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The emergence of tolerance of human disturbance in Neotropical birds

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Research Article

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Abstract

Animals living close to human settlements more often experience disturbance, but also reduced predation risk. Because an escape response is costly, behavioural adjustments of animals in terms of increased tolerance of humans occurs and is often reported in the literature. However, most such studies have been conducted in and around long-existing cities in Europe and North America, on well-established animal populations. Here, we investigate the degree of tolerance of human disturbance across 132 bird species occurring in disturbed (small farms) and undisturbed (intact wetlands and grasslands) areas in Pantanal, Mato Grosso (Brazil), a region with only a very recent history of human-induced disturbance. We found a clear across-species trend toward higher tolerance of human disturbance in birds near farms when compared with birds in wild areas. Such a flexible and perhaps also rapid emergence of tolerance when facing small-scale and very recent human disturbance presumably involves learning and might be attributed to behavioural plasticity. The ability of birds to modify their degree of tolerance of human disturbance may play a key role in the facilitation of wildlife–human coexistence.

Introduction

Anthropogenic environmental change is often responsible for biodiversity loss (Dirzo *et al.* 2014, McKinney 2002), and ecologists increasingly seek to study the effects of human activity on wild-living animals. However, many animal taxa, including birds, invade human settlements and capitalize on the sympatry with humans, for example, because of lower predation (Díaz *et al.* 2013) and lower parasitism risk (Calegaro-Marques & Amato 2014), increased food availability (Tryjanowski *et al.* 2015) and favourable microclimate (Stewart & Oke 2012). Anthropogenic activity considerably alters ecosystem patterns and processes in affected areas, hence appropriate behavioural adjustment may be an important factor that enables species to successfully invade urbanized areas and coexist with humans.

Animals often consider humans as a predatory threat and even non-lethal human activities affect animal behaviour equivalently to predation risk (Frid & Dill 2002). Proximity to humans leads to frequent disturbances and recurrent escape responses that are costly, both directly (metabolic costs) and indirectly (e.g. reduced food intake) (Cooper & Blumstein 2014, Tatner & Bryant 1986); hence it is advantageous to habituate and increase the degree of tolerance of human presence. Although behavioural adjustment to environmental settings is a very complex process, modified by a myriad of factors (Stankowich & Blumstein 2005), birds consistently increase their tolerance to humans in urbanized areas across the world (Díaz *et al.* 2013, Samia *et al.* 2015). However, most previous studies were conducted in and around long-established cities in Europe and North America, on well-established animal populations (Blumstein 2019, Díaz *et al.* 2013, Samia *et al.* 2015). Therefore, it is still unclear how animals respond to anthropogenic disturbance when only recently exposed to it, i.e. at the beginning of the process of urbanization.

Here, we used a field experiment to study the tolerance of wild birds (estimated as flight initiation distance, FID) to human disturbance in the tropical area of Pantanal, the largest freshwater wetland ecosystem in the world (a UNESCO World Heritage Site; Alho *et al.* 1988). Similar to many other remote tropical areas around the world, the Pantanal ecosystems are threatened by increased anthropogenic land-use; habitat loss due to its conversion to farmland and other anthropogenic uses (Richards & VanWey 2015, Zalles *et al.* 2019) and growing ecotourism (Bouton *et al.* 2005). However, annual flooding negatively affects the local economic activities of humans, causing the local human population to still be relatively small

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and penetration into many remote areas by humans is very recent, within the last 50 years (Alho *et al.* 1988, Silva *et al.* 2017). We studied the tolerance of humans of birds that occupy areas near small, recently established farms and surrounding undisturbed grassland areas. We predicted that birds associated with human settlements were expected to exhibit higher tolerance of human disturbance than birds in natural areas.

Methods

Study site

The study took place near Porto Jofre (17°21′51.8″S, 56°46′24.6″W), Pantanal, Mato Grosso, Brazil. The study site is a part of the Poconé subregion in the northern Pantanal which is characterized mainly by open areas, such as grasslands and temporal wetlands. Human settlements have only occurred here since the 1970s. The human population is concentrated in one city, Poconé, otherwise occupying single farms or small villages, hotels and resorts distributed close to the 140 km main road *Transpantaneira* to Porto Jofre. Human activities, such as farming, occur in and close to human settlements. Moreover, waste food and occasional deliberate bird feeding occur on farms. Hunting is not practiced very close to human settlements; in general, hunting pressure is greater in more remote tropical areas (Benítez-López *et al.* 2017). Altogether, opportunities for habituation by birds to non-lethal interactions with humans are greater near human settlements, such as farms, than in surrounding natural areas.

Data collection

Flight initiation distance. Tolerance of birds to human disturbance was estimated by a widely used technique, termed flight initiation distance (FID), that represents a trade-off between the benefits of staying put and the costs of escape (Díaz *et al.* 2013, Samia *et al.* 2015, Stankowich & Blumstein 2005). FID estimates were collected during two seasons (October–November, 2017 and 2018). Birds were approached during favourable weather conditions (sunny days with no rain or strong wind) during the morning (6:00–10:00). We approached birds in two habitat types significantly differing in the level of human activity. First, we collected data near recently established farms; the term ‘farm’ refers to area near human settlements used for crop production and pasture. Second, we focused on natural open areas, such as grasslands and temporal wetlands. In both farms and natural areas, we approached birds at sites characterized by low vegetation which were >100 hectares in size.

FID data were collected using a standard procedure (Blumstein 2006) adopted in our previous studies (Díaz *et al.* 2013, Mikula *et al.* 2018). In brief, when a target bird (either a singleton or a randomly selected bird in a single species flock) was spotted by a researcher (usually using binoculars), the researcher moved at a normal walking speed directly towards the target bird, while recording the number of ~1 m paces. The FID was then estimated as the distance (equal to the number of paces) from the researcher to the bird when the bird first started to escape. When the target bird was in vegetation or on an artificial structure, the researcher estimated its height above ground to the nearest metre; FID was then calculated as the Euclidean distance based on horizontal and vertical distances. Large FIDs indicate low tolerance, whereas small FIDs indicate a high tolerance of humans. FID estimates were sampled by systematic searches of the study area but simultaneously we avoided re-sampling by moving to another site (≥300 m away) after each sampling. We focused only on bird individuals engaged in foraging and comfort behaviour (e.g. roosting or preening). We did not approach birds sitting on nests or caring for fledglings or birds exhibiting highly vigilant behaviour. Almost all data were collected by a single person (PT = 90% and MH = 10% of all estimates) to avoid a multiple collector effect. When collecting FID data, researchers wore standardized dull outdoor clothing. We collected data also on starting distance (defined as the distance between the researcher's position and the bird when first spotted) and flock size in which the target bird occurred.

Starting distance. Starting distance has often been found to be strongly positively correlated with FID (Blumstein 2006, Mikula *et al.* 2018). Hence, we measured the starting distance, defined as the distance between the researcher's position and the bird when first spotted.

Flock size. When approached by humans, birds in flocks often behave differently compared with single birds, for example, because of ‘dilution’ or ‘many eyes’ effects (Mikula *et al.* 2018, Pulliam 1973, Roberts 1996). Hence, when estimating FID, we also collected data on flock size in which the target bird occurred.

Statistical analysis

Animal behaviour, including escape behaviour, is influenced by phylogenetic relatedness of taxa because related taxa have a higher probability of sharing similar characteristics from a common ancestor than from distant taxa. First, we tested for differences in mean FID (log10-transformed) of natural and farm-associated populations of same species (where available) by a phylogenetic paired two-tailed t-test, using the ‘phyl.pairedttest’ function implemented in the phytools R-package (Lindenfors *et al.* 2010).

However, potential differences in FID between birds in natural and farm areas can be affected by confounding factors such as starting distance, flock size, taxonomy or phylogenetic relationships between species. First, we built a multivariable linear mixed model (LMM) to explore variation in FID (response variable) in relation to habitat type (natural/farm), starting distance and flock size (predictors). We used lme4 R-package (Bates *et al.* 2014) for LMM with species introduced as a random factor; fitted by maximum likelihood. We also built a model where species was replaced by bird family but the conclusions were the same; hence, we present only results for the model with species as a random factor. All continuous variables were log10-transformed before analysis. The response variable and all continuous fixed effects were centred and scaled to allow comparison of estimated effect sizes. We assessed the degree of multicollinearity among the predictor variables by calculating variation inflation factors (VIFs) using the ‘vif’ function in car R-package (Fox & Weisberg 2016). In general, a VIF > 4 indicates a possible collinearity, and a VIF > 10 indicates strong collinearity (Neter *et al.* 1996). The VIFs were < 1.42 in all cases, suggesting weak multicollinearity between predictors. Variances explained by the fixed and random effects (conditional R^2) and by the fixed effects (marginal R^2) were calculated using the ‘r.squaredGLMM’ in MuMIn R-package (Nakagawa & Schielzeth 2013). A LMM revealed that birds near farms were more tolerant than birds in natural areas; tolerance of birds also positively correlated with starting distance and flock size (Table 1). This approach produced the same results as the phylogenetically informed mixed model (see below), hence, we report only the results from the latter model in the Results section.

Table 1. Associations between flight initiation distance (FID; response variable) and habitat type (natural/farm), starting distance and flock size (predictors) in birds of Pantanal, Brazil. We modelled FID–predictor associations by a linear mixed model (LMM) with species identity introduced as a random factor. Response and predictor variables were log10-transformed before analysis. A LMM explained > 80% of the variation present in the data (conditional $R^2 = 0.84$; marginal $R^2 = 0.81$)

Predictor	Estimate ± SE	df	t-value	P
Intercept	0.306 ± 0.027	84.059	11.562	<0.0001
Habitat (farm)	−0.511 ± 0.028	1114.111	−18.345	<0.0001
Starting distance	0.705 ± 0.017	457.030	41.089	<0.0001
Flock size	0.043 ± 0.013	934.900	3.179	0.0015

Table 2. Associations between flight initiation distance (FID; response variable) and habitat type (natural/farm), starting distance and flock size (predictors) in birds of Pantanal, Brazil. Associations were examined using a multivariable model based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with phylogeny (the maximum credibility tree) as a random effect. Response and predictor variables were log10-transformed before analysis. We report estimates of the posterior mean with 95% credible intervals (lower and upper CI), P values and posterior mode of the phylogenetic signal (lambda)

Predictor	Posterior mean	95% CI	lambda	P
Intercept	0.098	−0.014–0.223	0.243	0.0922
Habitat (farm)	−0.226	−0.249– −0.201		<0.0001
Starting distance	0.062	0.026–0.100		0.0008
Flock size	0.869	0.818–0.915		<0.0001

Then, we investigated association between FID (response variable) and habitat type (natural/farm), starting distance and flock size (predictors) by a phylogenetic generalized linear mixed-effect model (PGLMM) (Ives & Helmus 2011). All continuous variables were log10-transformed before analysis. We performed PGLMM by Bayesian inference using the Markov chain Monte Carlo technique (MCMCglmm; Hadfield 2010, Hadfield & Nakagawa 2010). To control for phylogenetic relationships among species, we entered a single maximum credibility phylogenetic tree as a random factor in the model. First, we generated 1000 trees using the Hackett backbone at the online platform available at http://birdtree.org/ (Jetz *et al.* 2012). The maximum credibility tree was then reconstructed using the TreeAnnotator tool v. 1.8.2 in BEAST software v. 1.8.2 (Drummond & Rambaut 2007). We used an uninformative inverse-gamma prior for random effects and an uninformative prior for the residual variance. The model was run for 1 million-iterations with a burn-in of 20 000 iterations and thinning of 100. We then checked convergence of model parameters (fixed and random effects) using the Gelman–Rubin statistic that compares within- to between-chain variance and calculates the potential scale reduction factor (Gelman & Rubin 1992). The posterior fixed effect distribution was examined for overlap with zero (i.e. the significance test), using a 95% highest posterior density as a credible interval. Finally, we estimated a value of the phylogenetic signal (lambda) to estimate the proportion of variance in FID in a multivariable model which is explained by the effect of phylogenetic relatedness.

All primary data (Supplementary Material 1), phylogenetic tree (Supplementary Material 2) and R code (Supplementary Material 3) are deposited as supplementary material. All statistical analyses were conducted in RStudio 0.98.1103 (R Development Core Team 2019).

Results

Altogether, we collected 1120 flight initiation distances (FIDs) from 132 bird species. The number of estimates per species ranged from 1 to 64 (mean ± SD = 8.49 ± 10.45, median = 4). FIDs of sampled birds were highly variable (raw mean ± SD = 23.31 ± 25.97 m; range = 1–221 m; median = 15 m). Sampling effort was similar in both habitat types (527 and 593 estimates for natural and farm areas, respectively).

The phylogenetically informed analysis of paired same-species populations revealed that birds showed a consistently larger tolerance (shorter FID) to humans in disturbed (farms) than in natural areas (phylogenetic paired t-test, $t = 21.64$, 95% CI (0.38, 0.46), $df = 82$, $\lambda = 0$, $P < 0.0001$, $N = 85$ species; raw mean ± SD (m) = 36.84 ± 25.79 for natural and 14.07 ± 10.08 for farm birds, respectively) (Fig. 1). The MCMCglmm supports these results and revealed significant associations between degree of tolerance of birds and habitat type, but also starting distance and flock size (Table 2). Birds approached near farms were more tolerant of approaching humans than birds in natural areas. Simultaneously, birds were more tolerant when approached from a shorter starting distance and when in smaller flocks.

Discussion

We found that birds approached around farms exhibited consistently higher tolerance toward humans than birds in natural areas. Although such a pattern is widely reported from elsewhere (Díaz *et al.* 2013, Samia *et al.* 2015, 2017), we document that the emergence of tolerance toward human disturbance is widespread also in bird populations which were only recently disturbed by anthropogenic activity. Therefore, our results may shed light on the behavioural adjustments of animals necessary for a successful exploitation of human-disturbed areas during the initial stage of their synurbanization. Moreover, this study may be useful for a more general understanding of the impact of urbanization on animal behaviour because our knowledge on this phenomenon is strongly skewed towards temperate regions (Blumstein 2019, Díaz *et al.* 2013, Ortega-Álvarez & MacGregor-Fors 2011).

Tolerance of animals toward humans is a gradual process with animal populations that have a longer history of inhabiting urbanized areas having a greater tolerance of humans (Møller *et al.* 2012, Symonds *et al.* 2016). However, the majority of previous studies focused on populations around long-established urban areas and the majority of birds became urbanized several decades ago (e.g. on average > 50 years ago in Europe; Møller *et al.* 2012). We have shown that individuals of numerous wild-living bird species in Pantanal respond flexibly to human-altered environmental conditions as indicated by a dramatic decrease of FID among synurbic populations. Flexible and perhaps rapidly emerging changes in behaviour can be attributed to behavioural plasticity which seems to be particularly important during the initial stages of establishment of populations in urbanized areas (Sol *et al.* 2013). However, although behavioural plasticity is surely important at this stage, one has to bear in mind that species

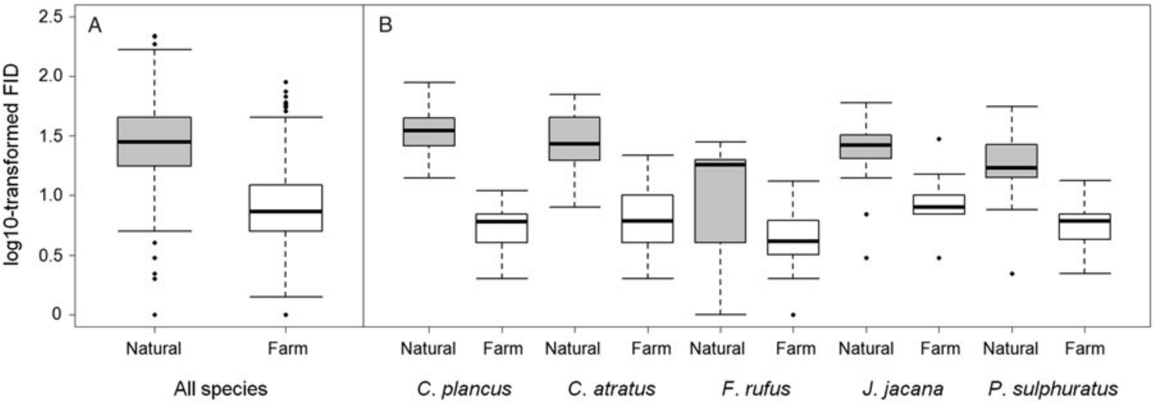

Figure 1. Flight initiation distance (FID) of birds approached in natural areas (grey) or near farms (white) in Pantanal, Brazil. (A) represents overall FID for all sampled bird species (N = 1120 FID estimates), (B) represents a subset of five most frequently examined species: *Caracara plancus* (N = 48), *Coragyps atratus* (N = 41), *Furnarius rufus* (N = 64), *Jacana jacana* (N = 37) and *Pitangus sulphuratus* (N = 43) (ordered in alphabetical order). Box plots show the median (horizontal line in the middle of the boxes), upper (75%) and lower (25%) quartiles (top and bottom of the box), 1.5 times the inter-quartile range (whiskers) and outliers (points outside of 1.5 times the inter-quartile range; black dots).

occupying invading urban areas usually represent a non-random subset of species available in the regional pool (Sol *et al.* 2013, 2014). Nevertheless, the ability of birds to modify their degree of tolerance of human disturbance may represent an important mechanism enabling wildlife–human coexistence. This may be crucial for their survival at a time of rapid human-induced environmental changes in the tropics in general, and in Brazil in particular (Richards & VanWey 2015, Zalles *et al.* 2019).

Large wild areas where human activity was not detectable until recently, such as many tropical regions, offer a valuable opportunity to study how and when birds and other animals begin to invade human settlements. For instance, it is almost impossible to precisely identify a time and place when and where some animal populations started to do this in long-term and heavily urbanized regions such as in Western Europe. Møller *et al.* (2012) have shown that a year of urbanization among same-species populations across Europe is highly repeatable, suggesting that the initial establishment of an urbanized population in one area is followed by a rapid spread of this behaviour across other populations. Extrapolating from this, small and recently established human settlements may, at least in some world regions such as Pantanal, represent starting points where synurbanization begins, facilitating subsequent penetration of animals into other urbanized areas. Moreover, given that most human settlements in our study site were built <40 years ago and are already widely exploited by birds indicates that the history of animal exploitation of urbanized areas may be significantly older in many world regions than previously thought.

In conclusion, we have demonstrated that individuals of many bird species, until recently occurring in intact areas with regard to human-driven habitat exploitation, exhibited increased tolerance of humans. This indicates that birds of at least some species are able to cope with human-altered conditions very flexibly by behavioural adjustments. Since our study was conducted in a region where urbanization is very recent, it may extend our knowledge of the fundamental aspects of behavioural adjustment in animals at the beginning of the synurbanization process. Finally, identification and understanding of behavioural processes and mechanisms which enable birds and other animals to cope with anthropogenically altered environments may contribute to designing effective conservation strategies that reduce the negative effects of human disturbance on biodiversity in a rapidly urbanizing world.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467419000282

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