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RESEARCH ARTICLE

Relating flight initiation distance in birds to tropical dry forest restoration

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ABSTRACT. Flight initiation distance (FID), defined as the distance at which an individual flees from an approaching predator, might depend on how the individual perceives the risk of being predated. Using a standardized walking approach method on focal bird individuals, we investigated whether different levels of vegetation cover (habitat) influence the perception of predation risk. To do this, we worked in an area of tropical dry forest in central Mexico that is currently part of a restoration ecology experiment. We hypothesized that restoration decreases individual's predation risk perception by increasing the complexity of the vegetation cover. The escape responses of three tropical birds with different diets and foraging strategies were also contrasted. There was no effect of habitat on FID, suggesting that birds in both habitats perceived predation risk in a similar manner. There was, however, a difference in FID among species: the Golden-cheeked Woodpecker tolerated closer human presence before flight than the Inca Dove and Streak-backed Oriole. This difference is likely due to the use of an alternative avoidance strategy of this species, which uses trunks for hiding. To decrease birds' perceived predation risk, restoration intervention plans should include a mosaic of larger excluded plots located near relatively well-conserved sites to increase the area covered by vegetation.

KEY WORDS. Escape from predators, foraging strategies, habitat quality, predation risk, tropical birds.

INTRODUCTION

Predation risk is one of the main selective forces shaping animal behavior (Lima and Dill 1990). In particular, behavioral strategies that reduce individuals' exposure or likelihood of attack by predators should be favored (Lima 1998, Valeix et al. 2009). Predation risk results from a combination of factors affecting both attack and capture probabilities that include the structure of the environment, vegetative cover, social factors, and distribution and abundance of predators (Frid and Dill 2002), besides intrinsic species characteristics (Lima and Zollner 1996, reviewed in Weston et al. 2012). Because antipredator behavior responds to changes in these factors rather than the predation rate per se, it is expected that animals' responses to nonlethal human disturbance follow the same decision rules (Frid and Dill 2002). Riskier human approaches could reduce the opportunities for foraging and habitat use in general if the level of human disturbance is high (Miller et al. 2001, Fernández-Juricic 2000). This effect could be stronger in open habitats (Finney et al. 2005), where high visibility could increase the distance at which threats are detected (Whittingham and Karl 2004); consequently, individual perception of security should improve as vegetation cover increases (see meta-analysis in Stankowich and Blumstein 2005). On the other hand, some species may feel more secure in open areas because they can escape faster (see Ripple et al. 2001) or because areas with higher vegetation cover may allow predators to hide (Hopcraft et al. 2005). In the Nuthatch *Sitta europaea* (Linneaus, 1758), Sittidae, lower predation risk, measured as the time investment in vigilance while foraging, was associated positively with closeness to vegetation (Mozetich and Carrascal 1995). In ground-foraging birds, denser habitat structure increases visual obstruction (Butler and Gillings 2004) and may increase predation risk; alternatively, denser structure may reduce predation risk if birds are cryptic when under cover (review in Whittingham and Karl 2004 for examples in both alternatives).

Fleeing is a main predator avoidance strategy. However, it involves large potential costs due to the energetic cost of flight itself and the many costs associated with abandoning fundamental activities such as courtship, breeding, and foraging (Lima and Dill 1990). Individuals should therefore adjust their sensitivity to an approaching predator based on this balance of costs and benefits. This decision may vary within the same population, depending, for instance, on the time of day and the condition of satiation (Piratelli et al. 2015).

Flight initiation distance (FID), or the distance at which potential prey initiates flight when approached by a predator (Ydenberg and Dill 1986) is a useful measure of this predation risk sensitivity. Measuring how behavior changes depending on environmental characteristics allows the comparison of derived fitness consequences among habitats with contrasting characteristics. For example, behavior measurements enable the identification of critical resources that determine whether or not a site is suitable for a particular species (Lindell 2008).

The study of escape behavior has an important potential role in evaluating habitat quality within the framework of restoration ecology. Restoration ecology not only aims for the recovery of biodiversity per se, but more broadly aims to re-establish natural processes reduced or eliminated by human-induced disturbance. Several studies have shown that after eliminating anthropogenic disturbance in an area, the structural complexity of vegetation (i.e. density, biomass, vertical strata, percent cover) increases by natural succession, from secondary vegetation to mature forest (Lamb and Erskinepd Parrotta 2005). Heterogeneous landscapes resulting from an experimental restoration approach often include a gradient of successional stages (Howe and Martínez-Garza 2014), making them ideal systems for testing the effectiveness of using escape behavior (FID) as an indicator of the restoration of ecological processes.

Animals respond to approaching humans similarly to terrestrial predators (Frid and Dill 2002). Therefore, a standardized walking approach to focal individuals mimics the effect of an approaching predator and allows the quantification of FID. We applied this standardized approach to compare FID in three bird species with different diet and foraging strategies to evaluate the success of one of the few long-term restoration ecology experiments performed within a tropical dry forest. This biome is particularly important for conservation and restoration goals due to its high biological value in terms of endemic species as well as human habitation and resource use (Quesada et al. 2009). In this experiment, we compared FID in two habitats: areas under continued human disturbance and plots where anthropogenic disturbance has been eliminated since 2006, when cattle were removed as part of a larger ongoing restoration experiment (Martínez-Garza et al. 2011). Since restoration intervention has increased vegetation complexity (for example, De la O-Toris et al. 2012), this may lead to decreased predation risk perception, and therefore, we would expect lower FID in the three focal bird species in restored areas than in areas under disturbance. On the other hand, if higher vegetation complexity increase predation risk, FID will be higher in the restored areas. In addition, we examined between-species differences in escape behavior among two canopy-foraging birds *Icterus pustulatus* (Wagler, 1829), Icteridae, and *Centurus chrysogenys* (Vigors, 1839), Picidae and one ground-forager *Columbina inca* (Lesson, 1847), Columbidae. We expected lower FID in *I. pustulatus* and *C. chrysogenys* than in *C. inca*, since canopy-foraging species should be less vulnerable to terrestrial predators.

MATERIAL AND METHODS

Study site

The Sierra de Huautla Biosphere Reserve is a federally protected area (ca. 59 030 ha) located in the southern part of the state of Morelos, Mexico. It borders the states of Guerrero and Puebla (18°20′10″, 18°34′20″ N and 98°51′20″, 98°08′15″ W). The topography is variable and elevation ranges from 900 to 1,300 m. The mean annual temperature is 24.5 °C and the average total rainfall is 850 mm, with peak rainfall occurring between June and October. Climate is classified as tropical subhumid with summer rains (CONAGUA, Gerencia Regional Balsas). The original vegetation is tropical dry forest (Trejo and Dirzo 2000), and nearly 60 % of the total area is relatively well-conserved, particularly in steeply sloped areas (CONANP 2005). However, around 40 % of the total surface has been degraded due to deforestation for agricultural fields, wood extraction, and cattle ranching.

A large portion of tropical dry forest near the town of El Limón de Cuauchichinola (ca. 300 inhabitants, 1220 m asl) was deforested in the early 1990s, used for maize cultivation for six years, and subsequently abandoned. Despite abandonment, the area is still degraded, since the secondary forest has been used mainly to sustain cattle ranching (~ 7 head/ha, De la O-Toris et al. 2012).

Study species

All observations were conducted on medium-sized species (Howell and Webb 1995) of resident birds. Trials were carried out when each focal bird was perched alone, and during the non-breeding season, since parental care could increase risky behavior (Frid and Dill 2002). Bird species were selected because they constitute a representative and resident avifauna in the Mexican tropical dry forest (Urbina-Torres 2000), and also for their contrasting foraging behavior. The Streak-backed Oriole (*I. pustulatus*, 19–23 cm) is a frugivorous-insectivorous species that feeds in the canopy; both sexes are ornately colored with carotenoid-based yellow-orange body plumage (Jaramillo and Burke 1999, Murphy et al. 2009). The Golden-cheeked Woodpecker (*C. chrysogenys*, 19–21.5 cm) is a bark insectivore that feeds while perching on branches. Males are barred black and white with bright yellow-orange colors on the nape whereas females have a grayish crown (Howell and Webb 1995). The Inca Dove (*C. inca*, 20.5–23 cm) is a granivorous ground feeder

(Howell and Webb 1995). This dove is a secretive species that hides in low, dense vegetation, but it also occurs in human settlements (Singhal et al. 2016).

Restoration context

In 2006, 14 experimental plots (50 × 50 m) with similar vegetation and history of use were located and marked (details in Martínez-Garza et al. 2011, 2016). The plots were situated within an area of some 50 ha near the biological station "El Limón". Distance among experimental plots ranged from 0.08 to 1.59 km (0.72 ± 0.46; mean ± standard deviation). The most abundant trees species in the disturbed areas were *Acacia cochliacantha* (Humbolt & Bonpland ex Willd, 1806), *Mimosa benthamii* (Macbr, 1919), Fabaceae and *Ipomoea pauciflora* (Martens & Galeotti, 1845), Convolvulaceae, these species dominate the post-agricultural landscape, and the experimental plots (Martínez-Garza et al. 2011). There were also a few *Bursera* spp. trees, specifically maintained by local people due to their ethnobotanical value (Maldonado et al. 2013).

Eight experimental plots were enclosed with electric fences to avoid the intrusion of small and large domestic animals, and the remaining plots were marked but remained open to domestic animals. By the sixth year after exclusion, marked differences in the vegetation matrix were detected. For example, herbaceous vegetation (Poaceae and Asteraceae) cover was 20 times greater in the excluded than in non-excluded plots (Hernández-Flores et al. 2016), and tree vegetation cover was 60-80 % in the excluded plots and less than 10% in the non-excluded plots (Santana-Huicochea et al. in review). Meanwhile, in non-excluded plots the soil remained bare and degraded, sustaining poor herb biomass due to constant grazing and soil compaction by cattle (De la O-Toris et al. 2012).

Experimental design

The observer walked slowly in the plot searching for a focal individual. Once a bird was identified, the distance between the observer and the individual was recorded as escape behavior is influenced by the intruder's starting distance (Blumstein 2003). The observer then scored FID by walking directly toward the bird at a constant pace (ca.1 m/s) while maintaining eye contact, recording both the perching height and the distance at which focal individual initiated flight. Distance measurements were done with a laser rangefinder (Leica DISO D5).

Direct starting distance calculated using the Pythagorean Theorem was used as a measurement of FID, since escape behavior is often influenced by the height at which the bird was perched at in the tree (Geist et al. 2005). Measurements of FID were carried out in restored and perturbed areas (n = 8 plots per habitat). The study was conducted during April and May 2012 between 6:30 and 8:30 am. Because birds were not banded, only one trial per species was carried out per day in each plot to minimize the possibility of pseudoreplication due to observing the same individual. In total, we performed 54 trials on *I. pustulatus*, 18 trials on *C. inca*, and 50 trials on *C. chrysogenys*.

Statistical analyses

An analysis of covariance (ANCOVA) with independent slopes was performed to evaluate the effect of habitat, species, and intruder starting distance on FID. The effect of habitat was included as a nominal variable with two levels (restored and perturbed plots) with fixed effects. Species identity was included as a three-level nominal variable with fixed effects, and intruder's starting distance was included as the covariate (Blumstein 2003). To understand the effect of habitat on the expected relationship between starting distance and FID, the interaction between starting distance and habitat was included as was the interaction between species and starting distance. Raw FID was log-transformed to fulfill the assumption of homoscedasticity of residuals. All statistical tests were performed using JMP statistical software (version 4.0.3, SAS Institute, Cary, NC).

RESULTS

The ANCOVA utilized to evaluate the effect of habitat, identity of birds on FID explained 22 % of the total variance. According to the effect tests of the analysis of covariance, the species identity and starting distance (the covariate) showed a marginal and a highly significant effect, respectively, on the variation in FID (Table 1). There was a positive relationship between FID and starting distance. There was no significant effect of habitat or the interaction terms on FID (Table 1).

Due to the fact that, in this ANCOVA, the effect of habitat and both interaction terms were non-significant, a model that included only the effect of species identity, the starting distance,

Table 1. ANCOVA results for species identity, habitat, the covariate and the interaction terms on FID.

Source	DF	Sum of Squares	F	p
Species (S)	2	2.99	2.51	> 0.05
Habitat (H)	1	0.36	0.61	> 0.05
Covariate (C)	1	6.75	11.31	< 0.005
S×C	2	0.72	0.61	> 0.050
H×C	1	0.31	0.52	> 0.050

Table 2. ANCOVA results for species identity, the covariate and the interaction term on FID.

Source	DF	Sum of Squares	F	p
Species (S)	2	3.66	3.08	< 0.05
Covariate (C)	1	6.38	10.75	< 0.005
S×C	2	0.77	0.65	> 0.05

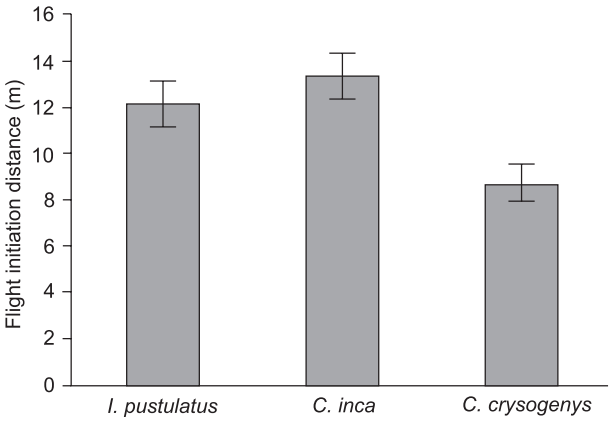

Figure 1. Mean (± SE) flight initiation distance scored in the three avian species evaluated.

and their interaction was also tested. The effect test of this ANCOVA showed statistical significance only for the effect of species identity and the covariate were statistically significant (Table 2). The post hoc mean comparison test (Tukey HSD) indicated that there was no difference in FID between *C. inca* and *I. pustulatus*, whereas the FID of *C. crysogenys* was significantly lower (they allowed a closer approach) than in the other two species (Fig. 1).

DISCUSSION

The significant effect of starting distance (the covariate) indicates that birds in our study, were on alert to potential predators. This is consistent with the hypothesis that animals should not pay the attentional cost for continued monitoring of an approaching predator and should flush at a greater distance as starting distance increases (Blumstein 2003). However, our results show no association between the escape behavior and habitat, demonstrating no effect yet of restoration intervention on FID for these three species after six years. In contrast, there was a significant between-species difference; the Golden-cheeked Woodpecker was more tolerant of human approach than Inca Doves or Streak-backed Orioles in both habitats. We discuss the likely explanation for the lack of effect of restoration intervention and the implication of our results on the design of restoration projects in tropical dry forests. We also discuss the causes explaining inter-specific differences in the perception of security independent of restoration intervention.

We propose three possible non-exclusive explanations for the lack of differences in FID between habitats. First, while restoration actions clearly increased cover of both herbaceous (Hernández-Flores et al. 2016) and tree vegetation, it is possible that the vertical complexity in the restored areas may have been insufficient to increase birds' perception of security. This is because although planted tree increased cover their vertical growth was still limited after six years.

Second, it is also possible that the lack of effect of habitat could result from the geographic scale at which restored plots are present within the landscape. The 50 × 50 m plots could represent very small vegetated patches in comparison with the overall landscape (~50 ha), which is mainly composed of open areas and a broken canopy of trees. Birds may have been unable to perceive the decreased risk at this scale, and the landscape's fragmented physiognomy may have even produced edge effects with higher predation risk. Small patches were perceived as risky sites by birds (Batary and Baldi 2004) and rodents (Baker and Brown 2010) in forest restoration plots in Costa Rica, whereas increased patch area and canopy cover were associated with longer duration of bird visits (Fink et al. 2009). Also in Costa Rica, restoration patches of tens to a few hundred square meters offered less cover from predation risk for insectivorous and omnivorous birds, including Cherriés tanager, *Rampochelus costaricensis* (Lesson, 1831), Thraupidae; Ruffous-capped warbler, *Basileuterus rufifrons* (Swainson, 1838), Parulidae; Common tody-fly-catcher, *Todirostrum cinereum* (Linnaeus, 1766), Tyrannidae; and Plain wren, *Thryothorus modestus* (Cabanis, 1861), Troglodytidae (Morrison et al. 2010). The authors therefore recommended that patches of at least a few thousand square meters be planted to reduce the predation risk perception of birds.

Third, the study site is within an ecologically fragmented matrix, surrounded by secondary forest, maize cultivation plots, open areas with limited vegetation and eroded soil. Individuals could have been sensitized by frequent proximity to humans or cows (i.e. perceive greater risk from repeated exposure to the predator type, see Stankowich and Blumstein 2005). Indeed, a meta-analysis found that experience with predators increased the prey's perception of predation risk by 38 % (Stankowich and Blumstein 2005), and the same study reported a greater FID in bird species during hunting seasons, when species face higher exposure to human predators than at other times. In the case of our study site, birds are frequently exposed to human and cow presence, since the plots are surrounded by paths where people frequently walk, ride on horseback, or travel in small trucks; these areas are also used by cattle during the rainy season. It is possible that habituation to repetitive human and cow stimuli resulted in similar levels of wariness both in open sites and those with more vegetative cover. On the other hand, it is possible that local birds have been selected for tolerance to humans and cows (see Dongen et al. 2015). It would be interesting to evaluate this hypothesis in our study site.

The decreased FID in the Golden-cheeked Woodpecker compared to the other two species was contrary to our prediction. This was also contrary to the general expectation that FID increases with body size (see Blumstein 2006, and Piratelli et al. 2015), since this was the largest of the three species studied. We suspect that the decrease in FID was due to specialized feeding habit. Golden-cheeked Woodpeckers perch on small branches and move around the trunks while gleaning prey from the bark. This behavior allows individuals to hide when a predator ap-

proaches, essentially providing an alternative strategy to flight. In this study, woodpeckers were observed moving around the trunk (i.e. maintaining the trunk between themselves and the "predator") and observing the "predator" before taking flight. This hiding behavior could account for the higher tolerance in terms of FID to an approaching predator than the other species studied. Streak-backed Orioles, on the other hand, are likely unable to apply this hiding strategy due to their conspicuous coloration. In this part of the species' geographic range, both sexes are ornately colored with carotenoid-based yellow-orange body plumage and vivid crimson-orange feathers on the head and breast (Murphy et al. 2009). In species where camouflage/hiding is not a predator avoidance option, individuals are likely to be less tolerant to an approaching predator in any habitat. It would be interesting to test this prediction in species where one sex has a more conspicuous ornamental trait to verify whether FID is larger in the more conspicuous sex (see Møller et al. 2015).

Interestingly, the Inca Dove, a species that occurs in urbanized sites, was less tolerant to human approach than Golden-cheeked Woodpeckers. The Inca Dove is a ground forager with low aspect ratio. Individuals find small seeds by picking at the soil surface in open sites. While foraging, individuals maintain their heads down and have limited predator detection capacity. Birds with a lower aspect ratio have longer FID as they have limited potential to escape from predation (Møller 2014). The Columbiforme clade has developed a greater mass-specific power output due to relatively shorter wings with higher beat frequencies (Jackson 2009), which enables an energetic vertical flight to escape from predation. Inca Dove behavior may be subject to a "flush early and avoid the rush" trade-off (Blumstein 2010), where the higher energetic investment of fleeing early is compensated by a reduction of the attention cost of monitoring an approaching predator (Samia et al. 2013).

Animals' behavior and decisions can be useful indicators to evaluate the success of habitat management actions for birds in different context as restoration ecology, urban parks and protected areas. In this study, we found that for medium sized bird species, small (ca. 2500 m^2) and isolated restored plots may not decrease perceived predation risk. Therefore, to decrease birds' perceived predation risk, restoration plans should include a mosaic of larger excluded plots located near relatively well-conserved sites to increase the area covered by vegetation. Wildlife managers should use FID in zones that are far removed from human impact on wild species to avoid possible sensitization or habituation effects. So, in conjunction with restoration plans it is important to identify buffer zones in order to avoid disturbance induced by human activity.

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