



Ecological and environmental predictors of escape among birds on a large tropical island

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Abstract

Ecological and environmental traits can influence avian escape behaviour but most data underpinning our current understanding relates to continental and temperate areas and species. We conducted a phylogenetically controlled comparative analysis of flight-initiation distance (FID) against a variety of environmental, behavioural and life history attributes for Sri Lankan birds (202 species; $n = 2540$). As with other studies, body mass was positively associated with FID, and longer FIDs occurred in areas where human population density was lower. We also found that the effect of human population density was more pronounced in larger birds. Birds that were in groups when approached tended to have longer FIDs. Unlike the findings of other comparative analyses, based mostly on continental, temperate populations, most other ecological variables did not feature in the best models predicting FID (time of year, breeding system, clutch size, habitat, migratory behaviour, development [altricial/precocial], elevation and diet). Thus, some associations (body mass and exposure to humans) may be universal, while others may not manifest themselves among tropical avifaunas. Further tropical datasets are required to confirm truly universal associations of environmental and ecological attributes and escape distances among birds.

Significance statement

Escape responses in birds are influenced by the environment in which they live, the conditions under which they face a threat and their own biological characteristics. The vast majority of our knowledge of avian escape behaviour is derived from continental, temperate species. We examined the environmental and ecological factors that shape flight-initiation distance (FID), the distance at which a bird reacts to an approaching threat (a walking human) by escaping, using 2540 observations of 202 bird species on a large tropical island—Sri Lanka. Several predictors of FIDs in birds are clearly influential for Sri Lankan birds: body mass, human population density and whether the bird is alone or in a group. However, many other putative predictors are not, suggesting that tropical island avifaunas may have different responses to approaching threats compared to their temperate continental counterparts.

Keywords Body mass · Comparative analysis · Flight-initiation distance · Group size · Human density · Sri Lanka

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Introduction

For wildlife, escape from predators is a critical part of survival, and is associated with a variety of ecological and environmental traits (Blumstein 2006; Møller 2014). Flight-initiation distance (FID), the distance at which animals commence escape from an approaching threat, potentially constitutes a general proximate measure influencing ecological and life history trade-offs and reflects the risks that individuals take when responding to a putative predator. A plethora of comparative studies have mapped prominent associations

between avian FIDs and ecological, environmental and contextual variables (Blumstein 2019). Among birds, life history influences the FIDs of individuals (Møller 2014) and life and natural history traits influence FIDs across species (Blumstein 2006). Environmental factors are also prominent in terms of their association with FIDs (Blumstein 2006; Samia et al. 2015a), with some factors potentially being universal mediators of FID.

Most comparative FID studies of birds report a positive association between FID and body mass across species, with larger birds having longer FIDs (see Weston et al. 2012). This might be due to lower agility and speed of escape (Blumstein 2006), and/or because larger birds are longer lived, and therefore more risk-averse as they trade off current survival with future reproductive potential (see Weston et al. 2012). Social and developmental contexts are also associated with FIDs (Blumstein 2006). Longer FIDs may occur among birds in groups (perhaps because vigilance may be more effective; Morelli et al. 2019) or for species which breed cooperatively (possibly due to highly coordinated alarm and response among such species; Blumstein 2006). Developmental mode (whether offspring are altricial or precocial) could conceivably influence FID (increased parental investment in young could reduce risk-taking; but see Blumstein 2006), and variation in clutch sizes (reproductive potential, possibly influencing risk-taking) may also be associated with FIDs (Møller and Liang 2013; but see Blumstein 2006). Migratory birds exhibit longer FIDs, perhaps because migratory species have lower familiarity with local environments and risks in comparison with resident species (Mikula et al. 2018a, b) or perhaps because migration is associated with heightened predator risk resulting in adaptations to avoid depredation (Simpson et al. 2015). Omnivorous and carnivorous diets are associated with longer FIDs, suggesting foraging ecology and/or adaptations may also influence FID (Blumstein 2006).

Environmental influences on FID are also apparent. Most comparative analyses of FID report longer response distances in rural compared with urban environments, a difference attributed to exposure to humans (Samia et al. 2015a). Elevation may influence FIDs, with longer FIDs in at least one upland bird (Andrade and Blumstein 2020). Habitat complexity/density may theoretically alter FID with shorter FIDs where more cover exists (Lomas et al. 2014), although some studies report no such effect (Blumstein 2006; Osorio-Beristain et al. 2018). Some environmental aspects which influence FIDs may vary temporally. Time of day may influence avian FIDs, perhaps due to energetic constraints early in the day (McQueen et al. 2021), and consequent trade-offs between starvation and predator risk (Moiron et al. 2018). Short FIDs in the morning have been shown for only one bird species, and time of day has been recommended to be included in analyses of FID (Ferguson et al. 2019).

Despite the recent growth in our understanding of associations between ecological and environmental traits, and escape among birds derived from comparative studies (Blumstein 2019), these have been dominated by datasets from continental, temperate areas (predominantly North America, Europe and Australia; e.g. Blumstein 2006), and more recently augmented for avifauna in equatorial mainland Africa (Weston et al. 2021). However, tropical (especially equatorial), non-continental avifaunas remain poorly studied in this regard (Møller and Liang 2013, and Gotanda 2020 are rare exceptions). Climate influences avian life histories, including FIDs, and some of the described life history/FID associations which have been studied may be absent from tropical populations (see Møller and Liang 2013). Avian life histories vary between tropical and temperate birds in many aspects; notably, tropical birds generally experience a greater risk of predation, more stable climate and more disease, and food resources may be more stable (Møller and Liang 2013). Avian FIDs decrease with increasing latitude (Diaz et al. 2013; Poddubnaya et al. 2019), and tropical birds exhibit longer FIDs than sister taxa in temperate areas, a finding attributed to different life histories and predator environments between climatic zones (Møller and Liang 2013). However, general patterns of associations with FIDs, derived from mostly temperate datasets, may not hold in tropical areas. For example, tropical birds may not exhibit lower FIDs in areas with more people (Møller and Liang 2013; Bjørvik et al. 2015; but see Piratelli et al. 2015 and Tryjanowski et al. 2020)—the latter generally being conceived as a possibly universal pattern as reported from mostly temperate, continental datasets (Samia et al. 2015a). This may reflect underlying differences in associations with life history, or the nature of human population density gradients between urban and rural areas, or both between tropical and temperate avifaunas.

Islands hold a disproportionate diversity of birds, and avian life histories are shaped by island isolation (Newton 2003). Unsurprisingly, FID varies between mainland and island vertebrates such as reptiles, mammals and birds, i.e. these taxa exhibit ‘island tameness’ on predator free islands (Humphrey et al. 1987; St Clair et al. 2010; Cooper et al. 2014; Cabrera et al. 2017). Although Sri Lanka is large and not particularly isolated, such differences may manifest themselves over fairly modest geographical scales. For example, even within one island group, avian FIDs can vary, being longer on islands with introduced predators or those visited infrequently by people (St Clair et al. 2010; Thibault et al. 2020). Thus, comparative analyses involving island avifaunas may reveal new or specific patterns in FID, potentially different from those derived from predominantly continental datasets (Blumstein 2019; Tryjanowski et al. 2020).

Data on tropical avian FIDs are relatively sparse (Piratelli et al. 2015), and this is especially so of islands, including

large, near-continental islands. Asia presents a gap in current knowledge of avian FIDs (Blumstein 2019). Here, we use a substantial dataset on FIDs of Sri Lankan birds to examine associations with life and natural history and environmental influences, while controlling for phylogeny and sampling effort. Our aim is to explore associations of available ecological and environmental traits used in existing comparative studies, in the context of a large tropical island avifauna. We compare a broad diversity of Sri Lankan species and present the most comprehensive comparative analysis of FID of a tropical island avifauna available, and the first account of FIDs for Sri Lankan birds in all climatic zones (see Gnana-pragasam et al. 2021). Given that tropical islands are under immense conservation pressure, sometimes hosting dense human populations (Qadeer 2000) and substantial nature and ecotourism (d’Hauteserre 2016), documenting response distances may also assist in informing suitable management of human disturbance (Guay et al. 2016).

Methods

We measured flight-initiation distance (FID), the distance at which birds commence escape from an approaching person, a widely used method of indexing escape behaviour in animals (Blumstein 2003). Observers wore dull pants, shirts and hats. We recorded the distance at which approaches commenced (StDist; starting distance), which is usually positively associated with FID (Blumstein 2003). We sampled singlets or single-species groups. 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. FIDs for perched birds were corrected for observer height (Livezey and Blumstein 2016), and straight line distances were calculated. Our dataset did not support the use of the Phi Index (Samia and Blumstein 2014), because we could not reliably measure alert distances (see Guay et al. 2013). Note that it was not possible to record data blind because our study involved focal animals in the field.

Ecological and environmental traits

We extracted 13 ecological and environmental variables which have been previously identified as influencing, or being candidates to influence, avian FIDs (Table 1). Every FID was geolocated, enabling each to be allocated a corresponding elevation, human population density and location (geographically proximate areas that exhibit the same prevailing regimes of human occurrence, land use and activity; $n = 124$ locations). Date and time of day were collected along

with StDist, for each FID. Other life and natural history traits were derived from the literature (see Table 1) and gaps filled with expert consultation and opinion which extended beyond the authorship team (U. Ekanayake; S. Seneviratne, banding data from Field Ornithological Group of Sri Lanka).

Phylogenetic comparative analysis

We constructed models of the response of FID to the following predictor variables: starting distance, body mass (for the species), human population density, group status (because these data were highly skewed towards single individuals and estimation of exact group size when with others was often ambiguous, this was categorised as either solitary or with other birds at the time of encounter), time of day, Julian date, elevation (this was clearly bimodally distributed and so was categorically divided into highland sites > 1500 m and lowland sites < 1000 m asl), breeding system, habitat type, migratory behaviour, clutch size, developmental type and diet (Table 1). Julian date was circular transformed to convert into radians. To improve normality and reduce skew of distributions, all continuous variables were \log_{10} -transformed and z -standardised. Finally, we also considered three interaction terms in our modelling: mass \times population density, to account for differences in the way different sized birds might respond to increased human presence (sensu Weston et al. 2021); starting distance \times habitat type, to account for the possibility that starting distance will have different relationships to FID in different habitats (Mayer et al. 2019); and elevation \times migration, to account for possible physiological constraints in escape at higher elevations, between residents and migrants (Barve et al. 2016). Additionally, differential parasite loads may exist in birds between elevations, which may also vary with migration and breeding status (Gonzalez et al. 2014), and could influence escape.

We performed analyses using a Bayesian Markov Chain Monte Carlo phylogenetic generalised linear mixed model approach, using the *MCMCglmm* package (Hadfield 2010) in R version 4.0.2 (R Core Team 2020). Here, in addition to the fixed effects, species identity was included as a random effect with a phylogenetic structure to control for non-independence of those species and to control for sampling of multiple individuals from the same species. Location was also included as a random effect to control for repeat sampling from the same locations. By including all individual observations in a phylogenetic comparative analysis, one automatically incorporates within-species variation and differences in sampling (Garamszegi and Møller 2010).

The phylogeny used as the basis for analysis was derived from www.birdtree.org (Jetz et al. 2012); 2000 trees were downloaded for the subset of species from the pseudo-posterior distribution of trees using the ‘backbone’ phylogeny

Table 1 Summary of variables associated with the 2540 observations of Sri Lankan birds used in the comparative analysis, justification for their inclusion in analyses and source. Categorical variables are indicated with the suffix '(categorical)'. *Response variable. Species-level natural and life history classifications are provided in Supplementary Material Table S1

Variable	Summary	Justification	Source
FID (m) *	Mean = 19.62, SD = 19.44, range = 0–279	Widely used measure of escape propensity (Blumstein 2003)	Methods follow Blumstein (2003). Most distances were collected using a laser range-finder, except where obscuring vegetation or reflection prevented use, in which case distances were paced. FIDs were collected in fine weather only
StDist (m)	Mean = 31.76, SD = 28.54, range = 2–362	Almost always positively related to FID (Blumstein 2003)	Measured in field, using same methods as for FID
Body mass (g)	Mean = 336.7, SD = 751.0, range = 6.4–5700	Almost always positively related to FID (see, for example, Weston et al. 2012)	Weighted average body mass from Dunning (2007) gaps filled with information in the Handbook of the Birds of the World (2019)
Date (Julian)	Range = 48–348 (mid-February to mid-December)	Seasonal events (migration, breeding) influence avian FIDs (Mikula et al. 2018a, b; Weston et al. 2019)	Collected in field
Time of day (minutes before or after dawn)	Range = 21 min before dawn to 12 h 31 min after dawn	Longer FIDs later in the day (Ferguson et al. 2019)	Time collected in field calculated from time of dawn on relevant day
Population density (humans km ⁻¹)	Mean = 558.7, SD = 1218.5, range = 2–21,777	Almost always shorter FIDs in urban versus rural context (Samia et al. 2015a)	In tropical settings with large human populations the classic urban versus rural distinction does not necessarily hold (see Tryjanowski et al. 2020). We therefore included prevailing population density (for 2015) mapped in 30 s resolution (https://sedac.ciesin.columbia.edu/data/collect/gpw-v4/sets/browse)
Elevation (categorical)	2378 lowland (< 1000 m above sea level), 162 highland (> 1500 m)	Predicted longer FIDs in uplands (Andrade and Blumstein 2020)	Community Surface Dynamics Modelling System topographic layer (CGIAR-SRTM). Data aggregated to 30 s grid resolution (https://csdms.colorado.edu/wiki/Data:CGIAR-CSL_SRTM)
Group status (categorical)	1868 solitary, 672 in group	Longer FIDs when in groups (Morelli et al. 2019)	Collected in the field when FIDs collected. Single-species groups approached, no mixed species flocks
Breeding system (categorical)	2140 solitary, 400 cooperative breeders	Longer FIDs for species which breed cooperatively (Blumstein 2006)	Cooperative breeders were birds other than a single pair contribute to incubation or raising the chicks at a non-trivial proportion of nests. Data were sourced from Handbook of the Birds of the World (2019) and expert review
Habitat (categorical)	1760 open, 272 closed, 508 both	Postulated longer FIDs in more open habitats (Blumstein 2003, 2006)	'Open' (e.g. wetland, grassland), 'closed' (i.e. forest, woodland) or 'both'. Finer habitat classifications are reduced to open, closed or both following Blumstein (2003). Data were sourced from Handbook of the Birds of the World (2019) and expert review. All approaches involved direct line of sight

Table 1 (continued)

Variable	Summary	Justification	Source
Migratory status (categorical)	2006 resident, 434 migrant, 100 partially migratory/resident	Migratory birds exhibit longer FIDs (Mikula et al. 2018a, b)	'Migratory' (regular movements in and out of Sri Lanka regardless of whether or not the species breeds there), 'resident' (non-migratory) or 'both' (i.e. partially migratory/resident). Data were sourced from Handbook of the Birds of the World (2019) and pertain to Sri Lankan populations
Clutch size	Mean = 3.69, SD = 1.45, range = 1–11	Clutch size reflects one aspect of reproductive potential, and explains some variation in FID between temperate and tropical bird faunas (Møller and Liang 2013)	Data were sourced from Handbook of the Birds of the World (2019) and expert review
Development type (categorical)	1901 altricial, 639 precocial	Developmental mode conceivably influences FID (Blumstein 2006)	'Altricial' or 'precocial'. Data were sourced from Handbook of the Birds of the World (2019) and expert review
Diet (categorical)	396 aquatic carnivore, 146 benthic, 339 carnivore, 43 frugivore, 128 generalist, 431 generalist granivore, 601 generalist insectivore, 456 insectivore	Diet influences FID (Blumstein 2006)	Diets were characterised by coding food items from accounts in Handbook of the Birds of the World (2019) (0/1) for: fruit nectar or pollen; seeds, foliage or herbs; corms or tubers; terrestrial invertebrates; terrestrial vertebrates; aquatic vertebrates; carrion; intertidal invertebrates; fish or marine invertebrates; and freshwater fish or invertebrates. K-means cluster analysis ($k = 6$) provided an initial classification, this was reviewed by several experts on Sri Lankan birds which resulted in the splitting of two clusters to reflect observed foraging niches/guilds. Expert review was necessary as not all food items were documented for all species, and guilds needed to reflect observed ecological patterns

from Hackett et al. (2008). From these 2000 trees, we generated a single maximum clade credibility tree using the `maxCladeCred` function in the R package *phangorn* version 2.7.1 (Schliep 2011).

The priors used for the MCMCglmm analysis were flat, uninformative priors ($V = 1$, $\nu = 0.02$, for random terms and residual variance) and the analysis was performed for 101,000 runs with a burn-in of 1000 and a thinning interval of 100, resulting in an effective sample size of the posterior distribution of 1,000 (after the first 1000 ‘burn-in’ runs are discarded, every 100th result is taken from 100,000 remaining runs, making 1000 selected runs in total). Convergence of the runs was confirmed through visual evaluation of convergence (trace) plots. Parameter estimates were then calculated as the means of the estimates in the posterior distribution, with 95% credibility intervals obtained and pMCMC values being the proportion of iterations in the posterior distribution where the estimate crossed 0. The extent to which the fixed effects in models described variation in FID was calculated via marginal R^2 values (Nakagawa and Schielzeth 2013).

We used a model selection approach to determine the most important variables influencing FID in Sri Lankan birds. Top models were selected based on Akaike’s information criterion (AIC; Burnham and Anderson 2002) corrected for small sample size (AICc) because, although our sample size is not small, a large number of predictors were included. ‘Top models’ within delta two AICc of the highest ranked model were selected using the ‘dredge’ function in the package *MuMIn* (Bartoń 2020). We repeated the dredge process for three global models, each including 13 fixed effects (described above) and one of the three interaction terms (i.e. separate models with mass \times population density, starting distance \times habitat and migration \times elevation). To reduce computation time, we fixed the variables ‘starting distance’ and ‘mass’ to be included in all models; both of these variables are known to strongly correlate with FIDs from previous studies (see Weston et al. 2012) and had large, statistically significant effects in our full model. We present top selected models from the global model including mass \times population density in our results, as this was the only interaction term that was included in top models (i.e. the interactions starting distance \times habitat and migration \times elevation were not included in the subset of models within $\Delta\text{AICc} \leq 2$). The full model was run in the same manner as the three global models described above, but with a larger effective sample size of 10,000 (number of iterations = 401,000; burn-in = 1000; thinning interval = 40, for explanation of how this results in this effective sample size see above).

We checked all fixed predictors in the best models for collinearity through correlation plots (continuous variables only) and variance inflation factors (VIF; all variables) which revealed no significant problems with collinearity

between predictors (Pearson’s $r \leq 0.4$; $\text{VIF} \leq 3$, with the exception of diet, which does not feature in any top models, see the ‘Results’ section).

Data availability

A summarised species average dataset is presented in Supplementary Material Table S1. The complete dataset of FID observations and associated location data is available through Dryad (datadryad.org) (Ekanayake et al. 2022).

Results

We obtained 2,540 observations of flight-initiation distances from 202 species of Sri Lankan birds. The birds represented individuals from a range of environments and with diverse biological and ecological characteristics (Supplementary Material Table S1).

Our model selection approach identified 12 top models whose AIC scores were within 2 units of each other (Table 2). The best approximating model identified starting distance, body mass, human population density and whether the focal bird was alone or in a group, as predictors. Additionally, time of day, and the interaction between body mass and population density, featured prominently in the list of top models. None of the other predictors or interaction terms featured strongly among the best models.

The best approximating model (Table 3) identified that, in addition to starting distance, body mass was positively associated with FID, with larger bodied species having longer FIDs (Fig. 1A). Birds that were alone had shorter FIDs compared to those that were associated with other individuals (Fig. 1B). Human population density was negatively associated with FID, with birds responding to an approaching human at shorter distances in areas that have higher population density (Fig. 1C). We also considered the most complex model in the list of top models that contained the other prominent predictors identified above (Table 3). This model indicated that birds observed later in the day tended to have longer FIDs (Fig. 1D); however, the effect was minimal, and the credibility intervals on the estimate spanned zero, suggesting it cannot be considered with much confidence. This model did, though, show an interaction effect between mass and population density indicating that larger birds show a steeper decline in FID with increasing population density compared to smaller birds (Fig. 2).

The full global model (Table 4) indicated two further effects where the credibility intervals on the estimates did not cross zero (and pMCMC values were less than 0.05). The first of these was elevation, with lowland birds tending to have longer FIDs than those in highland areas. The other (the migratory behaviour:elevation interaction) suggests

Table 2 Comparison of the generalised linear mixed models predicting flight-initiation distance (FID) in Sri Lankan birds. Variables included are those identified as producing almost equally good top models through model selection: starting distance of the FID approach, mass (average body mass for the species), group status (whether the focal bird was alone or in a group), population density (humans per km²) and time (minutes after dawn). All models include location and species (with a phylogenetic framework) as random effects. We present the AICc, delta AICc and marginal R² values for fixed effects

Model no	Model components	AICc	Delta score (ΔAIC)	R ²
1	StDist + mass + group status + population density	3644.9	0.00	0.62
2	StDist + mass + group status + population density + mass*pop. dens	3645.3	0.40	0.62
3	StDist + mass + group status + time	3645.4	0.46	0.56
4	Starting distance + mass + group status + population density + time + mass*pop. dens	3645.4	0.49	0.62
5	StDist + mass	3645.5	0.51	0.56
6	StDist + mass + time	3645.6	0.65	0.56
7	StDist + mass + population density	3646.1	1.11	0.62
8	StDist + mass + population density + mass*pop. dens	3646.1	1.19	0.62
9	StDist + mass + population density + time	3646.3	1.31	0.62
10	StDist + mass + population density + time + mass*pop. dens	3646.6	1.68	0.62
11	StDist + mass + group status + population density + time	3646.8	1.90	0.62
12	StDist + mass + time + migration	3646.9	1.92	0.58

Marginal R² for full model = 0.68

Table 3 Top generalised linear mixed model models predicting flight-initiation distance in Sri Lankan bird species. Shown is the highest ranked model (Model 1 in Table 2) and the model with the greatest number of predictors (Model 4 in Table 2) of the twelve selected ‘top’ models within ≤ 2 ΔAICc. FID and all continuous predictors were z-standardised. Mean estimate and 95% CI refer to the mean and 95% credible interval of the Bayesian posterior distribution obtained using *MCMCglmm*. λ is a measure of the phylogenetic signal in the model residuals (Pagel 1999). The ‘group status’ estimate applies to focal birds observed while standing alone (without other individuals). P values show the proportion of the posterior distribution estimated to cross zero

Model 1 (highest ranked model; marginal R ² =0.62; conditional R ² =0.71; λ=0.11)				
Random effects	Variance			
Phylogeny	0.036			
Species	0.009			
Location	0.036			
Residual	0.244			
Fixed effects	Post mean	Lower CI	Upper CI	P
Intercept	0.139	2 × 10 ⁻⁴	0.280	0.046
StDist	0.611	0.586	0.636	<0.001
Mass	0.099	0.047	0.157	0.004
Group status (single)	-0.049	-0.096	0.001	0.040
Population density	-0.150	-0.196	-0.105	<0.001
Model 4 (top model with the most variables; marginal R ² =0.62; conditional R ² =0.71; λ=0.11; ΔAIC 0.49)				
Random effects	Variance			
Phylogeny	0.034			
Species	0.009			
Location	0.035			
Residual	0.244			
Fixed effects	Post mean	Lower CI	Upper CI	P
Intercept	0.105	-0.051	0.249	0.150
StDist	0.612	0.586	0.639	<0.001
Mass	0.092	0.040	0.141	0.004
Group status (single)	-0.048	-0.095	2 × 10 ⁻⁴	0.046
Population density	-0.136	-0.178	-0.093	<0.001
Time	1 × 10 ⁻⁴	-3 × 10 ⁻⁵	2 × 10 ⁻⁴	0.182
Mass*population density	-0.039	-0.062	-0.014	<0.001

that the elevation pattern is more pronounced in migrant birds, with lowland migrant birds having the longest FIDs (Fig. 3). However, neither of these predictors featured in any top model set, and indeed the best model including elevation performed substantially worse than the top model (delta AICc = 5.842).

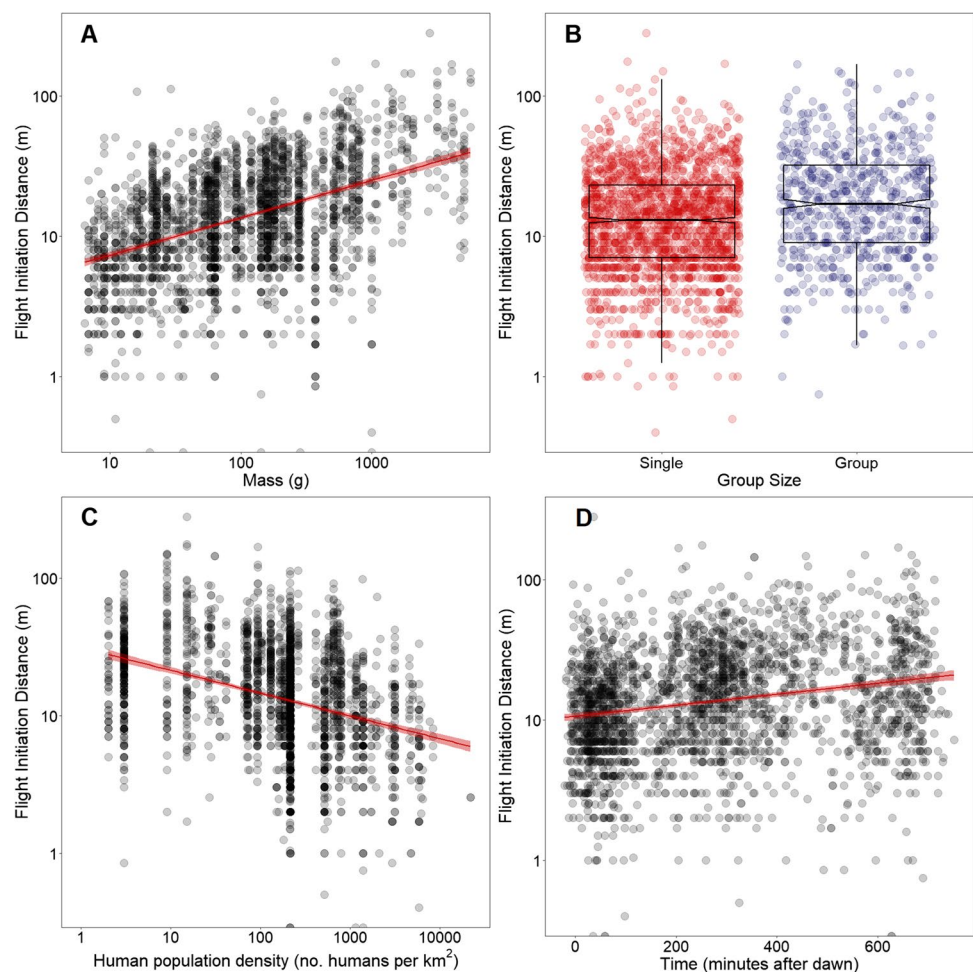
In total, the fixed effects in the global model explained 68% of the variation in FIDs, although starting distance and body mass accounted for the vast majority of that variance (Table 4).

Discussion

Our best model of FID featured positive effects of starting distance, body mass and group status and a negative effect of human density—effects which have been reported in comparative analyses from all or most other continents and localities for which data are available. Starting distance appears universally and positively related to avian FID perhaps because it permits birds to judge risk and ‘flush early

and avoid the rush’ (Blumstein 2003, 2010), or because it is a methodological artefact (Dumont et al. 2012), or both. Body mass is usually positively related to avian FID (e.g. Møller et al. 2014), although a comparative analysis of tropical east African birds recently revealed a slightly negative (though non-significant) effect of body mass on FID (Weston et al. 2021). Sri Lankan birds in groups had longer FIDs than when they were alone, which aligns with general patterns observed (Morelli et al. 2019) and is predicted from the benefits of anti-predator vigilance associated with occurring in groups (but see Tätté et al. 2019). We sampled birds in single-species flocks, and note that the prominence of mixed species flocks among Sri Lankan forest birds warrants further investigation of their FID (Mammides et al. 2018; Linley et al. 2019). We confirm the apparently universal influence of human density on avian FID, whereby shorter FIDs occur in areas with more people (Samia et al. 2015a). Our measure of local human density may have utility in contexts (common in many parts of the world) where the urban–rural distinction does not clearly apply. High human densities occur in rural areas in many parts of the world, especially in Asia (Qadeer 2000),

Fig. 1 Relationship between flight-initiation distance and **A** body mass, **B** group status, **C** human population density and **D** time of day for Sri Lankan birds. Flight-initiation distance (y-axes), mass and human population density are shown on a log scale (tick marks are labelled with untransformed values). Panels A, C and D show linear regression lines and 95% confidence interval in red. The boxplot in panel B shows the median (central line), interquartile range (box area) and predominant range minus outliers (whiskers), with raw data overlaid



meaning that the classic urban–rural distinction does not necessarily reflect the prevailing human regime experienced by birds. Urban and rural areas differ in aspects other than human activity (e.g. predator regimes, structural complexity, resources) which potentially confound comparisons of FIDs between urban and rural environments (Weston et al. 2012). Indeed, in studies within homogenous forest habitat, avian FIDs are lower in those areas with more humans, suggesting exposure to humans does influence FIDs independently of other confounding effects (Bötsch et al. 2018). Our use of the continuous measure of human population density, combined with our random effect of location, also suggests that birds exhibit shorter FIDs in relation to being exposed to more humans, regardless of whether or not areas are rural or urban. The effects of starting distance, body mass, group status and human density which we report are unremarkable, given that they have been described from similar studies on other avifaunas. However, we confirm for the first time their existence among Sri Lankan birds, and to our knowledge, our study represents the most comprehensive assessment of possible predictors of FID for a tropical island's avifauna.

The interaction between body mass and human population density also featured in four out of the 12 top models (Table 2), and was statistically significant (Table 3). This interaction indicated that the decline in FID with increasing exposure to humans is moderated by body size, with larger birds showing a steeper decline, such that, in areas of high human population density, the difference in FIDs between large and small birds is less pronounced. A broadly similar pattern has been reported between continents. Avian FIDs increase with body mass for Australian birds (comparatively sparsely populated) but not for African birds (densely populated) (Weston et al. 2021). The pattern we report is consistent with the idea that larger birds have the capacity to tolerate people more readily (Samia et al. 2015a), perhaps because of greater cognition associated with relatively larger brains (Samia et al. 2015b), higher costs associated with leaving a resource patch (Glover et al. 2011), or other as yet unidentified factors.

We also report two further effects which apply to Sri Lankan birds and which have, to date, been understudied: time of day and elevation. FIDs showed a very weak tendency to increase as the day progressed (this effect featured in seven of the top 12 models, but was minimal and not statistically significant). Links between time of day and FID have, to our knowledge, only previously been identified in only a couple of studies, and with contrasting patterns: Burger and Gochfeld (1991) found shorter FIDs later in the day in Indian birds, which they ascribed to greater human activity at those times. By contrast, Ferguson et al. (2019) for a single species of nectarivore argued that shorter FIDs *earlier* in the day were related to energetic constraints after nocturnal fasting. The extent to which this explanation applies to Sri Lankan birds is unclear, but it seems unlikely given Burger and Gochfeld's

(1991) results. Given the reported effect was non-significant, and the relationship may even be non-linear (see Fig. 1D), we refrain from further inference; however, further investigation of the time of day effect across birds in different climates and with different life histories seems warranted.

The global model indicated a significant effect of shorter FIDs occurring in highland birds. The only other study (a single-species), study of elevation and FID in birds, predicted shorter FIDs at higher elevations, in line with shorter FIDs which occur at higher latitudes, and the similar patterns of seasonality, climate and predator density that covary between latitude and elevation (Andrade and Blumstein 2020). Our results align with this prediction. Contrary to Andrade and Blumstein's (2020) prediction, they reported longer FIDs at higher elevations for their single study species. Thus, this study provides the first confirmatory comparative evidence for the proposed elevational effect. Furthermore, a significant interaction effect with migratory behaviour was also apparent in the global model, such that the longer FIDs of lowland birds are more pronounced for migrant species (Fig. 3). Other studies have documented that migrants have longer FIDs in both temperate (Mikula et al. 2018a, b) and tropical (Burger and Gochfeld 1991; Weston et al. 2021)

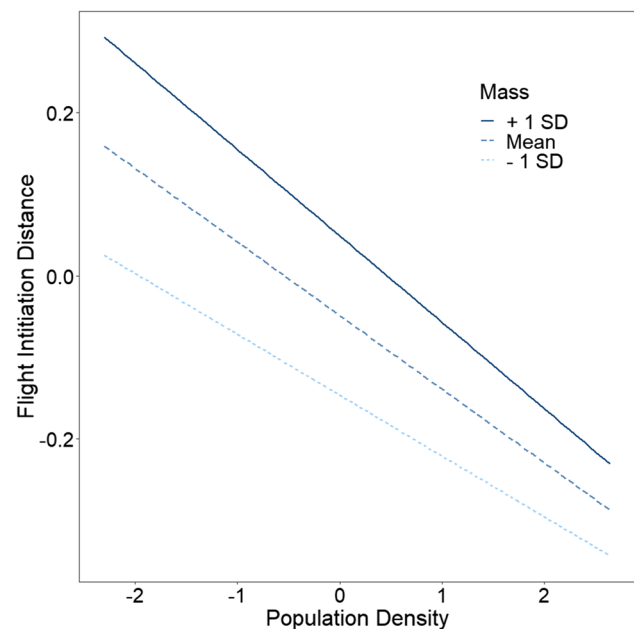


Fig. 2 Interaction effect of body mass and human population density on flight-initiation distances of Sri Lankan birds. Birds with greater mass generally have longer flight-initiation distances, but show a steeper reduction in flight-initiation distances in response to increased human population density. The three lines show the predicted linear relationship between flight-initiation distance (log-transformed and z-standardised) and human population density for averaged sized birds (mean mass), larger birds (mass one standard deviation above the mean) and smaller birds (mass one standard deviation below the mean)

Table 4 Full global generalised linear mixed model predicting flight-initiation distance (FID) in Sri Lankan bird species. FID and all continuous predictors were z -standardised. Mean estimate and 95% CI refer to the mean and 95% credible interval of the Bayesian posterior distribution obtained using *MCMCglmm*. Estimates are expressed relative to birds in open-and-closed habitats, in groups (surrounded by other individuals), and with cooperative breeding, altricial development, aquatic carnivore diet, partly migratory behaviour and at highland elevation. P values show the proportion of the posterior distribution estimated to cross zero. Model marginal $R^2=0.68$, conditional $R^2=0.74$, $\lambda=0.07$

	Variance			
	Post mean	Lower CI	Upper CI	P
Random effects				
Phylogeny	0.021			
Species	0.010			
Location	0.028			
Residual	0.245			
Fixed effects				
Intercept	-0.031	-0.318	0.304	0.818
Starting distance	0.581	0.523	0.632	<0.001
Habitat (closed)	0.085	-0.051	0.200	0.206
Habitat (open)	0.066	-0.037	0.157	0.178
Mass	0.107	0.051	0.161	0.002
Population density	-0.114	-0.165	-0.073	<0.001
Date	0.005	-0.024	0.036	0.708
Time	0.020	-0.010	0.049	0.144
Group status (single)	-0.054	-0.106	-0.007	0.022
Breeding (solitary)	0.032	-0.061	0.135	0.536
Development (precocial)	0.092	-0.098	0.247	0.290
Diet (benthic)	0.026	-0.171	0.265	0.838
Diet (carnivore)	0.011	-0.126	0.143	0.852
Diet (frugivore)	-0.042	-0.327	0.233	0.764
Diet (generalist)	-0.232	-0.464	-0.006	0.054
Diet (generalist granivore)	-0.093	-0.250	0.081	0.282
Diet (generalist insectivore)	-0.161	-0.327	0.017	0.072
Diet (insectivore)	-0.138	-0.304	0.038	0.120
Clutch size	0.021	-0.017	0.056	0.256
Migratory behaviour (migrant)	0.209	-0.078	0.451	0.130
Migratory behaviour (resident)	-0.154	-0.345	0.029	0.098
Elevation (lowland)	0.256	0.108	0.413	0.004
StDist: habitat (closed)	0.027	-0.064	0.119	0.562
StDist: habitat (open)	0.034	-0.027	0.096	0.262
Mass: population density	-0.037	-0.059	-0.012	0.002
Migrat. behav. (migrant): elev. (lowland)	-0.253	-0.470	-0.052	0.016

environments, possibly because they are less regularly exposed to (and hence habituated to) humans, or because, with their longer and more pointed wings (Lockwood et al. 1998), the costs of escape flights are lower for migrants. That the difference between migrants and residents is less pronounced at highland studies might possibly be a consequence of the physiological limitations of mounting energy-intensive behaviours at higher elevations (Barve et al. 2016).

It is curious that, despite these apparently significant patterns, neither elevation nor the migration \times elevation interaction featured in any top models from our model selection procedure. This is not due to any confounding effect with other fixed predictors (variance inflation factors for both elevation and migratory behaviour are low). However, we note that our sampling from highland locations was limited ($N=162-6.3\%$ of our observations), and elevation is inevitably somewhat confounded with

our random effect of location. Given the lack of model support, therefore, as with time of day, we must be circumspect in interpretation of the effects of elevation and migration. Ideally, more systematic sampling from across a greater range of elevations would be informative in future studies (we sampled only highland and lowland Sri Lankan locations, with no sampling at intermediate elevations).

A range of other variables did not feature in our best models (date, breeding system, habitat, clutch size, developmental mode, diet). All of these have been shown, or linked, with avian FIDs in other studies from other, usually temperate and continental areas (see references in Table 1). These effects therefore appear more localised, and further studies could confirm if they exist in other tropical localities. We note that seasonality is fundamentally different in tropical ecosystems, and that tropical birds may not experience seasonal food shortages (Bender et al. 2017).

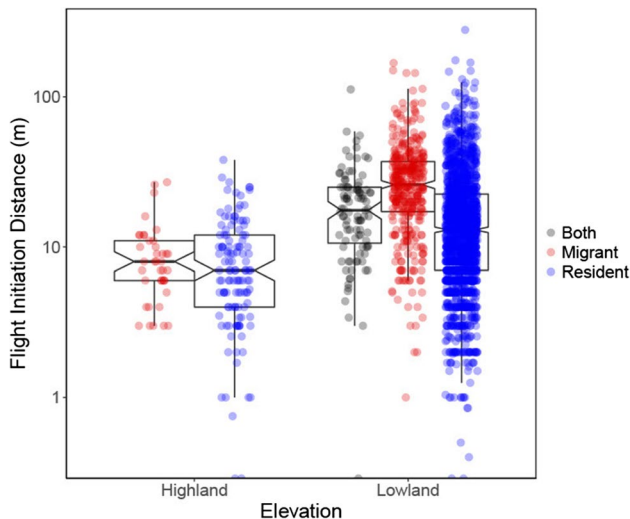


Fig. 3 Interaction effect of elevation (lowland or highland) and migratory status (resident, migratory or partial migrant) on flight-initiation distances of Sri Lankan birds. Lowland birds tend to have longer flight-initiation distances, and this effect is augmented in migratory species. Although these effects are significant in the global model, they did not feature in the list of top models from the model selection analysis. Boxplot shows the median (central line), interquartile range (box area) and predominant range minus outliers (whiskers), with raw data overlaid

Finally, escape distances can inform management of human disturbance (Guay et al. 2016). In Sri Lanka, nature and wildlife tourism is common, and challenges exist in ensuring these ventures are sustainable (Fernando and Shariff 2017). Some ecotourism activities are more disturbing, to some species, than the pedestrian approach we employed here (Radkovic et al. 2019; Slater et al. 2019). However, our FID data offer a guide for suitable buffers, albeit those which require refinement and adaptive implementation (Guay et al. 2016).

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Author contribution This study was conceived by KE, JGG, MAW and MRES. Data were collected by KE, JGG, MAW, DRV, UTA and CF. Logistics and permits: KR, MAW, KE, JGG and UTA. Analysis and write up: AM, MRES and MAW.

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Declarations

Ethics approval Animal ethics approvals were obtained (Deakin University Animal Ethics Committee Permits B32-2012, B11-2015, B10-2018) as was a Sri Lankan Department of Wildlife Conservation Permit (WL/3/2/61/15; K. Ranawana). All applicable international, national and institutional guidelines for the use of animals were followed.

Conflict of interest The authors declare no competing interests.

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