Human influences on antipredator behaviour in Darwin's finches

Kiyoko M. Gotanda[1]*

[1] Department of Zoology, University of Cambridge, Cambridge, United Kingdom CB2 3EJ

Telephone: +44 (0) 1223-767130, Fax: +44(0) 1223 336676, Email: kg419@cam.ac.uk

* Corresponding author

Running Title: Behaviour in Darwin's finches

Keywords: Galapagos, invasive predators, flight initiation distance, urbanization, post-eradication

Abstract

In the Galapagos, humans have established a permanent presence and have altered selective pressures on local and endemic species through influences such as invasive predators and urbanization. I quantified flight initiation distance (FID), an antipredator behaviour in Darwin's finches, across multiple islands in the Galapagos to address two questions: (i) does antipredator behaviour change in the presence of invasive predators and importantly, what happens once invasive predators have been eradicated and (ii) to what degree does urbanization affect antipredator behaviour? The Galapagos Islands offers a system of among island differences in invasive predator regime as well as degree of urbanization presenting an opportune place to answer these two questions. Furthermore, this is one of the first studies to look at behaviour in an endemic species after successful eradication of invasive predators. FID was higher on islands with invasive predators as compared to islands with no predators. On islands from which invasive predators were eradicated ~11 years previously, FID was also higher than on islands with no invasive predators. Within islands that had both urban and non-urban populations of finches, FID was lower in urban finch populations, but only above a threshold human population size. FID in larger urban areas on islands with invasive predators was similar to or *lower* than FID on islands with no history of invasive predators. Overall, these results suggest that for antipredator behaviour, invasive predators can have a lasting effect on antipredator behaviour, even after eradication, and that the effect of urbanization can strongly oppose the effect of invasive predators, reducing antipredator behaviour to levels lower than found on pristine islands with no human influences. Together, we can begin to understand how human influences are affecting antipredator behaviour which could help inform future conservation and management efforts on islands.

"All of [the terrestrial birds] are often approached sufficiently near to be killed with a switch, and sometimes, as I myself tried, with a cap or a hat." – Charles Darwin in "The Voyage of the Beagle"

Introduction

Human influences such as invasive species and urbanization can strongly affect the process of local adaptation [1–4]. Such effects are amplified on islands such as the Galapagos Islands, where small population sizes and strong isolation increase the vulnerability of local flora and fauna to human influences, often resulting in loss of island biodiversity through extinctions [5–8]. Among the endemic species on the Galapagos Islands are Darwin's finches, an iconic example of an adaptive radiation in which a single founding species has evolved into several species, each with different adaptions (e.g. beak shapes and body sizes) to exploit different ecological niches [9,10]. Humans began establishing settlements on the Galapagos in the early 19th century [11], and since then, human influences such as invasive predators and urbanization have affected several islands on the Galapagos. Many organisms initially respond to such human influences through behavioural adaptations. Here, I consider how two human influences – invasive predators and urbanization – might alter antipredator behaviour in Darwin's finches on the Galapagos Islands.

Invasive predators have strong ecological and evolutionary effects [1,2,12,13], and this impact is known to be correlated with local extinction events [14,15]. On islands, the lack of predators and correlated relaxed selection can result in reduced antipredator behaviour [16–19]. This evolutionary naïveté of isolated animals that have evolved without major predators can contribute to the extirpation of island species [17,18,20,21]. In particular, house cats (*Felis silvestris catus*) are of concern for island biodiversity because cats target small animals such as birds and reptiles [22–25], and invasive house cats now exist on four islands of the Galapagos [26], presenting a critical threat for Galapagos biodiversity [27,28]. Past research on the effects of invasive predators in the Galapagos has focused on behavioural adaptations in reptiles [e.g., 27,29], and thus, little is known about the effect of novel mammalian predators on endemic land birds. Given the resulting selective pressures, natural selection should favour an increase in antipredator behaviour after the introduction of an invasive predator to reduce mortality.

Effective conservation management, especially on islands, often involve eradication of invasive predators to protect the local and endemic species [30,31]. Post-eradication research typically follows local and endemic species population recovery [32–34], monitors the re-introduction of extirpated species to previously abandoned breeding grounds [35], or focus on major ecological effects such as changes in food web dynamics [32,36]. All this research contributes to the growing need to understand post-eradication effects [33,34,37], yet surprisingly little research has focused on post-eradication behavioural adaptations, nor how quickly such behavioural adaptations might occur. Post-eradication behavioural adaptations could have population-level consequences on fitness. For example, increased antipredator behaviour can have associated costs due to the reallocation of energy and time away from other important behaviours such as foraging, reproduction, and rearing of young [38–40], and so if antipredator behaviours are maintained even after eradication, that might result in a decrease in fitness for local and endemic species, which could struggle to recover as a result. Thus, understanding how local and endemic species will behaviourally adapt post-eradication could help improve conservation efforts. On the Galapagos, some islands have invasive house cats, some have remained free of invasive predators, and someislands have successfully eradicated invasive predators. This allows for among-island comparisons of antipredator behaviour in relation to the current and historical invasive-predator regime.

Urbanization has rapidly increased in the past century, with more than half the world's population occupying urban settlements, severely altering patterns of selection and adaptation [3,4,41]. In general, animals such as birds show decreased antipredator behaviour in urban areas compared to rural areas, likely due to habituation to humans [42–45]. However, such a reduction in antipredator behaviour in urban areas could make organisms more vulnerable to different threats, such as invasive predators. Quantifying the degree to which urbanization can reduce antipredator behaviours can inform our understanding of the impacts of urbanization. Can urbanization reduce antipredator behaviour to levels *before* the introduction of predators?

The Galapagos Islands represent an excellent opportunity to study the effects on invasive predators and urbanization for two key reasons that few, if any, other systems offer. First, few other archipelagos in the world have islands that vary not only in the presence or absence of invasive predators, but also in whether eradication of invasive predators has been accomplished. Second, islands differ not only in the presence or absence of urban centres, but also in the size of the urban centres, representing a novel opportunity to compare antipredator behaviour in urban and non-urban setting, as well as among islands that have or have not developed urban centres. The isolation of the Galapagos Islands removes potentially confounding factors such as high gene flow or continued influxes of introduced predators, allowing me to ask two key questions regarding human influences and antipredator behaviour. First, I ask how will antipredator change in the presence of invasive predators and perhaps more importantly, what will happen *after* eradication of invasive predators from an island? Very little research has been done on behavioural adaptations post-eradication. Second, I ask how much can urbanization reduce antipredator behaviour – can it be reduced to levels found on islands with no history of invasive predators? While we know how urbanization can affect behaviour, we have no sense of the *degree* to which urbanization is affecting behaviour because it is difficult to find a system in which we can assess baseline behaviour before urbanization occurred (e.g. islands with no history of permanent human populations). On the Galapagos, islands vary in their exposure to human influences, allowing me to answer these questions. Together, these two questions can inform how human influences are affecting antipredator behaviour on isolated islands.

Materials and methods

Site descriptions

The Galapagos Islands are a volcanic archipelago located ~1,000 km off the coast of Ecuador. Local or endemic predators such as owls, or snakes are found on all islands (Supplemental Table 1; Swash & Still 2005). Snakes are thought to prey on the nestlings of ground finches, and are thus an unlikely predator. However, short-eared owls are known predators of adult land birds such as Darwin's finches [47]. Galapagos Hawks, also predators of ground finches [48,49], are found on four (Santa Fe, Española, Isabela, and Santa Cruz) of the eight islands surveyed in this study [46,50]. Unfortunately, little data are available about the current densities of local and endemic predators on these islands; however the ecology of the local and endemic predators is well documented, and can thus be assumed to be predators of finches. The invasive predator regime (presence of house cats) on the islands (Supplemental Table 1) were classified as: present (Floreana, Isabela, San Cristobal, Santa Cruz), pristine (Santa Fe, Española), or successful eradication (Baltra, North Seymour). House cats and rodents were successfully eradicated from Baltra in 2003 [26,51], and rats from North Seymour in 2008 [52,53]; I will refer to these as "eradicated" below for brevity. The two pristine islands and two eradicated islands have no permanent human populations. On the four islands with human populations (Floreana, Isabela, San Cristobal, Santa Cruz), site urbanization categories were classified as: urban (in town) or non-urban (remote areas several kilometres away from town and not visited by tourists). Islands with permanent human populations and no presence of invasive predators nor pristine islands with permanent human populations exist in the Galapagos archipelago, and thus, I am restricted to the among island comparisons outlined above.

Data collection

Flight initiation distance (FID), the distance at which a prey flees an approaching predator, is a metric used to quantify antipredator behaviour [38–40]. An individual's decision to flee is influenced by the perceived costs and benefits of remaining or taking flight, which means FID can be an indicator of how an organism assesses risk, and thus, antipredator behaviour. Data were collected from 2015 to 2018 on eight islands of the Galapagos archipelago, generally between February and April (some data on San Cristobal were collected in November 2017).

FID measurements were performed with a human stimulus following methods from Blumstein [54]. A focal finch was located by walking and searching the landscape at a slow walking pace, and the finch's initial behaviour was noted. To minimize the possibility of pseudoreplication, in a given day, each trial ensured the focal finch was of a different sex, species, or age class (for male *Geospiza spp.*) than finches that had previously been approached. However, it is possible the same bird might have been approached on different days or years because the finches were not individually banded. Birds were located in areas that had relatively open habitat to ensure a straight approach by the human and a clear sightline from the human to the finch. The human would then approach the focal finch at a standardized speed (~2 m/s). Human stimuli always wore neutral-coloured clothing, and looked at the focal individual while approaching.

Flight was considered to have been initiated if the finch extended its wings and flew; the distance flown could be short (<0.5 m) or substantial (out of sight). Finches that hopped away instead of taking flight were omitted from the study, though this was a rare occurrence. A marker was placed where the finch originally was and where the stimulus was when the finch took flight, and the distance between these markers was the FID. Because of the complexity of the landscape, the distance at which the stimulus started from could not be standardized [54–56], and so I noted the distance from where the human started to the flight-initiation marker (starting distance). Alert distance, the distance at which an individual is aware of the approaching stimulus [57], could not be quantified because the focal individual was often foraging on the ground and would repeatedly raise its head, and so normal foraging behaviour was indistinguishable from an alert reaction to an approaching human.

Each data point collected included the island, invasive predator regime, urbanization category (on islands with permanent human populations), finch species and sex, time of day, and group size (was the focal finch in a group and if so, how large was the group). Finch sex was identified by plumage, and for ambiguous cases and non-sexually dimorphic species (e.g. warbler finches), sex was denoted as unknown. Time of day was noted because birds are most active at dawn and at dusk, so baseline activity levels and behaviours can vary throughout the day. Group size was noted because it could increase FID because larger groups mean more observers and thus, detection of a potential threat will occur when the threat is still a longer distance away [38]. Conversely, group size could decrease FID through the dilution effect where the probability a predator will target a specific individual decreases as group size increases [40]. Island size was also noted [58] to account for potential among island environmental differences due to different area.

Statistical analysis

All analyses were done in R (version 3.4.3). To meet assumptions of normal distributions, FID and starting distance (the distance between the focal finch and the stimulus starting position) were log-transformed. Then, FID and starting distance were centred by subtracting the mean from each value and then dividing by the standard deviation. Because starting distance could not be standardized and is known to affect FID, it was included as a covariate, as was group size, time of day, and island size. Lastly, sex was included as a fixed effect and species was included as a random effect. Sample sizes for some species across islands were unbalanced (Supplemental Table 2); therefore, I also repeated all analyses using one species, *Geospiza fuliginosa*. Further analysis details are below, but in general, linear mixed models were performed using lmer() from the lme4 package [59] and Anova() from the car package [60]. Random-effect significance (species and/or island) was determined with ranova(), and post-hoc pairwise comparisons for fixed factors in the linear mixed models used difflsmeans(), both from the lmerTest package [61]. R^2 values were calculated with the r.squaredGLMM() from the MuMIn package (version 1.42.1).

How does antipredator change in the presence of invasive predators and what happens following eradication of invasive predators from an island?

On islands that had both urban and non-urban populations, only data from non-urban sites were used for this analysis. A linear mixed model was performed with invasive-predator regime as a fixed factor, island and species as random factors, and time of day, starting distance, island size, and group size as covariates; post-hoc comparisons focused on pairwise comparisons between invasive-predator regimes. This analysis were performed twice, once with all finch species, and once with only small ground finches, *Geospiza fuliginosa*. To determine whether FID varied among islands within a given invasive-predator regime, I ran a linear mixed model with island as a fixed factor, species as a random factor, and time of day, starting distance, and group size as covariates; post-hoc comparisons were focused on pairwise comparisons between islands within a given invasive-predator regime. This analysis was repeated as a linear model with only small ground finches, *Geospiza fuliginosa*. For this analysis, post-hoc analyses were a Tukey's HSD (honestly significant difference) test.

How much can urbanization reduce antipredator behaviour?

Only data collected from the four islands with permanent populations were used for this analysis. A linear mixed model was performed with site urbanization as a fixed factor, island and species as random factors, and starting distance and group size as covariates. These analyses were performed twice, once with all finch species, and once with only small ground finches *Geospiza fuliginosa*.

Results

How does antipredator change in the presence of invasive predators and what happens following eradication of invasive predators from an island?

On islands with invasive predators and islands where predators have been eradicated, FID was significantly higher than on pristine islands (Table 1, Figure 1). Post-hoc comparisons showed that pristine islands (Santa Fe and Española) had marginally non-significant decreased FID when compared to islands with invasive predators (Figure 1; $p = 0.063$) and eradicated islands (Figure 1; $p = 0.014$), and eradicated islands did not differ in FID when compared to island with invasive predators (Figure 1, $p = 0.192$). As group size increased, FID increased (Table 1, Supplemental Figure 1). Analysis with data only for small ground finches had comparable results with the only differences being group size was no longer significantly correlated with FID (Table 1) and a post-hoc comparison of FID from islands with invasive predators was significantly lower than pristine islands ($p = 0.017$). When considering the effect of island independently of invasive predator regime, island and group size had a significant effect on FID (Figure 1; Table 2). Post-hoc comparisons within an invasive predator regime showed no significant difference between the two pristine islands ($p = 0.293$), among the four islands with invasive predators ($0.101 < p < 0.780$) with exception of Floreana having significantly lower FID than Santa Cruz ($p = 0.011$), and between the two eradicated islands, Baltra had significantly higher FID than North Seymour ($p = 0.010$) Analysis with data only for small ground finches had comparable results with the only differences being group size was no longer significantly correlated with FID (Table 2) and a post-hoc comparison of FID of islands within a predation regime found Baltra did not significantly differ from North Seymour ($p = 0.996$) and Floreana did not differ significantly from Santa Cruz ($p = 0.544$).

How much can urbanization reduce antipredator behaviour?

Urban finches had significantly lower FID as compared to non-urban finches (Table 3, Figs. 1 and 2). A post-hoc linear mixed model of FID on Floreana only showed no significant difference of FID between urban and non-urban populations ($\chi^2 = 0.030$, $p = 0.862$) whereas FID was significantly lower in urban areas as compared to non-urban areas on Isabela ($\chi^2 = 16.503$, $p < 0.001$), San Cristobal ($\chi^2 = 22.100$, $p < 0.001$), and Santa Cruz ($\chi^2 = 9.185$, $p = 0.002$). On San Cristobal, finches in urban populations had lower FID than found on pristine islands (Figure 1).

Group size was again positively correlated with FID (Table 3, Supplemental Figure 1). Time of day was also positively correlated with FID (the later in the day it was, the higher the FID; Table 2, Supplemental Figure 2). Analysis with data only for small ground finches had comparable results (Table 3) with the only differences being time of day and group size no longer had a significant effect on FID (Table 3).

Discussion

Increased antipredator behaviour is maintained after eradication of invasive predators

Finches exhibited increased antipredator behaviour on islands with invasive predators (Table 1; Figure 1). More interestingly, this increased antipredator behaviour was also observed on islands where invasive predators had been eradicated (in 2003 and 2008, 13 and 8 years prior to data collection; the mean generation time of finches is one year, by comparison). Since all islands have naturally occurring local or endemic predators of finches (Supplemental Table 1), this effect was most likely due to the presence of invasive predators, even after eradication. This is one of the first studies to show that increased antipredator behaviour has been maintained on islands that have had invasive predators removed. Several possible reasons exist for these observations, especially the apparent maintenance of elevated FID on eradicated islands. First, it is possible increased antipredator behaviour has evolved on islands that have and used to have invasive predators. However, without knowledge of heritability, and thus actual evolution, this cannot be confirmed, but would be an area for future research. Second, perhaps the expected costs of increased antipredator behaviour are not high enough to cause a reversion to pre-predator levels. Increased FID can have associated costs [38–40], suggesting that if this behavioural adaptation were costly then finches on eradicated islands would have FID comparable to finches on pristine islands. It could also be that not enough time has elapsed for reversion in antipredator behaviour. Third cultural transmission of increased FID [62,63] with learned behaviour transmitted from generation to generation could maintain the increased FID. Lastly, the increase in FID could be due to something other than predation, which could still be present on eradicated islands, or that for unknown historical reasons, antipredator behaviour on the eradicated islands have historically been high. The last reason is possible, but it would be a quite a coincidence if the eradicated islands that have this elevated FID for some reason unrelated to predation just happen to be exactly the islands where predation was introduced and then eradicated.

Regardless of the mechanism, the fact that antipredator behaviour levels did not revert post-eradication (when comparing FID on eradicated islands to FID on pristine islands; Figure 1) has potential consequences for evaluating the efficacy of eradication efforts. Recent studies of local animal populations post-eradication have focussed on demographic parameters such as population recovery [32–34] or on ecological parameters such as food-web dynamics [32,36]. However, such phenomena will be influenced by behavioural shifts. For example, increased antipredator behaviour correlates with decreased time and energy for behaviours such as foraging, courting, defending territories, or caring for offspring [38–40], which could affect population recovery and/or food-web dynamics. Thus, understanding how the eradication of invasive predators will affect the behaviour of local or endemic animals should be central to future conservation efforts [33,34,37].

Urbanization can decrease antipredator behaviour to levels lower than before the introduction of predators

Finches in urban areas had lower FID than finches in non-urban areas, supporting previous findings [42–45]. However, two interesting wrinkles are found in this general trend. First, the *degree* of urbanization appears to determine just how much lower FID is for urban finches when compared to non-urban finches. Finches in the town of Puerto Velasco Ibarra on Floreana had the highest FID compared to finches in other towns, and Puerto Velasco Ibarra is also the smallest town, with a permanent population of only 111 (Supplemental Table 1). The significantly lower FID of finches in larger towns as compared to non-urban finches suggests an urbanization “threshold”, such that the degree of urbanization needs to be high enough to exert sufficient selective pressure on finches to drive behavioural adaptation; in short, perhaps Puerto Velasco Ibarra is simply too small to be an “urban” site for the purposes of finch behavioural adaptation. The next largest town, Puerto Villamil on Isabela, with a population of 2,164 (Supplemental Table 1), had significantly lower FID than Puerto Velasco Ibarra on Floreana. Puerto Villamil is still a relatively small town (Supplemental Table 1), showing that the threshold amount of urbanization sufficient to produce differences in antipredator behaviour is not very high.

The second interesting wrinkle is that on some islands, urbanization can result in FID that is *lower* than FID on islands that have never been exposed to predators (Figure 1), even though urban areas invariably contain invasive predators such as cats and rats. In other words, in some towns, such as Puerto Baquizo Moreno on San Cristobal, FID has been reduced to levels below what was observed on islands with no history of invasive predators. Such reductions in FID in urban finches is likely due to habituation [64–67],) suggesting that habituation from urbanization is so strong that it results in FID lower than the baseline FID quantified on pristine islands, counteracting any increase in FID due to the presence of invasive predators. This suggests that the effects of urbanization on organisms can be quite strong, with likely evolutionary and ecological consequences [3,4,68].

Group size and species

For all analyses with all species, FID significantly increased with increasing finch group size (Supplemental Figure 1). This supports the "many-eyes hypothesis" that detection of predators occurs earlier in large groups, when the predator is further away, due to the larger number of individuals watching [38]. Because of the unbalanced design with respect to sample sizes of different species on different islands, and because Darwin's finches are closely related species (implying statistical non-independence among species), I repeated all analyses with a subset of the data utilizing FID from the one species, the Small Ground Finch, *Geospiza fuliginosa*. Species did not have a significant effect on FID in any of the main analyses, and these additional single-species results did not alter the interpretation of any of my results. Future work should use a more balanced sample size and to allow adjustment for non-independence among species.

Conclusions

Our current understanding of how humans affect the evolution and ecology of Darwin's finches has primarily focused on beak shape evolution and shifts in ecological niches in response to changes in food availability and diet [69–71]. However, humans have had effects on the environment of the Galapagos beyond diet, through creation of urban environments and the introduction of invasive mammalian predators. The Galapagos Islands represent an opportune system to study the effects of human influences due to the among island differences in invasive predator regime as well as the differences in the amount of urbanization. Such systems do not readily exist elsewhere. Here, I showed how antipredator behaviour increased in response to invasive predators and was maintained even after eradication of those invasive predators, and this can have possible demographic and ecological effects. This is one of the first studies to look at post-eradication behaviours in local and endemic species, which can have implications for future conservation efforts. I also found that urbanization can reduce antipredator behaviour to levels at or below what was found on pristine islands, attesting to the strength of the effect urbanization can have on behavioural traits. Understanding the effects of different human influences will help us predict how organisms might respond to their rapidly changing environments.

Acknowledgements

I wish to thank Marc-Olivier Beausoleil, Lara Bernasconi, Carlos Camacho, Sofia Carvajal, Angela Hansen, Célina Leuba, and Ashley Saulsberry for their assistance in the field. Permits were obtained with the assistance of Sofia Carvajal, Jaime Chaves, Jeff Podos, the Charles Darwin Research Centre, the Galápagos Science Centre, the Galápagos National Park, and the Universidad de San Francisco. I thank Sarah Knutie for numerous helpful suggestions on ideas and methods, Ben Haller, Andrew Hendry, and Claire Spottiswoode for extensive comments and friendly reviews of the manuscript, and Tom Houslay for guidance with statistics. My research has been generously supported by the Natural Sciences and Engineering Research Council of Canada (Banting Postdoctoral Fellowship), Le Fonds Québécois de la Recherche sur la Nature et les Technologies (postdoctoral research fellowship), Clare Hall (Whitehead Fund), Christ's College (Galápagos Islands Visiting Scholarship Scheme), Newnham College (Phyllis and Eileen Gibbs Travelling Research Fellowship), the British Ornithologists' Union, and McGill University (Department of Biology Vineberg Fellowship). Lastly, many thanks to Andrew Hendry, Jeff Podos, and Joost Raeymaekers for introducing me to the magical place that happened to be visited, some 185 years ago, by someone named Charles Darwin.

References

1. Low, T. *Feral Future: The Untold Story of Australia's Exotic Invaders*. (University of Chicago Press, 2002).

2. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human domination of Earth's ecosystems. *Science* **277,** 494–499 (1997).

3. Johnson, M. T. J. & Munshi-South, J. Evolution of life in urban environments. *Science* **358,** eaam8237 (2017).

4. Alberti, M. *et al.* Global urban signatures of phenotypic change in animal and plant populations. *Proc. Natl. Acad. Sci.* **114,** 8651–8956 (2017).

5. Sax, D. F. & Gaines, S. D. Species invasions and extinction: the future of native biodiversity on islands. *Proc. Natl. Acad. Sci.* **105,** 11490–11497 (2008).

6. Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. & Gaston, K. J. Avian extinction and mammalian introductions on oceanic islands. *Science* **305,** 1955–1958 (2004).

7. Fritts, T. H. & Rodda, G. H. The role of introduced species in the degredation of island ecosystems: a case history of Guam. *Annu. Rev. Ecol. Syst.* **29,** 113–140 (1998).

8. MacArthur, R. H. & Wilson, E. O. *The Theory of Island Biogeography*. (Princeton University Press, 1967).

9. Grant, P. R. & Grant, R. B. *How and Why Species Multiply: The Radiation of Darwin's Finches*. (Princeton University Press, 2008).

10. Grant, P. R. & Grant, R. B. *40 Years of Evolution: Darwin's Finches on Daphne Major Island*. (Princeton University Press, 2014).

11. Fitter, J., Fitter, D. & Hosking, D. *Wildlife of the Galápagos*. (Princeton University Press,

2016).

12. Clavero, M., Brotons, L., Pons, P. & Sol, D. Prominent role of invasive species in avian biodiversity loss. *Biol. Conserv.* **142,** 2043–2049 (2009).

13. Lever, C. *Naturalized Animals: The Ecology of Successfully Introduced Species*. (Poyser Natural History, 1994).

14. McKinney, M. L. & Lockwood, J. L. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* **14,** 450–453 (1999).

15. Clavero, M. & García-Berthou, E. Invasive species are a leading cause of animal extinctions. *Trends Ecol. Evol.* **20,** 110 (2005).

16. Beauchamp, G. Reduced flocking by birds on islands with relaxed predation. *Proc. R. Soc. B Biol. Sci.* **271,** 1039–1042 (2004).

17. Blumstein, D. T., Daniel, J. C. & Springett, B. P. A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* **110,** 919–934 (2004).

18. Blumstein, D. T. Moving to suburbia: ontogenetic and evolutionary consequences of life on predator-free islands. *J. Biogeogr.* **29,** 685–692 (2002).

19. Jolly, C. J., Webb, J. K. & Phillips, B. L. The perils of paradise: an endangered species conserved on an island loses antipredator behaviours within 13 generations. *Biol. Lett.* **14,** 20180222 (2018).

20. Cooper, W. E., Pyron, R. A. & Garland, T. Island tameness: living on islands reduces flight initiation distance. *Proc. R. Soc. B Biol. Sci.* **281,** 20133019 (2014).

21. Blumstein, D. T. & Daniel, J. C. The loss of anti-predator behaviour following isolation on islands. *Proc. R. Soc. B Biol. Sci.* **272,** 1663–1668 (2005).

22. Loss, S. R., Will, T. & Marra, P. P. The impact of free-ranging domestic cats on wildlife of the United States. *Nat. Commun.* **4,** 2961 (2013).

23. Blancher, P. Estimated number of birds killed by house cats (*Felis catus*) in Canada. *Avian Conserv. Ecol.* **8,** 3 (2013).

24. Woods, M., Mcdonald, R. A. & Har Ris, S. Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Rev . Mammal Rev. Blackwell Sci.* **33,** 174–188 (2003).

25. Woinarski, J. C. Z. *et al.* How many reptiles are killed by cats in Australia? *Wildl. Res.* **45,** 247–266 (2018).

26. Phillips, R. B., Wiedenfeld, D. A. & Snell, H. L. Current status of alien vertebrates in the Galápagos Islands: invasion history, distribution, and potential impacts. *Biol. Invasions* **14,** 461–480 (2012).

27. Stone, P. A., Snell, H. L. & Snell, H. M. Behavioral diversity as biological diversity: introduced cats and lava lizard wariness. *Conserv. Biol.* **8,** 569–573 (1994).

28. Wiedenfeld, D. A. & Jiménez-Uzcátegui. Critical problems for bird conservation in the Galápagos Islands. *Cotinga* **29,** 22–27 (2008).

29. Berger, S., Wikelski, M., Romero, L. M., Kalko, E. K. & Roedl, T. Behavioral and physiological adjustments to new predators in an endemic island species, the Galápagos marine iguana. *Horm. Behav.* **52,** 653–663 (2007).

30. Nogales, M. *et al.* Feral cats and biodiversity conservation: the urgent prioritization of island management. *Bioscience* **63,** 804–810 (2013).

31. Jones, H. P. *et al.* Invasive mammal eradication on islands results in substantial conservation gains. *Proc. Natl. Acad. Sci.* **113,** 4033–4038 (2016).

32. Hughes, B. J., Martin, G. R. & Reynolds, S. J. Cats and seabirds: effects of feral domestic

cat *Felis silvestris catus* eradication on the population of Sooty Terns *Onychoprion fuscata* on Ascension Island, South Atlantic. *Ibis (Lond. 1859).* **150,** 122–131 (2008).

33. Lavers, J. L., Wilcox, C. & Donlan, C. J. Bird demographic responses to predator removal programs. *Biol. Invasions* **12,** 3839–3859 (2010).

34. Côté, I. M. & Sutherland, W. J. The effectiveness of removing predators to protect bird populations. *Conserv. Biol.* **11,** 395–405 (1997).

35. Campbell, K. J. *et al.* in *Island Invasives: Eradication and Management* (eds. Veitch, C. R., Clout, M. N. & Towns, D. R.) (IUCN and CBB, 2011).

36. Zavaleta, E. S., Hobbs, R. J. & Mooney, H. A. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* **16,** 454–459 (2001).

37. Phillips, R. A. Eradications of invasive mammals from islands: Why, where, how and what next? *Emu* **110,** (2010).

38. Ydenberg, R. C. & Dill, L. M. The economics of fleeing from predators. *Adv. Study Behav.* **16,** 229–249 (1986).

39. Cooper, W. E. & Frederick, W. G. Optimal flight initiation distance. *J. Theor. Biol.* **244,** 59–67 (2007).

40. *Escaping From Predators: An Integrative View of Escape Decisions*. (Cambridge University Press, 2015).

41. Hendry, A. P., Gotanda, K. M. & Svensson, E. I. Human influences on evolution, and the ecological and societal consequences. *Philos. Trans. R. Soc. B* **372,** 20160028 (2017).

42. Díaz, M. *et al.* The geography of fear: a latitudinal gradient in anti-predator escape distances of birds across Europe. *PLoS One* **8,** e64634 (2013).

43. Samia, D. S. M. *et al.* Rural-urban differences in escape behavior of European birds across

a latitudinal gradient. *Front. Ecol. Evol.* **5,** 1–13 (2017).

44. Møller, A. P. & Tryjanowski, P. Direction of approach by predators and flight initiation distance of urban and rural populations of birds. *Behav. Ecol.* **25,** 960–966 (2014).

45. Møller, A. P. Successful city dwellers: a comparative study of the ecological characteristics of urban birds in the Western Palearctic. *Oecologia* **159,** 849–858 (2009).

46. Swash, A. & Still, R. *Birds, Mammals, and Reptiles of the Galápagos Islands - An Identification Guide*. (Yale University Press, 2005).

47. Groot, R. S. D. E. Origin, status and ecology of the owls in Galapagos. *Ardea* **71,** 167–182 (1982).

48. Vries, T. De. Prey selection and hunting methods of the Galapagos Hawk, *Buteo galapagoensis*. *Le Gerfaut* **66,** 3–43 (1976).

49. Vries, T. De. *The Galapagos Hawk/El gavilán de Galápagos*. (Tundra Ediciones, 2015).

50. Vries, T. De. in *Raptors in the Modern World* (eds. Meyburg, B.-U. & Chancellor, R. D.) 327–330 (WWGBP, 1989).

51. Phillips, R. B. *et al.* Eradicating feral cats to protect Galapagos Land Iguanas: methods and strategies. *Pacific Conserv. Biol.* **11,** 257–267 (2005).

52. Harper, G. A. & Carrión, V. in *Island Invasives: Eradication and Management* (eds. Veitch, C. R., Clout, M. N. & Towns, D. R.) 63–66 (IUCN, 2011).

53. Carrión, V., Sevilla, C. & Tapia, W. Management of introduced animals in Galapagos. *Galapagos Res.* **65,** 46–48 (2008).

54. Blumstein, D. T. Developing an evolutionary ecology of fear: how life history and natural history traits affect disturbance tolerance in birds. *Anim. Behav.* **71,** 389–399 (2006).

55. Blumstein, D. T. Flight-initiation distance in birds is dependent on intruder starting

distance. *J. Wildl. Manage.* **67,** 852–857 (2003).

56. Samia, D. S. M., Nomura, F. & Blumstein, D. T. Do animals generally flush early and avoid the rush? A meta-analysis. *Biol. Lett.* **9,** 20130016–20130016 (2013).

57. Cooper, W. E., Samia, D. S. M. & Blumstein, D. T. in *Advances in the Study of Behavior* **47,** 147–197 (2015).

58. Jackson, M. H. *Galapagos*. (The University of Calgary Press, 1991).

59. Bates, D. M., Maechler, M., Bolker, B. M. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67,** 1–48 (2015).

60. Fox, J. & Weisberg, S. *An {R} Companion to Applied Regression*. (Sage, 2011).

61. Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82,** 1–26 (2017).

62. Aplin, L. M. Culture and cultural evolution in birds: a review of the evidence. *Anim. Behav.* (2018). doi:10.1016/j.anbehav.2018.05.001

63. Aplin, L. M. *et al.* Experimentally induced innovations lead to persistent culture via conformity in wild birds. *Nature* **518,** 538–541 (2015).

64. Cavalli, M., Baladrón, A. V., Isacch, J. P., Biondi, L. M. & Bó, M. S. The role of habituation in the adjustment to urban life: An experimental approach with burrowing owls. *Behav. Processes* **157,** 250–255 (2018).

65. Møller, A. P. Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* **63,** 63–75 (2008).

66. Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F. & Blumstein, D. T. Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* **6,** 1–8 (2016).

67. Blumstein, D. T., Fernandez-Juricic, E., Zollner, P. A. & Garity, S. C. Inter-specific

variation in avian responses to human disturbance. *J. Appl. Ecol.* **42,** 943–953 (2005).

68. Alberti, M. Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol. Evol.* **30,** 114–126 (2015).

69. De León, L. F. *et al.* Urbanization erodes niche segregation in Darwin's finches. *Evol. Appl.* 1–15 (2018). doi:10.1111/eva.12721

70. De León, L. F. *et al.* Exploring possible human influences on the evolution of Darwin's finches. *Evolution* **65,** 2258–2272 (2011).

71. Hendry, A. P. *et al.* Possible human impacts on adaptive radiation: beak size bimodality in Darwin's finches. *Proc. R. Soc. B Biol. Sci.* **273,** 1887–1894 (2006).

Table 1. Results for the first question: does antipredator vary in relation to invasive predator regime (present, pristine, or eradicated)? A general linear mixed model was performed with FID as the dependent variable, invasive predator regime and sex as fixed factors, time of day, starting distance, and group size as covariates, and species and island as random factors. R^2 for full model with all species was 0.281. This analysis was repeated using only small ground finches. Data used for this analysis were from eight islands that varied in invasive predator regime. For data collected on islands with permanent human populations, only data from non-urban sites used here. Bold indicates significant P values.

		χ^2	d.f.	P
All finches	Predation	13.797	2	**0.001**
	Sex	2.416	2	0.299
	Time of Day	1.683	1	0.164
	Start Distance	0.340	1	0.560
	Group Size	18.166	1	**<0.001**
	Island Size	0.152	1	0.697
	Predation * Sex	0.849	3	0.838
	Species	0.000	1	1.000
	Island	5.209	1	**0.022**
Small ground finches only	Predation	12.370	2	**0.002**
	Sex	4.034	2	0.133
	Time of Day	1.444	1	0.229
	Start Distance	0.021	1	0.886
	Group Size	1.551	1	0.213
	Island Size	0.320	1	0.572
	Predation * Sex	1.527	2	0.466
	Island	0.2025	1	0.653

Table 2. Results looking at the effect of islands on FID. A linear mixed model was performed with FID as the dependent variable, island and sex as fixed factors, species as a random factor, and time of day, starting distance, and group size as covariates. R^2 for full model with all species was 0.269. This analysis was repeated as a linear model with only small ground finches Data used for this analysis were from eight islands that varied in invasive predator regime. On islands with human populations, only data from non-urban sites are included. Bold indicates significant P values.

		χ^2	d.f.	P
	Island	39.287	7	**<0.001**
	Sex	0.310	2	0.856
	Time of Day	2.930	1	0.087
All finches	Start Distance	0.367	1	0.545
	Group Size	17.291	1	**<0.001**
	Island * Sex	5.358	10	0.866
	Species	0.023	1	0.880
		F	d.f.	P
	Island	3.587	7	**0.001**
	Sex	1.677	2	0.191
Small ground finches only	Time of Day	1.693	1	0.195
	Start Distance	0.112	1	0.739
	Group Size	1.850	1	0.176
	Island * Sex	0.604	7	0.752

Table 3. Results from the second question asking if urbanization affects antipredator behaviour A general linear mixed model was performed with FID as the dependent variable, site urbanization category and sex as fixed factors, time of day, starting distance, and group size as covariates, and species and island as random factors. R^2 for full model was 0.275. This analysis was repeated using only small ground finches. Data used in this analysis were from urban and non-urban sites on the four islands with permanent human populations. Bold indicates significant P values.

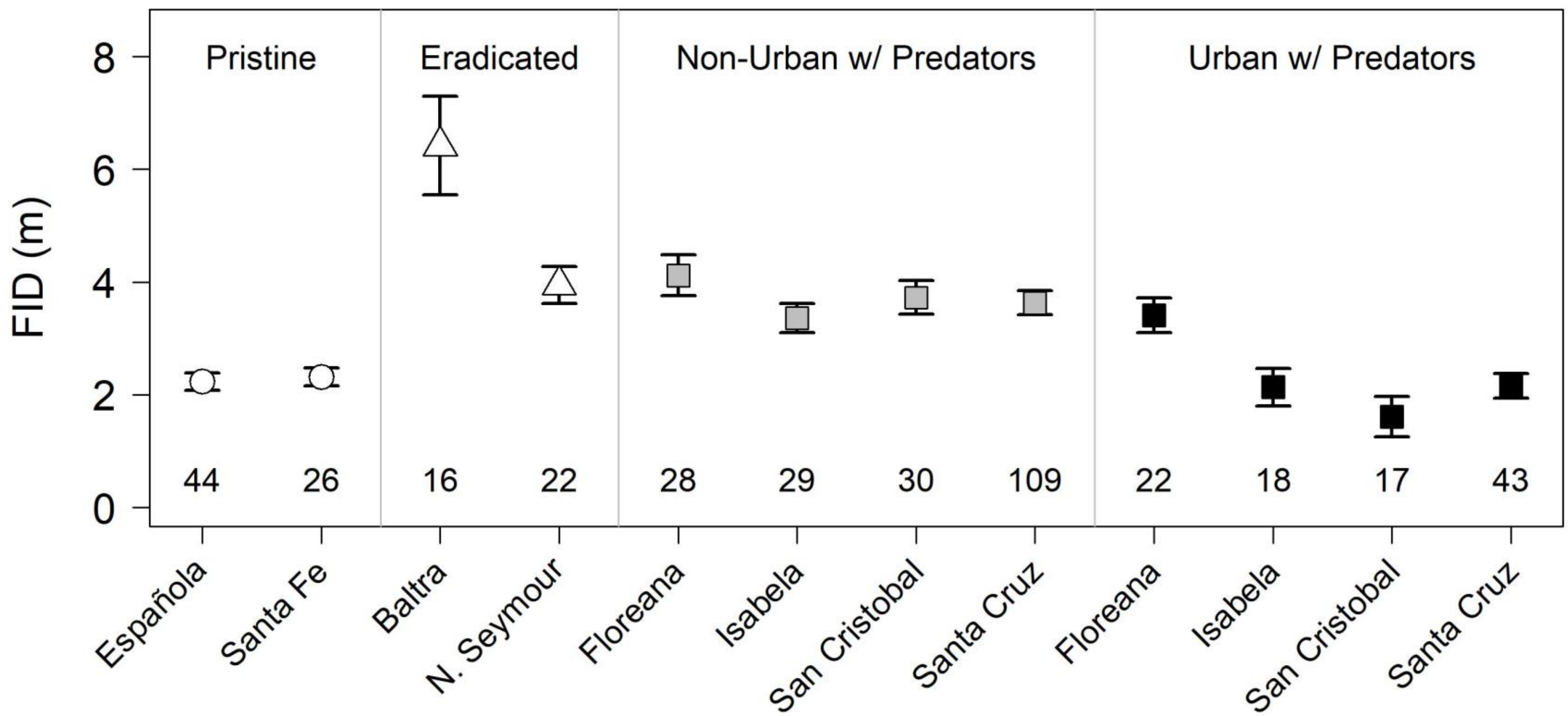
		χ^2	d.f.	P
All finches	Site Category	44.890	1	**<0.001**
	Sex	0.482	2	0.786
	Time of Day	11.650	1	**<0.001**
	Starting Distance	0.450	1	0.502
	Group Size	13.165	1	**<0.001**
	Island Size	0.687	1	0.407
	Site Category * Sex	0.416	1	0.518
	Species	0.000	1	1.000
	Island	3.684	1	0.055
Only small ground finches	Site Category	14.456	1	**<0.001**
	Sex	0.911	1	0.340
	Time of Day	2.252	1	0.133
	Starting Distance	1.987	1	0.159
	Group Size	5.015	1	0.025
	Island Size	0.199	1	0.655
	Site Category * Sex	1.178	1	0.278
	Island	1.928	1	0.165

Figure Legends

Figure 1. Mean FID and standard error on the eight islands data were collected from. Symbol shape denotes the invasive predator regime (pristine, eradicated, or present). Island and site categorization are listed on the top, and numbers indicate sample sizes. Symbol colour indicates the site urbanization category on the four islands with permanent human populations and invasive predators (Floreana, Isabela, San Cristobal, and Santa Cruz). Gray colour indicates non-urban finches, and black indicates urban finches. Open symbols indicate islands with no permanent human populations. The two far left islands, Española and Santa Fe are pristine islands with no history of invasive predators. The next two islands, Baltra and North Seymour are where invasive predators have been successfully eradicated in 2003 and 2008 respectively, and show maintained increased antipredator behaviour. Islands with predators are ordered by population size with Floreana having the smallest urban population and Santa Cruz the largest urban population. In non-urban sites that have invasive predators, antipredator behaviour is increased, and in non-urban sites, antipredator is significantly decreased on all islands except Floreana. On San Cristobal, the antipredator behaviour is lower than on islands untouched by predators and humans.

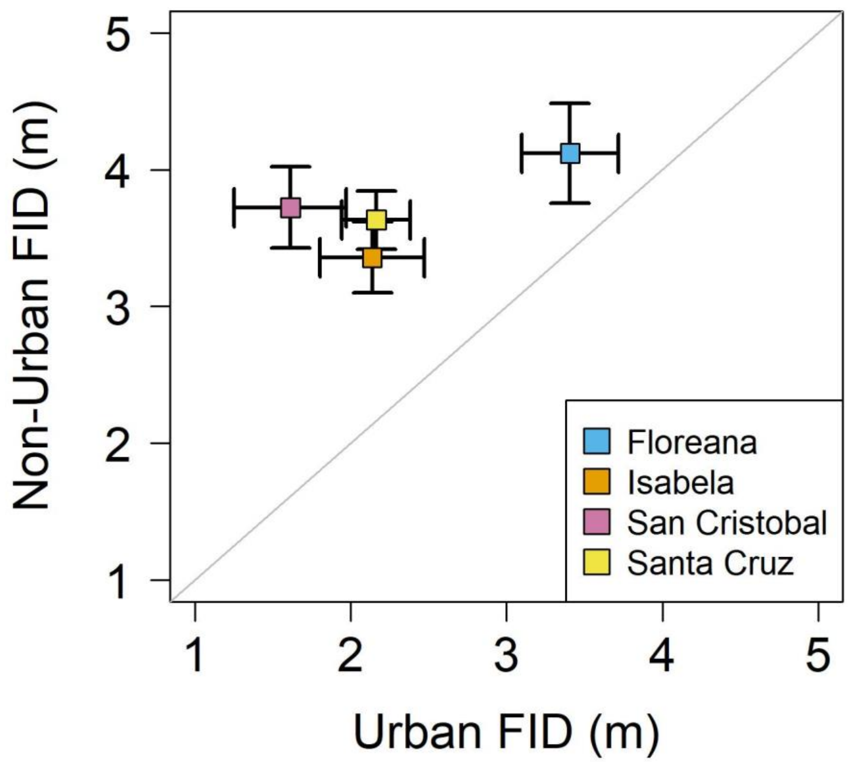
Figure 2. Mean FID and standard error contrasting urban finches with non-urban finches from the four islands that have permanent human populations. Colour indicates island. Above the 1:1 line indicates FID in non-urban areas is higher than FID in urban areas. Floreana, the island with the smallest human population size, has the least difference in FID between urban and non-urban finches.

Figure 1.



Pristine
Eradicated
Non-Urban w/ Predators
Urban w/ Predators
FID (m)
8
6
4
2
0
44
26
16
22
28
29
30
109
22
18
17
43
Española
Santa Fe
Baltra
N. Seymour
Floreana
Isabela
San Cristobal
Santa Cruz
Floreana
Isabela
San Cristobal
Santa Cruz

Figure 2.


5
4
3
2
1
Non-Urban FID (m)
1
2
3
4
5
Urban FID (m)
Floreana
Isabela
San Cristobal
Santa Cruz