and park) and continuous factors (starting distance, PCA factors, distance to nearest cover, and number of conspecifics). We used planned comparisons to determine differences between parks.

We also used a general linear model to analyze the variation in FID between morning and evening and among parks. We used only one type of attacker (pedestrians) in both mornings and evenings. Hence, we gathered FID data for pedestrian attacks in the mornings and compared it with the same data from evening pedestrian attacks used in the previous analysis. A total of 241 observations were used for this test, with a minimum of 25 observations for each period/park combination. We eliminated total number of birds from the model because it was highly correlated ($r > 0.6$) with other factors. The final model included categorical (period and park) and continuous factors (starting distance, PCA factors, distance to nearest cover, and number of conspecifics). We used planned comparisons to determine differences between time periods within parks.

RESULTS

Pedestrian rates and vegetation structure

In Table 1, we summarize the size, daily patterns of pedestrian rates, shrub density, and tree cover and height of the studied parks to help in the interpretation of the Figures.

We found significant differences in pedestrian rates among parks ($F_{3,74} = 600.81$, $P < 0.001$; Figure 2). Capricho received the lowest levels of visitation, whereas Retiro was the most visited park, with Moro and Oeste receiving intermediate levels of visitation (Figure 2). The temporal pattern of visitation also varied among parks ($F_{3,125} = 31.36$, $P < 0.001$; Figure 2). Retiro and Oeste received significantly more visitors in the evenings than in the mornings. Capricho is a park closed to

the public, so there are no visitors in the evenings but there were always some gardeners working in the mornings. We did not find significant differences in human visitation between mornings and evenings in the Moro park (Figure 2). These results confirmed that we applied our treatments to animals living in parks with different conditions: 1) higher visitation rates in the mornings than in the evenings (Capricho), 2) higher visitation rates in the evenings than in the mornings (Oeste and Retiro), and 3) similar levels of visitation in both mornings and evenings (Moro).

Vegetation structure variables for each park were reduced to 2 principal components (percentage of total variance explained; PC1, 28.82%; PC2, 25.62%). PC1 correlated positively with the distance to nearest shrub (factor loading = 0.85) and negatively with shrub cover (factor loading = −0.92), hence representing a gradient from shrubby areas to areas with sparse shrub abundance. PC2 correlated positively with tree height (factor loading = 0.68) and tree cover (factor loading = 0.78), hence representing a gradient from areas with small to large proportion of higher trees.

Both PC factors varied among parks (PC1, $F_{3,71} = 20.01$, $P < 0.0001$; PC2, $F_{3,71} = 13.70$, $P < 0.0001$). Oeste was the park with the lowest shrub and tree cover; Moro had a tall and dense tree canopy; Capricho had the highest shrub density; and tree and shrub structure in Retiro was intermediate among the 4 parks (Figure 3). The variation in vegetation structure among parks did not follow the same pattern as the variation in pedestrian rate among parks (compare Figures 2 and 3).

Flight initiation distance

Effects of park and type of attacker on FID

Blackbird FID was significantly affected by starting distance, park, and type of attacker, with the interaction between park and type of attacker being significant (Table 2, Figure 4). Planned comparisons showed that the FID differences among the least visited park (Capricho), the most visited park (Retiro), and the 2 parks with intermediate levels of human visitation (Moro and Oeste) were all significant, with higher FID

Table 1

Summary of the size, daily patterns of pedestrian rates, shrub density, and tree cover and height of each of the studied parks

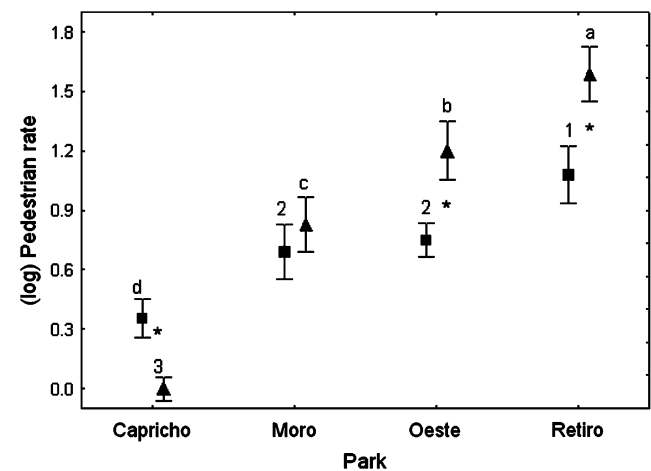| Park	Capricho	Moro	Oeste	Retiro
Size	19 ha	19 ha	60 ha	114 ha
AM versus PM pedestrian rate	AM > PM	AM = PM	AM < PM	AM < PM
Shrub density	High	Medium	Low	Medium
Tree cover and height	Medium	High	Low	Medium

Figure 2
Pedestrian rate variation among the 4 studied parks. The results of planned comparisons for morning pedestrian rate differences among parks are expressed with numbers, whereas the results for differences in evening pedestrian rates are expressed with letters. Different numbers or different letters denote significant differences in pedestrian rate in the morning or evening, respectively. An asterisk denotes a significant difference in pedestrian rate between morning and evening for a given park.
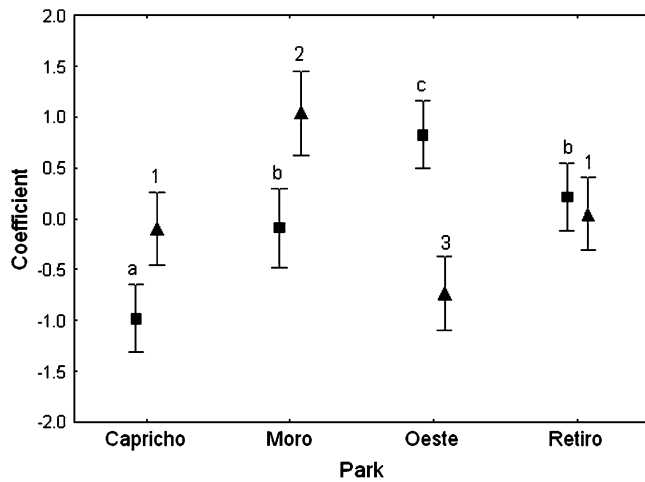
Figure 3
Vegetation structure variation among the 4 studied parks. PC1 correlates positively with shrub density, whereas PC2 correlates positively with tree height and cover. Different letters or numbers between parks denote significant differences in PC1 or PC2 coefficients, respectively.

in the parks with less visitation (Table 3). This pattern was similar whether the blackbirds were attacked by a human or a vehicle (Table 3). If we did not include Moro and Oeste in the same level of the planned comparisons, we still obtained the same results, with significantly higher FID in parks with less visitation, except for the FID differences for vehicle attacks between Moro and Oeste that were not significant ($F = 0.14$, $P = 0.713$).

Pattern of FID variation between morning and evening among parks
Starting distance, park, and period significantly affected blackbird FID in response to human approaches. The interaction between park and period was significant (Figure 5, Table 4). In parks with higher visitation rates in the evenings than in the mornings (Retiro and Oeste), FID was significantly lower in the evenings than in the mornings (Retiro AM 10.9 ± 6.9 m, PM 6.7 ± 2.3 m, $F_{1,226} = 23.27$, $P < 0.0001$; Oeste AM 16.2 ± 6.1 m, PM 10.2 ± 6.2 m, $F_{1,226} = 12.06$, $P < 0.001$). In the park with lower visitation rates in the evenings than in the mornings (Capricho), FID was significantly higher in the evenings than in the mornings (Capricho AM 26.3 ± 11.2 m, PM 39.5 ± 16.9 m, $F_{1,226} = 12.31$, $P < 0.001$). In the park with similar visitation in the evenings and in the mornings (Moro),
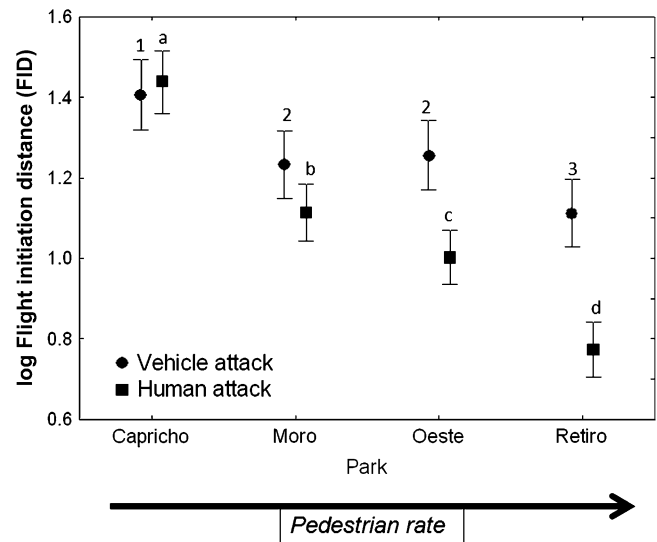

Figure 4
Blackbird FIDs in response to human and radio-controlled vehicle approaches in different parks. Parks are arranged from left to right in a gradient of increasing pedestrian rate. Different numbers or letters denote significant differences in FID to vehicle or human attacks, respectively.

FID was not significantly different between the 2 periods (Moro AM 12.3 ± 6.4 m, PM 14.0 ± 5.5 m, $F_{1,226} = 0.09$, $P = 0.769$).

DISCUSSION

Our results show that 1) risk allocation is involved in the pattern of blackbird FID reduction with increasing predator density among populations and 2) habituation is also present in our system, enhancing the effect of risk allocation when FID varies in relation to pedestrian approaches, but not to novel stimulus (radio-controlled vehicle) approaches.

We obtained the same pattern of FID reduction with increasing pedestrian rate among parks as in a previous study in this system (Fernández-Juricic et al. 2001) and elsewhere (reviewed in Stankowich and Blumstein 2005). Vegetation structure variation among parks could be an alternative explanation for FID differences. However, our results show that variation in FID was not associated with variation in vegetation structure, and the effect of microhabitat structure on the individual responses was comparatively low.

Table 2
Effects of park, type of attacker, and their interaction, as well as some confounding factors, on blackbird FIDs

	F	Degrees of freedom	P
Intercept	1.16	1, 192	0.28
Park	34.94	3, 192	**<0.0001**
Type of attacker	38.33	1, 192	**<0.0001**
Interaction park × type of attacker	9.86	3, 192	**<0.0001**
Starting distance	53.72	1, 192	**<0.0001**
Number of conspecifics	0.18	1, 192	0.669
Distance to cover	0.01	1, 192	0.901
Vegetation structure PC1	0.63	1, 192	0.428
Vegetation structure PC2	0.78	1, 192	0.379

Significant factors in bold.

Table 3
Differences in blackbird FID between parks for human and radio-controlled vehicle attacks

	$F_{1,192}$	P
Human attacks		
Capricho > Moro + Oeste	63.61	**<0.0001**
Capricho > Retiro	158.81	**<0.0001**
Moro + Oeste > Retiro	46.56	**<0.0001**
Vehicle attacks		
Capricho > Moro + Oeste	8.20	**<0.01**
Capricho > Retiro	19.57	**<0.0001**
Moro + Oeste > Retiro	7.07	**<0.01**

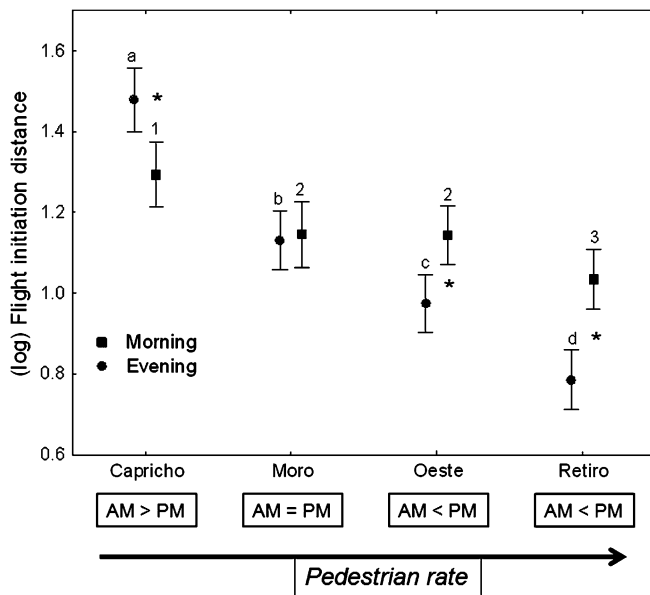Results of planned comparisons. Significant differences in bold.

Figure 5
Blackbird FID variation between morning and evening for each park. Different numbers or letters denote significant differences in FID in the morning or evening, respectively. An asterisk denotes a significant difference between morning and evening for a given park. Parks are placed from left to right in a gradient of increasing pedestrian rate. The specific pattern of pedestrian rate temporal variation is shown in the gray boxes.

The FID reduction in highly visited parks occurred not only with pedestrian approaches but also with novel predator approaches, supporting our first risk allocation prediction. This suggests that habituation could not be the sole process responsible for the observed patterns because blackbirds could not be habituated to the novel predator, as radio-controlled vehicles are not used frequently in the studied parks (e.g., we did not see any during the duration of this study).

We also found that blackbirds adjusted their antipredator behavior to the level of pedestrian rate encountered every morning and evening in each park, with higher FID in the period with lower pedestrian rate, further supporting our risk allocation predictions. Habituation is not likely to vary within a few hours every day. Had the lowest FID and highest pedestrian rate been found always in the evenings for all parks or vice versa, our interpretation could have been confounded by some potential association of FID with temperature or with the rate of body mass gain at different parts of the day (Cresswell 1998; MacLeod et al.

Table 4
Effects of park, period (and their interaction), and some confounding factors on blackbird FID

	F	Degrees of freedom	*P*
Intercept	4.76	1, 226	0.030
Park	38.58	3, 226	**<0.0001**
Period	5.96	1, 226	**0.015**
Interaction park × period	14.50	3, 226	**<0.0001**
Starting distance	36.07	1, 226	**<0.0001**
Number of conspecifics	0.18	1, 226	0.671
Distance to cover	0.32	1, 226	0.569
Vegetation structure PC1	3.74	1, 226	0.054
Vegetation structure PC2	0.15	1, 226	0.700

Significant factors in bold.

2005). However, blackbirds adjusted their FIDs to the specific temporal variation in pedestrian rate in each park. FID was higher in the mornings than in the evenings in Retiro and Oeste (2 parks with higher pedestrian rate in the evenings); the opposite trend occurred in Capricho (a park with higher pedestrian rate in the mornings); and no difference in FID was encountered in Moro between morning and evening, matching the lack of daily pedestrian rate variation in this park.

Some risk allocation studies could not rule out habituation as a confounding factor (Hamilton and Heithaus 2001; Pecor and Hazlett 2003; Mirza et al. 2006). Although our results support the risk allocation hypothesis, they also suggest that habituation plays a complementary role in the variation in FID, but only for pedestrian approaches. As predicted, we found an interaction effect, with the decrease in FID among parks being more pronounced for human than for vehicle approaches. Predators with different size and approach speed have been found to influence FID (Stankowich and Blumstein 2005). However, we were not interested in the direct FID differences between human and radio-controlled vehicles, but instead we examined the pattern of variation in FID among parks for each type of attacker. The size and speed of our radio-controlled vehicle remained constant among parks, as well as the size and speed of approaching pedestrians. Thus, we believe that the more pronounced FID reduction considering pedestrian approaches can be associated with the development of a learned tolerance toward pedestrians in highly visited areas. In other words, habituation may enhance the effect of risk allocation on blackbird FID when individuals are approached by a known potential predator. This additional effect would be expected in those systems where the potential predators are not very dangerous for prey (like humans or opportunistic predators).

In natural systems, higher predator densities usually have negative implications on predator fitness because prey depletion, prey habitat shifts, and prey refuge use can lead to a reduction in the per capita predator–prey encounter rate (Krivan and Vrkoc 2004; Schenk et al. 2005). In our high–predator density system, we show that the prey escape responses could be less strong due to the effect of risk allocation. This reduction in the strength of escape responses could increase the probability of prey being captured in any given encounter (Cooper and Frederick 2007), particularly if prey do not show compensatory effects (Rodriguez-Prieto et al. 2008). Future models on density-dependent predator–prey dynamics could benefit from considering the negative effect of predator density on prey antipredator behavior.

Our findings have also applied implications. The reduction in FID with increasing human visitation in natural areas is usually associated with habituation to humans (Louis and Le Berre 2000; Cooper et al. 2003). Animals with enhanced tolerance are considered less affected by human visitation (Madsen 1998; Evans and Day 2001). However, our results show that the reduction in FID can also be produced by risk allocation, which could make animals reduce antipredator effort to survive in an environment with high levels of recreational activities. The reduction in FID could cause negative effects in wildlife populations, such as an increase in stress levels (Fowler 1999) and mortality due to reduced anti-predation behavior. Our results propose a potential mechanism to explain why the most responsive animals (e.g., high FID) may not be necessarily the most negatively affected by human disturbance (Gill et al. 2001; Beale and Monaghan 2004).

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