

Civil War Is Associated with Longer Escape Distances among Sri Lankan Birds

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ABSTRACT: War influences wildlife in a variety of ways but may influence their escape responses to approaching threats, including humans, because of its effect on human populations and behavior and landscape change. We collected 1,400 flight initiation distances (FIDs) from 157 bird species in the dry zone of Sri Lanka, where civil war raged for 26 years, ending in 2009. Accounting for factors known to influence FIDs (phylogeny, starting distance of approaches, body mass, prevailing human density, group size, and location), we found that birds have longer FIDs in the part of the dry zone that experienced civil war. Larger birds—often preferred by human hunters—showed greater increases in FID in the war zone, consistent with the idea that war was associated with greater hunting pressure and that larger birds experienced longer-lasting trauma or had more plastic escape behavior than smaller species. While the mechanisms linking the war and avian escape responses remain ambiguous, wars evidently leave legacies that extend to behavioral responses in birds.

Keywords: dry zone, fear, flight initiation distance, human conflict.

Introduction

War has implications for humans and wildlife alike (Gaynor et al. 2016). Direct deleterious effects of war on wildlife include those caused by direct use of munitions, chemicals, and land mines (Dudley et al. 2002). Sometimes wildlife may be targeted specifically, to deny their utilization by the enemy for food or economic gain. Other direct effects of military conflict on wildlife include deforestation, draining of wetlands, and pollution. Compromised governance and in-

vestment means protected area and wildlife management are often weakened (Dudley et al. 2002; Gaynor et al. 2016). Additionally, people are displaced within or from conflict zones and are usually food poor, relying on wildlife and natural food sources for sustenance or trade (Santiapillai and Wijeyamohan 2003). Human hunting of wildlife is often more intense in war zones (Dudley et al. 2002), with humans preferentially hunting larger species of wildlife (Benítez-López et al. 2017), so it may be that larger species are especially impacted by war-related increases in hunting. War can also lead to overharvesting, overextraction (e.g., logging) in protected areas, and relaxed barriers to the illegal wildlife trade (Dudley et al. 2002; Santiapillai and Wijeyamohan 2003). Additionally, cognitively complex species of wildlife can harbor behavioral and neurological legacies of human-induced trauma, such as that caused by war (Shannon et al. 2013; Zanette and Clinchy 2020). Unsurprisingly, war zones have been associated with wildlife declines, but war can also benefit wildlife under certain circumstances (Dudley et al. 2002; Gaynor et al. 2016; Daskin and Pringle 2018). War can reduce interactions with people as they are displaced or less inclined to venture into natural areas (Korf 2004; Gaynor et al. 2016). Other benefits can include reduced poaching and the creation of war zone refuges, in which human activities and disturbance are severely curtailed (Dudley et al. 2002; Santiapillai and Wijeyamohan 2003). Such areas (e.g., the Korean demilitarized zone) can permit wildlife to thrive (Havlic 2018). Few studies quantify the impact of war on wildlife, and apparently none compares war zones with adjacent but ecologically matched areas (but see Daskin and Pringle 2018). Existing studies document wildlife population declines with war (Daskin and Pringle 2018), but no studies known to us document multispecies behavioral changes in wildlife associated with armed conflict.

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Birds exhibit distinct antipredator escape behaviors, which are used when responding to people and other predators (Blumstein 2006). One way of evaluating this escape behavior is to measure flight initiation distance (FID), the distance from an approaching threat at which the bird initiates escape. FIDs may conceivably be influenced by several consequences of war. We predict that birds from war zone areas will escape earlier from approaching threats (i.e., have longer FIDs) than those that are outside such areas. Our prediction is based on several tenets. First, birds are generally considered to respond to humans at longer distances in areas where humans are less common (Samia et al. 2015), as may be expected if war displaces humans (Santiapillai and Wijeyamohan 2003; Gaynor et al. 2016). Second, during wars, direct persecution or harvesting of birds may increase, even though humans may be less common (Santiapillai and Wijeyamohan 2003; Daskin and Pringle 2018), making birds more wary of humans and increasing their FIDs (Sreekar et al. 2015; Fujioka 2020). Finally, in theory, habitat degradation caused by war may influence FIDs, possibly with longer FIDs in degraded or open habitats (but see Samia et al. 2015; Osorio-Beristain et al. 2018).

The Sri Lankan civil war raged for 26 years (1983–2009) and reshaped human populations, causing displacement and poverty (Korf and Silva 2003). The National Parks Service was directly attacked, the war diverted public expenditure away from nature conservation, and enhanced exploitation of natural resources occurred and led to more overharvesting and poaching (Dudley et al. 2002; Santiapillai and Wijeyamohan 2003). Postwar periods can be characterized by a variety of human social and economic factors, which means that impacts on wildlife continue or intensify, and this has arguably been the case in Sri Lanka (Dudley et al. 2002; Gaynor et al. 2016; Ratnayake and Hapugoda 2017; Morrison 2020; Rathnayake et al. 2020). Here we document the escape distances evoked by human approaches to the rich dry

zone avifauna of Sri Lanka (Warakagoda et al. 2020). We compare these between the area where the civil war saw active conflict and other parts of the dry zone, while controlling for other factors that may influence avian escape. We test our hypothesis that longer FIDs occur among birds in the zones that saw active combat. Further, given that humans likely preferentially hunt larger species of birds (Benítez-López et al. 2017) and that war intensifies human hunting pressure (Santiapillai and Wijeyamohan 2003), we predict an interaction whereby larger birds will exhibit greater increases in their FIDs in the war zone compared with outside the war zone.

Methods

Detailed field methods are presented in Ekanayake et al. (forthcoming). We measured FID—a widely used method of indexing escape behavior in animals—according to protocols outlined by Blumstein (2003). We recorded the distance at which approaches commenced (starting distance), which is usually positively associated with FID. Repeat sampling of individuals was avoided by collecting data at many sites, not resampling the same location, and not sampling the same species <50 m from a point at which it had already been sampled. FIDs were recorded in a range of habitats by opportunistically collecting FIDs across as many habitats as could be visited (treed areas, such as woodland and savannah areas, and open areas, including grasslands, agricultural areas, and wetlands). Observers were blind to the comparison being conducted in this paper, which was conceived after data collection was completed.

A variety of factors influence FID, and while not of primary interest here, they need to be accounted for in our examination of whether birds in the war zone differed in their FIDs (see table 1). Our sampling controlled for several potentially confounding variables: season (sampling occurred late

Table 1: Comparison of top generalized linear mixed models with Δ AIC score <4, predicting flight initiation distance (FID) in Sri Lankan birds

Model no.	Model components	AICc	Akaike weight	Delta score (Δ AIC)	R^2
1	War + mass + war \times mass + group size + starting distance	1,887.6	.329	.000	.640
2	War + mass + war \times mass + starting distance	1,888.1	.249	.562	.637
3	War + mass + war \times mass + group size + population density + starting distance	1,890.1	.092	2.545	.642
4	War + mass + war \times mass + population density + starting distance	1,890.6	.073	3.026	.641
5	War + mass + group size + starting distance	1,891.1	.057	3.512	.638

Note: Variables included in the models are war (whether the species was living in a former war zone), mass (average body mass for the species), population density (humans/km²), group size (number of birds in the group in which the focal bird was observed), and starting distance of the FID approach. All models included location and species (with a phylogenetic framework) as random effects. Corrected Akaike information criterion (AICc), Akaike weight, Δ AICc, and R^2 values for fixed effects are presented.

October–December; see Mikula et al. 2018), breeding (we sampled only nonbreeding birds; Weston et al. 2018), latitude (the latitudinal span was a modest 3.5°, 6.2°–9.7°N; see Poddubnaya et al. 2019), altitude (all locations were in lowland parts of the dry zone below 400 m), and clothing (observers wore dull pants and shirts and wore hats; see Feng and Liang 2020). In a separate study, we showed a series of factors that do not evidently influence FID in Sri Lankan birds: breeding system, habitat, conservation status, migratory status, development (altricial/precocial), nativeness, and diet (Ekanayake et al., forthcoming). However, some life history, behavioral, and morphological traits can influence avian FID, so we accounted for these statistically by including them in our models. Prominent among these is body mass (Blumstein 2006), so we extracted the weighted average body mass of species (from Dunning 2007; filling gaps with Del Hoyo et al. 2017). We did not include sex in our analyses, because it was often not possible to sex birds on the field, and sex may not influence avian FID (Guay et al. 2017). Human population density can influence avian FID (Samia et al. 2015), so we used a measure of local human population density as a covariate in our models (2015 adjusted human population density data in 30-s resolution; see <https://sedac.ciesin.columbia.edu/data/collection/gpw-v4/sets/browse>). At our sampling locations, prevailing human densities did not differ between war and no-war zones ($F_{1,61} = 0.189, P = .577$). Social context—specifically, group size—can influence avian FID (Morelli et al. 2019), so group size was included in our models. We also specified location as a random effect in our models to account for differences in prevailing human or predator regimes.

Phylogenetic Comparative Analysis

Our analyses comprised 1,400 estimates of FID across 157 species of Sri Lankan birds, of which 857 observations were from parts of Sri Lanka that were formerly part of the war zone. We constructed models of the response of FID (m) to the following predictor variables: war zone (0/1), starting distance (m), body mass (g), human population density (people/km²), and group size (number of birds in the group with which the focal bird was associated). Because there may also be differential responses to war related to body size (e.g., larger birds may be subject to hunting; Benítez-López et al. 2017), we also considered the interaction between body mass and war zone. To improve normality and reduce skew of distributions, all continuous variables were log₁₀ transformed. Group size was strongly skewed and so was double log transformed (with one added after the first round of transformation). We also *z*-standardized all continuous variables in the analysis.

Since this was a cross-species comparative analysis, it was necessary to control for the effect of phylogenetic relation-

ships. The phylogeny used was derived from <http://www.birdtree.org> (Jetz et al. 2012); 2,000 trees were downloaded for the subset of species from the pseudoposterior distribution of trees using the backbone phylogeny from Hackett et al. (2008). A 50% majority rule consensus phylogeny tree was calculated using the consensus function in the package *ape* (Paradis and Schliep 2019), with polytomies randomly resolved. Ultrametric branch lengths were calculated using Grafen's (1989) algorithm as implemented in the *compute.brlen* function in *ape*.

We conducted analyses using phylogenetic generalized linear mixed models, implemented in the package *MCMCglmm* (Hadfield 2010). In addition to the fixed effects (starting distance, mass, group size, population density, and war zone—which were checked for autocorrelation through calculation of variance inflation factors, all of which were less than 1.5, well below the level that would suggest high autocorrelation), species identity is included twice as a random effect in the models, first to account for repeat sampling of the same species and second with an expected covariance matrix overlaid to account for phylogenetic relatedness (De Villemereuil and Nakagawa 2014). Because there was also repeat sampling from individual locations, location was included as an additional random term in all models. Because this approach involves all the data collected for individual birds (1–63 FIDs per species), it automatically incorporates the effect of within-species variation and sample size.

MCMCglmm employs a Bayesian framework using Markov chain Monte Carlo to fit models, producing a posterior distribution of most probable models explaining the response variable. The priors used for the analysis were flat, uninformative priors ($V = 1, \nu = 0.02$), and the analysis was performed for 401,000 runs with a burn-in of 1,000 and a thinning interval of 40, resulting in an effective sample size of the posterior distribution of 10,000. Convergence of the runs was confirmed through visual evaluation of convergence plots, and density plots of the posterior estimates were checked to confirm normality. Parameter estimates were then calculated as the means of the estimates in the posterior distribution, with 95% credibility intervals obtained and pMCMC values, the latter being the proportion of the Markov chain Monte Carlo iterations in the posterior distribution where the estimate crossed zero and is equivalent to a probability value. The extent to which models described variation in FID was calculated via marginal R^2 values (Nakagawa and Schielzeth 2013).

We initially obtained estimates for a full (global) model comprising all predictors but then identified the combination of variables that provided the best approximating model for the data using a model selection approach based on the Akaike information criterion (AIC; Symonds and Mousalli 2011). All possible combinations of fixed effects were

Table 2: Top phylogenetic generalized linear mixed model predicting flight initiation distance (FID) in Sri Lankan bird species

Coefficient	Mean estimate	95% CI	pMCMC
War	.175	.076 to .275	<.001
Mass	.188	.609 to .674	<.001
War × mass	−.071	−.128 to −.015	.013
Group size	.030	.001 to .060	.048
Starting distance	.642	.608 to .673	<.001
Intercept	−.066	−.359 to .212	.637

Note: FID and all continuous predictors were z-standardized. Mean estimate and 95% CI refer to the mean and 95% credibility interval of the Bayesian posterior distribution obtained using MCMCglmm. For war zone, the estimate applies to species that were observed from the former conflict zone. pMCMC values (approximate probability values based on Markov chain Monte Carlo) give the proportion of the posterior distribution where the estimate crossed zero. Marginal R^2 for fixed effects = 0.640.

compared (random effects were included in every model) using the dredge function of the MuMIn package in R (Bartoń 2019).

Results

Model selection identified that the best model predicting FIDs included whether the bird was in a former war zone, species body mass, and the interaction between these two variables, alongside starting distance and group size. Human population density did not feature as a predictor in this best model (table 1). The best model had an Akaike weight of 0.329, and the fixed effects explained 64% of the variation in FID. War zone, body mass, and their interaction were included (along with starting distance) in the top four models (combined Akaike weight = 0.743), and all models with $\Delta AIC < 4$ featured war zone as a predictor of FID. However, when considered by itself as a predictor, war zone explained only ~1.8% of the variance in FID ($R^2 = 0.018$), whereas starting distance and mass combined explained 62.5% of the variance in FID.

The best approximating generalized linear mixed model shows a clear but slight effect of war zone on FIDs, with birds in the former conflict zone having longer FIDs (table 2; fig. 1A). However, the interaction term shows that this effect of war zone on FIDs is moderated by bird body mass, with larger birds exhibiting greater differences in FIDs between the two zones (fig. 1B). The other predictors all showed positive relationships with FID (longer FIDs are associated with longer starting distances, heavier body masses, and larger group sizes).

Discussion

Human behavior is intimately linked with adaptive responses among wildlife (Sullivan et al. 2017), and human

conflict has significant repercussions for wildlife (Daskin and Pringle 2018; Stalmans et al. 2019). We identify a behavioral legacy of war and/or postwar recovery in an index of increased fear of humans among birds. This effect, albeit modest, has evidently persisted into the postwar period (sensu Dudley et al. 2002; Gaynor et al. 2016). Our results of longer FIDs in the war zone are consistent with our expectation that war resulted in either/or fewer humans and that humans possibly exhibited less benign behaviors. Unfortunately, we have no reliable data on alterations to human dispersal and behaviors during the war. However,

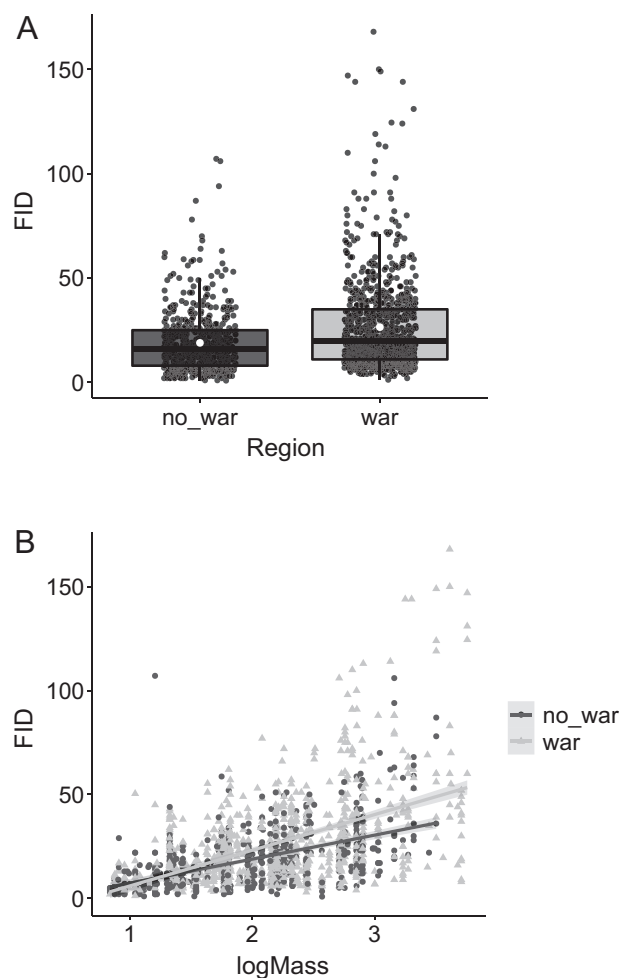


Figure 1: A, Boxplot of flight initiation distances (FIDs) in Sri Lankan dry zone birds from areas that were (war) and were not (no_war) formerly active combat zones during the Sri Lankan civil war. Boxes show median (thick black line) and interquartile ranges, and stems show the main range of the data (excluding outliers). White points within boxes represent mean values. B, Relationship of FIDs in Sri Lankan dry zone birds to log body mass and whether the bird was observed in the former war zone. Best-fit lines with confidence intervals are from the linear regression of raw FID against log body mass and are for indicative purposes.

the war radically redistributed people in northern Sri Lanka, resulting in displacement into camps (Mahees 2019) and spatially restricting many to safer, agricultural areas (Korf 2004). We did not consider the human population estimates available as reliable for the war period, and by 2015 (post-war) human densities at our sampling sites did not differ between war and no-war zones. Thus, prevailing human densities at the time of sampling do not explain the shorter FIDs outside the war zone.

Both sides of the Sri Lankan war hunted wildlife, as did the civilian population, and poaching may have increased or decreased depending on the area considered (Santiapillai and Wijeyamohan 2003; Gaynor et al. 2016). It therefore seems likely that some areas experienced reduced human population densities during the war (areas where avian FIDs may be high; Samia et al. 2015), followed by relocation and resettlement, which increased human densities (avian FIDs are longer in more recently established urban areas; Symonds et al. 2016). This, in combination with a recent history of more threatening human behavior in the form of hunting (which increases avian FIDs; Sreekar et al. 2015; Fujioka 2020) or trauma of individual birds accrued during the war (essentially learning; Zanette and Clinchy 2020), may explain the increase in avian fear in the war zone.

Human hunting of birds is likely biased toward larger species (Benítez-López et al. 2017), and we found a significant interaction between FID and body mass featured in four of the top five models. The pattern of greater increases in FID among larger birds in the war zone is consistent with reduced tolerance of humans among the size class of birds most likely to be hunted. However, several non-mutually exclusive candidate explanations exist regarding hunting and nonhunting mechanisms by which larger birds in the war zone may exhibit longer FIDs. First, the particularly pronounced increase in FID in the largest species we sampled, in the war zone, could reflect greater underlying cognitive capacity, behavioral flexibility, and visual acuity of larger species (Kiltie 2000; Jiménez-Ortega et al. 2020), enabling greater plasticity in FID than for smaller species and in this case an increase of FID in the war zone. Second, larger birds are on average longer lived (Bennett and Owens 2002) and so may harbor trauma, which could alter their behavioral responses throughout their lives (Shannon et al. 2013; Zanette and Clinchy 2020), and persist for longer periods of time after war than would be the case for smaller, shorter-lived species. Indeed, larger birds with relatively large brains (i.e., those that are capable of cognitively buffering themselves from risks by exhibiting behavioral plasticity) are especially long lived (Jiménez-Ortega et al. 2020). Finally, war-related hunting may have selected for wary individuals in the war zone, perhaps through enhanced mortality of bolder individuals that may have been more vulnerable to hunters (i.e., selection; sensu van Dongen et al. 2015).

Specific tests of these mechanisms are required to establish which, if any—acting separately or interactively via hunting and/or direct exposure to armed conflict—explain the patterns we report.

A competing or contributing explanation of FID change is that it was associated with habitat change. Areas of Sri Lanka that experienced active armed conflict experienced substantial and ongoing habitat change (Kaleel 2017; Rathnayake et al. 2020). Forest loss was initially modest but increased (2000–2004) after a cease-fire. A second period of notable clearance occurred in 2010–2018, after the war, when socioeconomic stability allowed greater land clearing, investment opportunities, and relocation initiatives (Rathnayake et al. 2020). War-driven deforestation may have redistributed some wildlife, intensifying farmer-wildlife conflict, with farmers sometimes hazing troublesome wildlife (Korf and Silva 2003; Horgan and Kudavidanage 2020). We cannot rule out habitat clearance as a contributing factor to the increased FIDs in the war zone but note that apart from nesting birds (Amat and Masero 2004), which we did not study, cover has not been unambiguously linked to avian FIDs (Blumstein 2006; Osorio-Beristain et al. 2018). In a recent comparative analysis of Sri Lankan birds, cover did not explain FIDs (Ekanayake et al., forthcoming). Therefore, on balance, habitat change as a mechanism driving longer FIDs in the war zone does not enjoy clear support, although future studies of land use change on FID would be desirable.

An emerging understanding of fear of humans by wildlife also points to individual learning by birds as a possible contributing factor. War may have imparted trauma among birds, with certain interactions between wildlife and humans causing behavioral and neuroanatomical changes. Some long-lived, cognitively complex species even exhibit behavior consistent with posttraumatic stress disorder, decades after the conflict ceased (Zanette and Clinchy 2020). The average longevity of the species we sampled and for which we had information (36 species) was 15.6 ± 1.1 (SE) years (5–33; Del Hoyo et al. 2017); our data collection occurred 6–9 years after conclusion of the conflict. Thus, some individuals that we sampled from some species possibly experienced armed conflict, and all experienced the postwar anthropogenic changes that occurred. Responses to humans may be drastically altered by even a single negative interaction (Zanette and Clinchy 2020). While we have no direct evidence of this possible explanation of our results, we cannot definitely exclude it as a potential mechanism, and further research could establish whether and how birds exhibit trauma.

Armed human conflict is a poorly understood driver of ecological change (Daskin and Pringle 2018; Stalmans et al. 2019). We cannot definitely identify the mechanisms through which avian FIDs have changed with the Sri Lankan war. However, we here confirm the previous suggestion that,

among the array of consequences for wildlife, war may induce behavioral change, which persists after conflict ceases (sensu Dudley et al. 2002). War may induce fear and create landscapes of fear, which in turn may entail long-lasting individual-, population-, community-, and ecosystem-level changes (Zanette and Clinchy 2020).

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Statement of Authorship

M.A.W. and M.R.E.S. conceptualized the study; J.J.G., K.B.E., M.A.W., and K.R. handled data collection, permissions, and logistics; M.R.E.S. conducted the analysis; and J.J.G., K.B.E., M.A.W., K.R., and M.R.E.S. wrote the manuscript.

Data and Code Availability

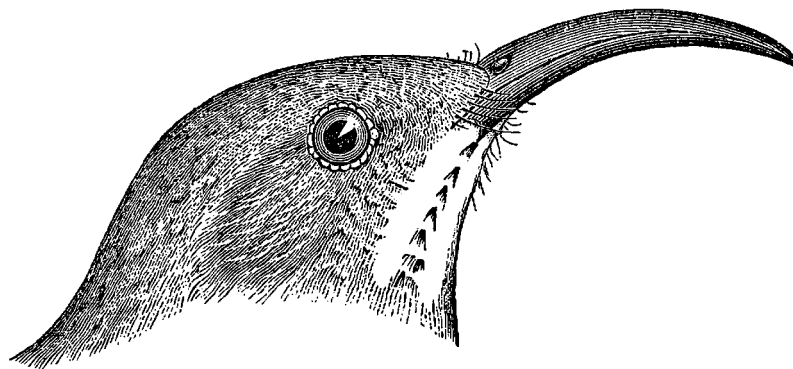
Data and code are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.q83bk3jj2>; Weston and Symonds 2021).

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