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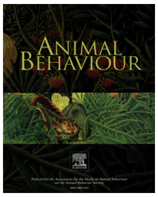

# Differences in flight initiation distances between African and Australian birds

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Associations between escape behaviours of birds approached by humans and life history traits differ between continents. This suggests environment and history have shaped the evolution of escape at the continental scale. We compared the escape behaviour of birds between eastern Australia (relatively low density and shorter history of human presence) and eastern Africa (high density and substantially longer history of human presence), in relation to life and natural history traits known to influence escape behaviour. We examined associations between flight initiation distance (FID) and life and natural history variables, using phylogenetically controlled analysis and model selection procedures, for 9372 FIDs from 516 bird species. Overall, African birds had shorter FIDs than Australian birds; however, this difference was only observed among nonmigratory (resident) species. Migratory birds showed no continental level differences in FIDs. Across continents, birds in 'wetland' and 'treed' habitats both had significantly longer FIDs than birds in 'scrub' habitats. Diet and social traits (cooperative breeding and flocking) did not significantly influence FID. The relationship between body mass and FID was positive for Australian birds but not so for African birds. This study (1) suggests that resident eastern African birds are more tolerant of humans and (2) supports the contention that some principles regarding escape behaviour of birds might represent universal patterns (e.g. longer FIDs in open wetland habitats), others (e.g. longer FIDs in larger birds) vary geographically or with habituation, perhaps in relation to the history of cohabitation between humans (and other predators) and birds.

Humans are ecosystem architects, having altered many land- and seascapes, and changed the evolutionary trajectories of many species (Bürgi, Östlund, & Mladenoff, 2017; Corlett, 2015; Sullivan, Bird, & Perry, 2017). Human dependence on wild plants and animals (e.g. for food and shelter) means humans and biodiversity have, to some extent, coevolved (Lu et al., 2018; Sullivan et al., 2017). Anthropogenic change, in many cases, has altered the distributions, life history and behaviour of wildlife, as well as causing some extinctions (Sullivan et al., 2017). The coevolution between humans and birds has driven adaptation in some species which has enabled them to exploit human-modified environments (Ducatez, Sayol, Sol, & Lefebvre, 2018). The capacity of some species to live in proximity to humans is thought to be partly driven by the cognitive capacity to judge risk in complex human environments (Griffin, Tebbich, & Bugnyar, 2017), and so is linked to decisions around antipredator escape responses (Sol et al., 2018). Specifically, where humans are common and mostly benign, antipredator responsiveness may be reduced (Blumstein, 2016; Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015).

From the perspective of wildlife, humans have acted as natural predators for lengthy periods of history and still hunt some species (i.e. prey upon them; Washburn & Lancaster, 2017). Although humans elicit specific responses from wildlife such as birds (McLeod, Guay, Taysom, Robinson, & Weston, 2013), it is generally

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considered that animals respond to people as they would to a nonhuman predator: humans usually elicit escape responses when they are close to birds (Frid & Dill, 2002). The propensity of birds to escape varies interspecifically and is generally regarded to be greater for large birds and species that are carnivorous and social (Blumstein, 2006; Blumstein, Anthony, Harcourt, & Ross, 2003; Møller, 2015). However, larger bird species may be especially able to habituate to humans (Blumstein, 2006; Samia et al., 2015). Furthermore, there are some suggestions that flightiness is, at least partly, genetically determined and thus can be passed from one generation to the next (van Dongen, Robinson, Weston, Mulder, & Guay, 2015). Intercontinental differences in the association between life history traits and escape also exist (Møller et al., 2014, 2016). The causes of some of these intercontinental differences are perplexing (Møller et al., 2014) and, for birds, comparisons are currently only available from three continents: Europe, North America and Australia.

One potential explanation of intercontinental differences in avian flightiness is the ‘depth of human history’ hypothesis which posits that the exposure of a species to humans over evolutionary time has resulted in modifications of escape responses. Exposure to humans over evolutionary time is a product of the duration of human occurrence and human density. Two continents exhibit especially stark differences in the exposure to humans: Africa (200 000+ years; currently, 80 people/km$^2$ [Kenya 82 people/km$^2$]; agricultural and nomadic heritage) and Australia (60 000+ years; currently, 3 people/km$^2$ [6.6/km$^2$ for eastern mainland states; www.population.net.au]; historically, largely nomadic in small groups; CIA, 2015; Dani and Mohen, 2005). The depth of hominid history in Africa means there is an even starker difference between the continents in this aspect of their history, with hominids ancestral to humans known to prey upon a diverse array of wildlife (Braun et al., 2010) and some extant nonhuman primates continuing to prey on birds and their eggs in Africa (Baudains & Lloyd, 2007; M.A. Weston, A. Radkovic, L. Kirao, P-J. Guay, W.F.D. Van Dongen, P Malaki, D.T. Blumstein & M.R.E. Symonds, personal observations). A comparison of avian responsiveness to humans on these continents could shed light on the role of the depth of human history on antipredator responses of birds, provided other life history traits are accounted for. Specifically, we predicted that flightiness will be lower in Africa than in Australia, because the depth of human history in Africa has resulted in more intense evolutionary processes which have enabled African birds to reduce flightiness that enables coexistence with humans, including through selective processes (e.g. by causing extinctions). Certainly, in Europe, the greater the time since urbanization the greater the tolerance of humans ($N = 42$ European bird species, Symonds et al., 2016) suggesting longer durations of coexistence underpin greater tolerance. While avian responses to humans can increase among birds subject to hunting (Fujioka, 2020; Sreekar, Goodale, & Harrison, 2015), many species appear to be able to differentiate humans engaged in hunting-like activities and respond earlier (Radkovic, Van Dongen, Kirao, Guay, & Weston, 2019; Slater et al., 2019), thereby cognitively buffering themselves from human impacts by exhibiting nuanced responses that are likely to have developed through exposure to humans (Sol, Székely, Liker, & Lefebvre, 2007). Finally, where humans are more abundant (urban areas) birds are more tolerant of human proximity (Samia et al., 2015). Contemporary processes such as habituation (through either or both of ontogenetic or genetic processes) may also play a role (but see Bjørvik, Dale, Hermansen, Munishi, & Moe, 2015), and cannot be readily disentangled from those acting over longer timescales.

Should intercontinental differences exist in avian flightiness, we expected that this will be mediated by whether a given species remains exclusively within a continent (resident) or regularly leaves it (intercontinental migrants). Given that migrants are exposed to a variety of prevailing human regimes during migration (Clemens et al., 2016), and that different life and natural history constraints may operate at different stages of migration (Mikula et al., 2018), we expected any intercontinental differences in avian flightiness to be most evident among resident species. While evolutionary shifts in residence/migration are known among birds, major migratory behaviour occurs in deep evolutionary time for at least some lineages (e.g. Passeriformes), and the development of migration in major groups occurred at least 6.6 million years ago in other groups (Dufour et al., 2020).

Here, we examined whether continental differences exist in flight initiation distances (FIDs) using a substantial database of avian escape responses from both continents.

## METHODS

### *FID Measurement*

We measured FID, a widely used method of indexing escape behaviour in animals, according to protocols outlined by Blumstein (2003). FID is the distance at which an animal commences escape from a stimulus, such as an approaching human. Wearing dull clothing and walking at ca. 1 m/s, we approached birds and measured their FID (direct line distances, measured using paces or rangefinders) and starting distance (SD, the distance between the person and bird at the beginning of an approach). Birds were not associating with other species and were behaving normally. Repeated 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; in both continents this involved suburban and rural data collection. Avian FIDs can vary with proxies of human density, such as suburban versus rural contexts (Samia et al., 2015). However, in Africa these proxies, to some extent, do not hold. Rural environments there can harbour comparatively high human densities, and species may not adjust their FIDs in relation to these gradients (Bjørvik et al., 2015; CIA, 2015). We therefore broadly matched sampling contexts between continents, avoiding city centres and wilderness areas.

### *Data*

Few African FIDs are currently available (Bateman & Fleming, 2011, Bjørvik et al., 2015; Blumstein, 2019; Braimoh et al., 2018; Coetzer & Bouwman, 2017; John, 2015; Magige, Holmern, Stokke, Mlingwa, & Røskaft, 2009; Radkovic et al., 2019). Kenya was chosen as the location for collecting African FIDs because it was accessible, has a high diversity of birds and involves an eastern continental seaboard making it most comparable to the area sampled in Australia (wetter coastal areas with deserts on the western fringes). FIDs of East African birds were collected from across the country, i.e. the general Nairobi area (1.2863°S, 36.8172°), the Watamu–Malindi area (3.2236°S, 40.1300°E) and around Lake Victoria near the Kenya–Tanzania border (1.0290°S, 34.0943°E). The data for Australian FIDs were taken from an existing data set of FIDs from throughout eastern Australia, but mostly from Victoria and New South Wales (94.3%; see Guay, van Dongen, Robinson, Blumstein, & Weston, 2016). The jurisdictions we sampled cover 2% (Africa) and 13% (Australia) of the continents, and we sampled 9% and 34% of the bird species that occur in the continents, respectively. In each continent, we sampled the eastern seaboard, especially the wetter areas, with our sampling in arid areas being mostly on the eastern margin of the respective inland deserts. We sampled in suburban, rural and park areas (accessible to people) in both continents but not in city centres or in strict wilderness areas. We assumed our sampling was representative of each continent (but future work over the entire expanse and taxonomic breadth of avifauna of both continents would be confirmatory). FID was measured by 31 trained observers, using the same methods, across both continents (three collected FID data on both continents), and previous work has demonstrated that estimates of FID do not vary significantly between observers (Guay et al., 2013).

### Ethical Note

Animal ethics approval was obtained (Deakin University Animal Ethics Committee Permits B32-2012, B11-2015, B10-2018 and Macquarie University Animal Research Committee 99021), as were permits (where required, e.g. Australia, Vic. DEWLP 10008731, SA DEWNR Y26590-1, NSW NPWS, SL101622; NT NPWS, 55233; Kenya, NACOSTI 25493, KWS 5001). Otherwise, explicit permission was obtained where permits were not required.

### Response and Predictor Variables

We required an index of escape that was consistent across species and continents. Being positively related to FID, SD explains significant and substantial variation in FID (Blumstein, 2003). Our study used species averages and considered $FID_{Adj}$ (the estimated FID at mean SD), calculated using the residual values from a phylogenetically controlled regression of $\log_{10}$(FID) on $\log_{10}$(SD) (after Glover, Guay, & Weston, 2015).

Comparative life history traits were chosen as predictor variables based on their likely influence on FID (see Appendix Table A1 for details). These were body mass (weighted average), diet (whether the bird ate live prey), whether it was a cooperative breeder, whether it was a flocking species at some point during the annual cycle and its main habitat (treed, scrub or wetland, following Blumstein, 2006; Møller, 2015). Additionally, we coded each taxon in regard to whether it was an intercontinental migrant at the population scale, because migrants may experience different depths of human history at different points of their migration. Of 531 species of African and Australian birds for which $FID_{Adj}$ was available, initially 518 species were selected for which all life history and natural history information was available. However, two species, *Lybius melanopterus* and *Francolinus coqui*, which had single observations each of FID that were unusually low (1 m) and unduly influential, were removed from the analysis.

Our data set did not support the use of the phi index (the complement of the average standardized distance between expected alert distance and observed FID; Samia & Blumstein, 2014) to index propensity to escape. This was because not all observations had alert distance (the distance at which vigilance commences) associated with FID measurements, and we were less confident in reliable measurements of those that did (see Guay et al., 2013).

### Statistical Analysis

We constructed models of the response of $FID_{Adj}$ to the following predictor variables: mass, diet, sociality (flocking and cooperative breeding), habitat, migratory status and continent. We also included all two-way interactions with continent (mass*continent, diet*continent etc.) to establish whether there are continent level differences in the way FID relates to other ecological predictors. For example, larger bird species are thought to habituate more to humans yet also tend to be flightier, so if the depth of human history influenced FID, it could interact with mass (Blumstein, 2006; Samia et al., 2015). Where interactions were shown to be important, we also analysed the data separately by continent to establish differences in responses to these other predictors between the two continents. We *z* standardized the continuous variables in the analysis (FID and mass). Predictors were also checked for covariance by calculating variance inflation factors, all of which were low ($< 1.6$).

Since this was a cross-species comparative analysis, it was potentially necessary to control for the effect of phylogenetic relationships. Species are not phylogenetically independent; hence they may resemble each other because of shared ancestry (Harvey & Pagel, 1991). The phylogeny used as the basis for analysis was derived from www.birdtree.org (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012); 2000 trees were downloaded for the subset of species from the pseudo-posterior distribution of trees using the ‘backbone’ phylogeny from Ericson et al. (2006). A majority rules consensus phylogeny tree was formed using Mesquite (Maddison & Maddison, 2010). The polytomies remaining in the phylogeny were arbitrarily resolved with internal branches assigned zero length. Where the same species was found in both Africa and Australia, they were coded as different taxa and placed as closest relatives to each other in the phylogenetic topology. This ensured that FIDs were not pooled across continents for these taxa. For branch lengths, Grafen's (1989) method was used where the depths of nodes in the phylogeny is proportional to the number of species descended from them.

Phylogenetic generalized least squares (PGLS) were implemented through the R packages nlme v.3.1-148, ape v.5.4-1 and phytools v.0.7-47 (Paradis & Schliep, 2019; Pinheiro, Bates, DebRoy & Sarkar, 2020; Revell, 2012). These control for nonindependence of species by incorporating information on the expected covariance between traits based on the species’ phylogenetic relatedness (Symonds & Blomberg, 2014). The amount of phylogenetic signal in the residuals of each model was calculated using the maximum-likelihood value of the parameter $\lambda$, which transforms the internal branch lengths of the phylogeny (Pagel, 1997; Pagel, 1999). When $\lambda = 1$, the internal branch lengths remain untransformed, indicating that the observed data strongly match the expected phylogenetic patterns given a Brownian motion model of evolution. When $\lambda = 0$, all internal branches of the phylogeny collapse to zero, indicating there is no phylogenetic signal in the data and the results are identical to analyses conducted using ordinary least squares regression on the raw data.

Because we also had different sample sizes for each species, we also considered this in the comparative analysis where each observation is weighted by the square root of the sample sizes for FIDs for each species (using the weights argument in the gls function in nlme).

A model selection and model averaging approach was adopted, based on the Akaike information criterion (AIC; Burnham & Anderson, 2002; Symonds & Moussalli, 2011). ΔAIC values of 0−2 indicate models that are essentially equally as good as the best model (Burnham, Anderson, & Huyvaert, 2011).

We applied this model selection approach in two stages. The first stage was used to compare model fit of the global models that either did or did not control for phylogenetic effects and sample size weighting (or both). For this we employed the R code provided in the supplementary material to Garamszegi and Mundry (2014). We then used the dredge function of MuMIn v.1.43.17 (Bartoń, 2020) on the best model derived above, to compare models containing all possible combinations of the selected parameters, and conditional model averaging using AICcmodavg v.2.3-1 (Mazerolle, 2020). Through this approach we were able to identify both the top models and an indication of the relative importance (i.e. the summed Akaike weights) and nature of the effect of each predictor on $FID_{Adj}$.

## RESULTS

We conducted 1223 FID approaches on 223 different species of African birds of which 987 FIDs and 210 species were suitable for the comparative analysis (see Appendix Table A2). We had a data set containing 9961 FIDs on 371 species of Australian birds of which 8385 FIDs on 306 species were suitable for comparative analysis.

Initial model selection based on the global model revealed that the best model was the simplest ordinary least squares model (see Appendix Table A3). There was no improvement of fit gained by controlling for phylogenetic relatedness or species sample sizes, so all subsequent model comparisons were run without controlling for phylogeny or sample size weighting (Appendix Table A3). The model comparison revealed there was no strongly supported best approximating model, with the top model having an Akaike weight of only 0.141 and four models having ΔAIC of < 2 (effectively equally as good). All four models included continent, mass, the interaction between mass and continent, migratory status, the interaction between migratory status and continent, and habitat as important predictors of FID (Table 1). Model averaging identified that these predictors were all strongly influential with parameter importance > 0.95 and confidence intervals for averaged estimates that did not cross zero (Table 2). Overall, birds were flightier (i.e. had longer FIDs) in Australia than in Africa (Table 2); however, a significant interaction effect with migratory status revealed that this difference in FID between continents only applied to nonmigratory species (Fig. 1). Migratory species showed no difference in FID between the continents. Likewise, while nonmigratory species were less flighty than migrants, this difference was confined to African and not Australian birds.

There was also a significant interaction between body mass and continent. In Australia, heavier species of birds were more flighty than smaller species, whereas no such relationship existed in African birds (Fig. 2). Habitat had a significant effect on the flightiness of birds. Birds in ‘wetland’ and ‘treed’ habitats both had significantly longer FIDs than birds in ‘scrub’ habitats. Birds in wetlands had the longest FIDs but their FIDs were not significantly longer than species in treed habitats (Fig. 3).

While diet and flocking behaviour were present in some of the best models (Table 1), these were only found in models that were more complex versions of the top model and the overall importance value for these predictors was low (< 0.6). Cooperative breeding was not an influential predictor, nor were any other interactions with continent.

## DISCUSSION

We found a difference between continents in the escape distances of birds approached by humans. As predicted, resident (although not migratory) birds were less fearful of people in Africa than they were in Australia. Furthermore, predictors for FID did not all have the same influence on FID on both continents: mass had a positive relationship with FID in Australia, but no such relationship (indeed the trend was slightly negative) in Africa, and migrants had longer FIDs than residents in Africa, but no such difference existed in Australia. The modest explanatory power ($R^2 = 0.26$) of our models is not unexpected from such a diverse range of species and comparisons across continents.

### Continent and Residency

Comparisons of the behaviour of fauna between continents are imperfect, and are potentially confounded by a myriad of geological, climatological, evolutionary and ecological histories and regimes, and some patterns defy ready explanation (Møller et al.,

**Table 1**
Composition of the top general linear models with a delta score < 2 (plus null model for comparison) explaining the relationship of flight initiation distance in eastern African and eastern Australian birds

| Model number | Model components | AICc | Akaike weight | ΔAIC | $R^2$ |
|---|---|---|---|---|---|
| 1 | Continent + Mass + Habitat + Migration + Continent*Mass + Continent*Migration | −456.9 | 0.141 | 0.00 | 0.261 |
| 2 | Continent + Mass + Diet + Habitat + Migration + Continent*Mass + Continent*Migration | −456.6 | 0.118 | 0.35 | 0.263 |
| 3 | Continent + Mass + Flocking + Habitat + Migration + Continent*Mass + Continent*Migration | −455.8 | 0.081 | 1.11 | 0.262 |
| 4 | Continent + Mass + Diet + Habitat + Flocking + Migration + Continent*Mass + Continent*Migration | −455.0 | 0.055 | 1.88 | 0.264 |
| Null | Intercept only | −315.5 | 0 | 141.4 | 0 |

Thirteen predictor variables were examined: continent, the average body mass of the species, diet (whether the bird ate live prey), whether it was a cooperative breeder, whether it was a flocking species, whether the species migrated outside the respective continent, the habitat type it was sampled in (treed, scrub and wetland; scrub is set as the reference variable) and the interactions of continent with each of the other predictors. The AICc, Akaike weight, ΔAIC and $R^2$ values are included, ranked by ΔAIC score.

**Table 2**
Model averaged coefficients for predictors of flight initiation distance (FID) in eastern African and eastern Australian bird species

| Coefficient | Estimate | Lower 95%CI | Upper 95%CI | Weight |
|---|---|---|---|---|
| **Continent (Australia)** | **0.155** | **0.111** | **0.198** | **1.00** |
| **Mass** | **−0.030** | **−0.054** | **−0.006** | **0.98** |
| **Habitat (Treed)** | **0.058** | **0.019** | **0.097** | **0.98** |
| **Habitat (Wetland)** | **0.057** | **0.007** | **0.107** | **0.98** |
| **Migration** | **0.121** | **0.049** | **0.193** | **0.99** |
| Diet (Carnivore) | 0.019 | −0.022 | 0.060 | 0.52 |
| Flocking | −0.009 | −0.050 | 0.031 | 0.43 |
| Cooperative Breeding | −0.005 | −0.054 | 0.044 | 0.34 |
| **Continent*Mass** | **0.051** | **0.022** | **0.081** | **0.97** |
| **Continent*Migration** | **−0.139** | **−0.226** | **−0.051** | **0.96** |
| Continent*Habitat (Treed) | −0.020 | −0.092 | 0.052 | 0.14 |
| Continent*Habitat (Wetland) | −0.018 | −0.120 | 0.083 | 0.14 |
| Continent*Diet | 0.017 | −0.052 | 0.085 | 0.15 |
| Continent*Flocking | −0.022 | −0.085 | 0.042 | 0.13 |
| Continent*Cooperative Breeding | 0.024 | −0.055 | 0.103 | 0.10 |

FID values were adjusted relative to starting distance (see Methods). FID and body mass values were *z* standardized. Habitat estimates are relative to scrub habitats. Diet estimates are relative to noncarnivorous species. Estimates for migration, flocking and cooperative breeding are for species that show these traits relative to those that do not. Important effects with high summed parameter weight (importance) and confidence intervals (CI) that do not cross zero are indicated in bold.

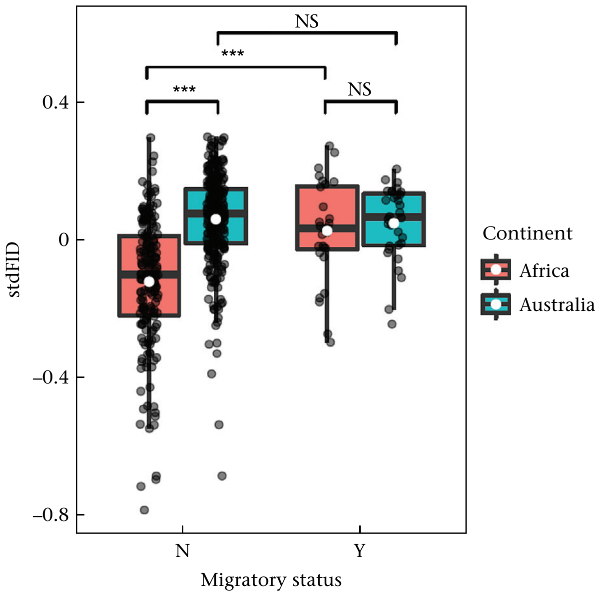


**Figure 1.** Box plot of standardized flight initiation distance (FID) in eastern African and eastern Australian birds, and in relation to the migratory status (i.e. whether they are nonmigratory (N) or migratory (Y) species). Boxes show median (thick black line) and interquartile ranges, while stems show the main range of the data (excluding outliers, defined as more than 1.5 times the interquartile range away from the median). White points within boxes are mean values. Significance values (*** $P < 0.001$) from separate linear models for Australian and African birds and for migratory and nonmigratory birds are also indicated.

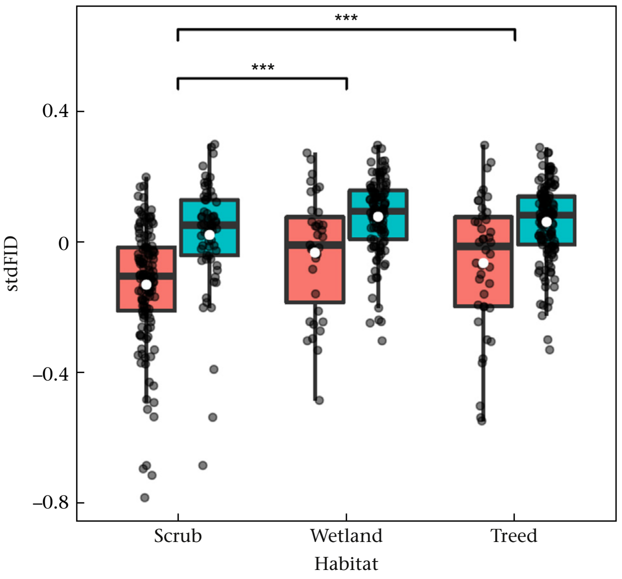
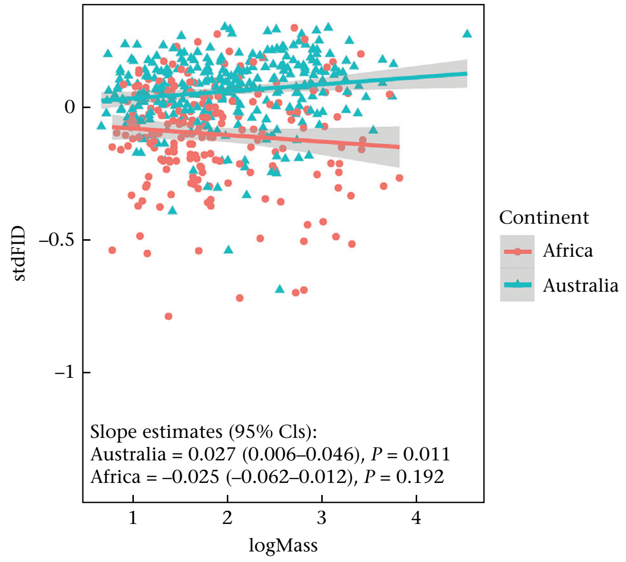


**Figure 3.** Box plot of standardized flight initiation distance (FID) for birds in three different habitats (scrub, wetland and treed) across eastern Africa and eastern Australia. Significant differences from the linear model of FID against Habitat are indicated: ***$P$ <0.001. Other box plot details as per Fig. 1.

2014). Despite these differences (which could explain at least some of the variation in avian FIDs between Africa and Australia that we documented), the history of human habitation, population and human behaviour has perhaps influenced avian antipredator responses to humans. Such processes may involve within-animal behavioural adaptations such as learning (Blumstein, 2016) or across-animal selective processes favouring bolder birds in areas with more humans (both of these have been demonstrated at smaller scales; e.g. van Dongen et al., 2015; Thibault, Weston, Ravache, & Vidal, 2020). Another possibility is that less flighty species have survived in areas with more humans, a pattern consistent with filtering. Very few species have been recorded as going extinct in Africa during the last 500 years or so, suggesting that species sensitive to early disturbance from humans became extinct before 1500, while the more resilient species have survived until modern times (Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007; Sol et al., 2007; Vitousek, Mooney, Lubchenco, & Melillo, 1997). The human history in Australia might have increased the fear among birds and their sensitivity to disturbance. Australia has had human populations for a quarter of the length of Africa and humans have apparently mostly been small, scattered populations of hunter-gatherers (Miller et al., 1999). Since European colonization the human population has increased dramatically in Australia, and some birds now experience disturbance to the extent it is viewed as a conservation problem (Weston, McLeod, Blumstein, & Guay, 2012). Encounters where birds are hunted as prey have also likely increased with European colonization (i.e. the last 250 years; Grayson, 2001; Miller et al., 1999), potentially amplifying fear of humans. Furthermore, fearfulness is negatively associated with population size trends of birds in Australia and Europe (but not North America), with no current information available for Africa because of a lack of reliable population trends (Møller et al., 2014).



Slope estimates (95% CIs):
Australia = 0.027 (0.006–0.046), $P = 0.011$
Africa = –0.025 (–0.062–0.012), $P = 0.192$

**Figure 2.** Scatterplot of relationship between standardized flight initiation distance (FID) and log body mass in eastern African and eastern Australian birds. Best-fit lines are linear regression lines with confidence intervals (CI) from the linear models of FID against mass for each continent.

Further support for the idea that the continental differences in FID are associated with prevailing and different human regimes between Africa and Australia comes from the significant interaction of continent with migratory status. The predicted shorter FIDs in Africa than in Australia occurred only in resident species, those whose exposure to people is confined to the bounds of their respective continents. African migrants had longer FIDs than African residents, perhaps because they visit somewhat less populous areas during migration. For shorebirds that migrate to Africa (i.e. a subset of species classified as 'migrants' in our analyses), the shortest FIDs are when breeding in Europe, the longest FIDs are during stopover at staging sites and intermediate FIDs occur during the nonbreeding period in Africa (Mikula et al., 2018). Thus, FIDs of at least some migrants are plastic (Mikula et al., 2018). In Australia, no difference in FIDs occurred between resident and migratory species, although at least some migratory birds pass through the densely populated east Asian coast on stopover (Clemens et al., 2016). While exposure to high human densities during migration may conceivably lead to reduced FIDs in Australia (but see Mikula et al., 2018), many migrants in the East Asian–Australasian Flyway are threatened or declining (Clemens et al., 2016), and such species may exhibit longer FIDs (Møller et al., 2014). Associations between life and natural history traits and FID can change during migration (Mikula et al., 2018), and a fuller understanding of any influence of human regimes experienced during migration, and its influence (if any) on FIDs, is desirable. Clearly, comparisons of FIDs between geographical areas should account for migratory status of the species sampled.

The patterns of fearfulness reported here are consistent with the idea that humans have shaped different escape responses of birds on continents over evolutionary time. We cannot exclude likely, although undocumented, contemporary processes as having played a role in these differences, such as exposure to hunting or prevailing predator risk, or the role of known contemporary processes, such as different prevailing human densities (Fujioka, 2020; Møller et al., 2014). Interestingly, variation in FID among African birds may only vary modestly in relation to human density, perhaps because these gradients are shallower in Africa (Bjørvik et al., 2015). We acknowledge that other processes may influence avian fear and may interact with or explain the patterns we report. These might include predator regimes and energetic or thermal constraints associated with different seasonal patterns of rainfall (Kenya has two wet seasons, Australia has one), or other factors. At least one of these seems an unlikely candidate explanation: greater predator abundance and diversity at lower latitudes (Díaz et al., 2013) could predict longer FIDs in our Africa data yet we found the opposite pattern. A global analysis of fear versus coevolution with humans would be helpful to further test this hypothesis.

### Body Mass

A result that emerged from many comparative studies and meta-analyses is that FID increases with body mass (Blumstein, 2006; Møller, 2015). The positive association between FID and body mass has been demonstrated in Australia, Europe, North America and elsewhere (see Møller, 2015). However, this study shows that this relationship is not universal and that it possibly varies between continents or that East African birds are an exception to the usual pattern. Australian birds followed the established pattern whereby smaller birds are not as flighty as larger birds (Møller, 2015). In Africa, a nonsignificant but slightly negative trend was apparent. The reasons for this difference are not perfectly known, but it has been suggested that larger birds have the capacity to habituate to humans more readily, although they are initially more flighty (Samia et al., 2015). Three possible reasons could contribute to the faster habituation of large birds. First, large birds have larger brains; they learn faster and make calculated risk assessments (Sol et al., 2007). Second, large birds need more food in absolute terms and may not leave a foraging patch unless it is necessary (Glover, Weston, Maguire, Miller, & Christie, 2011). If large birds learn that humans pose no direct threat, they might risk close proximity to continue foraging without expending energy on escape, and the positive association between body mass and FID may reduce or disappear. Finally, extinction trends may have selected against flightiness in larger Africa birds but towards it in Australia. Perhaps in Africa large species fear humans less than smaller species because large species sensitive to disturbance have already become extinct (sensu Chichorro et al., 2020). An extension of these inferred patterns is that sensitive Australian birds may be under heightened extinction risk. Further study of FIDs across the globe would confirm or refute whether human history has influenced the associations between avian FIDs and body mass.

### Habitat

Habitats offer differing degrees of refuge and detectability of approaching threats, and FIDs in different habitats may reflect a trade-off between proximity to refuge and risk of ambush (Blumstein, 2003, 2006; Blumstein et al., 2003; Møller, 2015). Birds in open areas may be especially sensitive to humans (Heil, Fernández-Juricic, Renison, Cingolani, & Blumstein, 2007). Alternatively, species typically found in dense habitats might be more wary than those found in more open habitats so as not to be surprised by nearby unseen predators; however, this has not been unambiguously demonstrated (Blumstein, 2006). Species in wetlands had significantly longer FIDs than birds inhabiting scrub (this study); water within wetlands can represent refuges from predators in some circumstances (Dear, Guay, Robinson, & Weston, 2015). The wetlands we sampled were very open habitats, giving birds high visibility but also possibly increasing the need for predator vigilance and perhaps exposing potential prey species to attack. We also found species in treed areas had longer FIDs than those inhabiting scrub. This could also result from greater subcanopy openness in woodlands compared with scrublands, or perhaps species–habitat associations (Grundel & Pavlovic, 2007). The effect of habitat openness on FID could be a universal principle and would usefully be tested on other continents.

Another possible explanation of differences in FIDs between habitats is the contiguous habitat hypothesis (Blumstein, 2014) which suggests that birds inhabiting fragmented, patchy habitats such as wetlands may habituate to humans whereas those in contiguous habitats may not do so. It is possible that the wetland habitats were more contiguous than the terrestrial ones in our study, perhaps due to fragmentation of the latter (see, for example, Howes, Byholm, & Symes, 2020). Further confirmatory research is required to test this hypothesis (Blumstein, 2014), and quantification of habitat connectivity across species is required to test these ideas.

### Sociality and Diet

Birds in larger groups benefit from communicated alarm signals and are generally regarded as flightier than less social species (Glover et al., 2011; Linley, Guay, & Weston, 2020; Møller, 2015). Flocking did not have a significant effect on FID in either continent. Cooperative breeders have previously been found to be more flighty (Blumstein, 2006); however, we found no such effect. In both Africa and Australia, birds that eat live prey were no more flightier than birds that did not (contra Blumstein, 2006). The reason for these different findings is unclear but the analyses use a different mix of species from different continents. The effects may also be context specific and are evidently not universal. Further analyses from more species and continents should confirm the universality or otherwise of these effects on escape responses of birds.

### Conclusions

We confirmed that fear in resident birds differed between the areas we studied on each continent. Although most of the mediating factors of FID recognized by Blumstein (2006) are the same across continents, the association between FID and mass (one of the main life history associations with FID), and between FID and migratory status, varied geographically in this study and in a manner consistent with the idea that the depth of human history has shaped FID. Other drivers of FID may not be universal either, such as sociality and diet and other associations with FID, for example the nature of associations between FID and population size trends, which can also vary between continents (Møller et al., 2014). Our understanding of associations between life and natural history traits and FID will inevitably develop as data from a greater variety of evolutionary histories become available.

## Author Contributions

Data collection was carried out by A.R., M.A.W., L.K. and P.M. M.A.W., M.R.E.S., S.T.B., P.G. and W.V.D. analysed the data and wrote the manuscript.

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## Appendix

**Table A1**
Details of life and natural history traits

| Trait | Details | Source | Precedence for inclusion |
|---|---|---|---|
| Body mass (g) | Weighted average between sexes | Dunning (2007) | Blumstein (2006), Møller (2015) |
| Diet | Whether the bird ate live prey | HANZAB (1981-2007), Zimmerman, Turner, and Pearson (1999) | Blumstein (2006), Møller (2015) |
| Flocking status | Whether the species formed flocks at any point of the life cycle | HANZAB (1981-2007), Zimmerman et al. (1999) | Blumstein (2006), Møller (2015) |
| Cooperative breeder | Whether the species bred cooperatively, i.e. with more than two adults tending nests/young | HANZAB (1981-2007), Zimmerman et al. (1999) | Blumstein (2006), Møller (2015) |
| Habitat | Main habitat: wooded, scrub or wetland (the latter includes other open habitats for a few species) | HANZAB (1981-2007), Zimmerman et al. (1999) | Blumstein (2006), Møller (2015) |
| Migration | Taxa were coded as to whether they undertook unambiguous population scale movements that extended beyond the continents in which they were sampled[1] | Del Hoyo, Del Hoyo, Elliott, and Sargatal (2021) | Mikula et al. (2018), and migrants may experience regimes in human occurrence that extend beyond the continents being studied |

[1] Extracontinental movements included those to adjacent islands (e.g. Madagascar for the Madagascan pratincole, or New Zealand for the double-banded plover). Thus, intracontinental movements (which can be substantial, and involve nomadism and migration) were not coded as intercontinental migrants (e.g. African golden oriole). In cases where population-specific differences in movements occurred, the population most representative of our sampling area was selected for the assignment of movement status (e.g. sacred kingfisher [migratory], Wahlberg's eagle [not migratory]). The vast majority of taxa could be unambiguously assigned to the movement status. Where ambiguity existed (e.g. leaden flycatcher, rufous fantail), these were assigned to 'nonmigratory'. We acknowledge that for some taxa, both intercontinentally migratory and nonmigratory individuals could have been present in our data (e.g. little bittern, spangled drongo).

**Table A2**
Complete list of bird species for which flight initiation distance (FID) was collected in Africa with the number sampled and mean ± SE FID and starting distance (SD)

| Common name | Scientific name | *N* | FID (m) | SD (m) |
|---|---|---|---|---|
| African darter | *Anhinga rufa* | 1 | 12.0±0.0 | 86.0±0.0 |
| African fish eagle | *Haliaeetus vocifer* | 2 | 68.0±28.0 | 228.0±8.0 |
| African golden oriole | *Oriolus auratus* | 1 | 5.0±0.0 | 25.0±0.0 |
| African golden weaver | *Ploceus subaureus* | 4 | 11.8±1.3 | 26.0±5.4 |
| African green pigeon | *Treron calvus* | 3 | 10.7±4.1 | 30.7±5.3 |
| African grey flycatcher | *Bradornis microrhynchus* | 2 | 3.0±1.0 | 14.5±0.5 |
| African jacana | *Actophilornis africanus* | 4 | 18.8±4.1 | 39.5±3.5 |
| African marsh harrier | *Circus ranivorus* | 1 | 61.0±0.0 | 71.0±0.0 |
| African mourning dove | *Streptopelia decipiens* | 3 | 8.3±3.2 | 29.3±7.6 |
| African paradise flycatcher | *Terpsiphone viridis* | 6 | 4.5±0.43 | 187.0±5.9 |
| African pied wagtail | *Motacilla aguimp* | 13 | 8.5±0.8 | 26.9±3.2 |
| African pygmy kingfisher | *Ceyx pictus* | 3 | 14.7±1.2 | 26.0±2.0 |
| African spoonbill | *Platalea alba* | 4 | 19.3±3.1 | 72.5±8.0 |
| Amethyst sunbird | *Nectarinia amethystina* | 5 | 4.6±0.8 | 35.6±8.7 |
| Angola swallow | *Hirundo angolensis* | 2 | 10.5±2.5 | 19.0±3.0 |
| Augur buzzard | *Buteo augur* | 1 | 131.0±0.0 | 235.0±0.0 |
| Bare-eyed thrush | *Turdus tephronotus* | 1 | 5.0±0.0 | 38.0±0.0 |
| Bare-faced go-away bird | *Corythaixoides personatus* | 5 | 9.0±3.8 | 44.2±19.9 |
| Black and white mannikin | *Lonchura bicolor* | 21 | 8.7±0.6 | 19.3±1.0 |
| Black crake | *Amaurornis flavirostra* | 1 | 15.0±0.0 | 38.0±0.0 |
| Black-crowned tchagra | *Tchagra senegalus* | 9 | 9.9±2.1 | 27.6±6.2 |
| Black-headed heron | *Ardea melanocephala* | 5 | 24.8±7.9 | 67.4±19.4 |
| Black heron | *Egretta ardesiaca* | 2 | 29.5±2.5 | 125.0±71.0 |
| Black kite | *Milvus migrans* | 8 | 26.7±9.7 | 57.4±10.2 |
| Black-backed puffback | *Dryoscopus cubla* | 2 | 17.5±9.5 | 37.0±2.0 |
| Black-bellied starling | *Lamprotornis corruscus* | 7 | 10.4±1.3 | 26.3±4.6 |
| Black-chested snake eagle | *Circaetus pectoralis* | 1 | 28.0±0.0 | 54.0±0.0 |
| Black-crowned night heron | *Nycticorax nycticorax* | 1 | 17.0±0.0 | 32.0±0.0 |
| Black-faced waxbill | *Estrilda erythronotos* | 3 | 8.0±1.5 | 16.7±2.2 |
| Black-headed gonolek | *Laniarius erythrogaster* | 5 | 6.2±1.0 | 26.8±4.3 |
| Black-headed oriole | *Oriolus larvatus* | 2 | 4.0±2.0 | 18.5±6.5 |
| Black-winged red bishop | *Euplectes hordeaceus* | 16 | 9.4±0.8 | 32.1±3.9 |
| Blue-capped cordon-bleu | *Uraeginthus cyanocephalus* | 15 | 9.3±1.1 | 22.1±2.2 |
| Blue-naped mousebird | *Urocolius macrourus* | 4 | 7.3±2.3 | 23.2±3.6 |
| Bronze mannikin | *Lonchura cucullata* | 6 | 7.8±1.5 | 18.3±3.8 |
| Brown-crowned tchagra | *Tchagra australis* | 1 | 12.0±0.0 | 18.0±0.0 |
| Buff-bellied warbler | *Phyllolais pulchella* | 2 | 11.5±0.5 | 35.5±0.5 |
| Carruther's cisticola | *Cisticola carruthersi* | 1 | 5.0±0.0 | 25.0±0.0 |
| Caspian tern | *Sterna caspia* | 10 | 38.0±6.5 | 57.5±8.2 |
| Cattle egret | *Bubulcus ibis* | 13 | 55.8±12.9 | 82.2±18.7 |
| Chestnut weaver | *Ploceus rubiginosus* | 1 | 9.0±0.0 | 22.0±0.0 |
| Cliff chat | *Myrmecocichla cinnamomeiventris* | 1 | 24.0±0.0 | 43.0±0.0 |
| Coastal cisticola | *Cisticola galactotes* | 21 | 10.9±1.3 | 24.5±1.9 |
| Collared sunbird | *Anthreptes collaris* | 7 | 5.4±1.3 | 16.1±3.9 |
| Common bulbul | *Pycnonotus barbatus* | 35 | 11.31±1.0 | 27.4±2.0 |
| Common drongo | *Dicrurus adsimilis* | 15 | 14.9±1.6 | 33.8±4.8 |
| Common fiscal | *Lanius collaris* | 11 | 5.8±1.0 | 23.8±2.3 |
| Common greenshank | *Tringa nebularia* | 27 | 51.3±4.7 | 99.8±13.4 |
| Common snipe | *Gallinago gallinago* | 1 | 38.0±0.0 | 53.0±0.0 |
| Common waxbill | *Estrilda astrild* | 2 | 9.0±3.0 | 17.5±3.5 |
| Crab plover | *Dromas ardeola* | 14 | 26.6±1.2 | 58.2±4.7 |
| Crowned hornbill | *Tockus alboterminatus* | 2 | 9.0±1.0 | 24.0±4.0 |
| Curlew sandpiper | *Calidris ferruginea* | 41 | 24.9±1.1 | 60.4±6.1 |
| D'Arnaud's barbet | *Trachyphonus darnaudii* | 3 | 12.0±3.1 | 42.3±12.8 |
| Diederik cuckoo | *Chrysococcyx caprius* | 2 | 10.5±8.5 | 29.5±3.5 |
| East coast batis | *Batis soror* | 1 | 5.0±0.0 | 12.0±0.0 |
| Eastern bearded scrub-robin | *Erythropygia quadrivirgata* | 1 | 17.0±0.0 | 25.0±0.0 |
| Egyptian goose | *Alopochen aegyptiaca* | 1 | 19.0±0.0 | 37.0±0.0 |
| Emerald spotted wood-dove | *Turtur chalcospilos* | 7 | 10.7±1.2 | 25.0±4.4 |
| Eurasian bee-eater | *Merops apiaster* | 4 | 17.5±3.1 | 60.3±10.3 |
| Eurasian golden oriole | *Oriolus oriolus* | 1 | 24.0±0.0 | 49.0±0.0 |
| Fan-tailed widowbird | *Euplectes axillaris* | 1 | 14.0±0.0 | 26.0±0.0 |
| Fiery-necked nightjar | *Caprimulgus pectoralis* | 1 | 3.0±0.0 | 10.0±0.0 |
| Fischer's greenbul | *Phyllastrephus fischeri* | 1 | 22.0±0.0 | 28.0±0.0 |
| Fischer's lovebird | *Agapornis fischeri* | 1 | 16.0±0.0 | 19.0±0.0 |
| Glossy ibis | *Plegadis falcinellus* | 17 | 38.8±6.7 | 83.2±12.2 |
| Golden-breasted bunting | *Emberiza flaviventris* | 1 | 8.0±0.0 | 17.0±0.0 |
| Golden-breasted starling | *Cosmopsarus regius* | 1 | 13.0±0.0 | 27.0±0.0 |
| Golden palm weaver | *Ploceus bojeri* | 5 | 5.6±0.7 | 18.4±4.9 |
| Goliath heron | *Ardea goliath* | 1 | 35.0±0.0 | 171.0±0.0 |
| Grassland pipit | *Anthus novaeseelandiae* | 6 | 10.3±2.0 | 30.5±4.4 |
| Great cormorant | *Phalacrocorax carbo* | 43 | 37.9±3.8 | 60.9±4.2 |
| Great egret | *Casmerodius albus* | 53 | 45.8±3.3 | 75.7±5.9 |
| Great sparrowhawk | *Accipiter melanoleucus* | 1 | 15.0±0.0 | 98.0±0.0 |

(*continued on next page*)

**Table A2** (*continued*)

| Common name | Scientific name | *N* | FID (m) | SD (m) |
|---|---|---|---|---|
| Greater blue-eared starling | *Lamprotornis chalybaeus* | 4 | 15.0±6.5 | 35.8±11.7 |
| Greater crested tern | *Sterna bergii* | 1 | 29.0±0.0 | 53.0±0.0 |
| Greater sandplover | *Charadrius leschenaultii* | 5 | 24.0±2.1 | 42.6±4.9 |
| Greater swamp warbler | *Acrocephalus rufescens* | 1 | 8.0±0.0 | 16.0±0.0 |
| Green-winged pytilia | *Pytilia melba* | 4 | 7.3±1.9 | 15.0±2.3 |
| Grey-capped social weaver | *Pseudonigrita arnaudi* | 15 | 9.9±1.3 | 22.4±1.9 |
| Grey-headed kingfisher | *Halcyon leucocephala* | 6 | 9.7±1.7 | 26.0±3.5 |
| Grey-headed sparrow | *Passer griseus* | 2 | 14.0±3.0 | 21.5±6.5 |
| Grey heron | *Ardea cinerea* | 3 | 26.7±8.8 | 66.7±22.3 |
| Grey plover | *Pluvialis squatarola* | 7 | 38.2±5.8 | 73.1±11.2 |
| Grey-backed cameroptera | *Camaroptera brachyura* | 1 | 15.0±0.0 | 29.0±0.0 |
| Grey-backed fiscal | *Lanius excubitoroides* | 4 | 15.0±5.5 | 60.0±12.3 |
| Grosbeak-weaver | *Amblyospiza albifrons* | 1 | 8.0±0.0 | 12.0±0.0 |
| Gull-billed tern | *Sterna nilotica* | 3 | 54.7±5.8 | 81.7±14.2 |
| Hadada ibis | *Bostrychia hagedash* | 3 | 19.7±4.9 | 74.0±10.0 |
| Hamerkop | *Scopus umbretta* | 2 | 13.0±3.0 | 31.5±3.5 |
| Helmeted guinea fowl | *Numida meleagris* | 1 | 28.0±0.0 | 42.0±0.0 |
| Hildebrandt's starling | *Lamprotornis hildebrandti* | 1 | 17.0±0.0 | 34.0±0.0 |
| Holub's golden weaver | *Ploceus xanthops* | 2 | 4.5±0.5 | 12.5±0.5 |
| Hunter's sunbird | *Nectarinia hunteri* | 1 | 4.0±0.0 | 26.0±0.0 |
| Indian house crow | *Corvus splendens* | 5 | 7.8±2.5 | 27.8±6.8 |
| Jackson's golden-backed weaver | *Ploceus jacksoni* | 6 | 6.5±1.3 | 22.0±4.3 |
| Jacobin cuckoo | *Clamator jacobinus* | 2 | 29.0±15.0 | 51.0±4.0 |
| Kittlitz's plover | *Charadrius pecuarius* | 4 | 18.3±2.5 | 44.3±8.5 |
| Knob-billed duck | *Sarkidiornis melanotos* | 2 | 26.0±2.0 | 88.0±2.0 |
| Laughing dove | *Stigmatopelia senegalensis* | 2 | 4.5±1.5 | 18.0±1.0 |
| Lesser black-backed gull | *Larus fuscus* | 3 | 37.7±6.2 | 92.3±3.3 |
| Lesser crested tern | *Sterna bengalensis* | 2 | 24.0±1.0 | 48.0±2.0 |
| Lesser flamingo | *Phoeniconaias minor* | 5 | 33.0±6.5 | 141.0±56.3 |
| Lesser masked weaver | *Ploceus intermedius* | 6 | 7.3±3.3 | 24.8±4.3 |
| Lesser sandplover | *Charadrius mongolus* | 9 | 24.4±2.2 | 45.6±3.4 |
| Lesser striped swallow | *Hirundo abyssinica* | 7 | 6.6±1.7 | 17.7±2.0 |
| Lilac breasted roller | *Coracias caudatus* | 9 | 22.4±4.3 | 43.1±7.4 |
| Little bee-eater | *Merops pusillus* | 23 | 8.3±0.8 | 24.2±2.5 |
| Little egret | *Egretta garzetta* | 29 | 35.6±5.0 | 75.4±7.8 |
| Little stint | *Calidris minuta* | 1 | 20.0±0.0 | 29.0±0.0 |
| Little yellow flycatcher | *Erythrocercus holochlorus* | 1 | 2.0±0.0 | 14.0±0.0 |
| Lizard buzzard | *Kaupifalco monogrammicus* | 9 | 17.3±2.7 | 37.2±5.1 |
| Long-tailed cormorant | *Phalacrocorax africanus* | 3 | 11.7±1.3 | 26.0±4.6 |
| Long-tailed fiscal shrike | *Lanius cabanisi* | 9 | 17.7±2.7 | 41.3±4.4 |
| Madagascar pratincole | *Glareola ocularis* | 1 | 40.0±0.0 | 63.0±0.0 |
| Magpie shrike | *Urolestes melanoleucus* | 2 | 6.0±2.0 | 20.0±8.0 |
| Malachite kingfisher | *Alcedo cristata* | 4 | 10.3±0.6 | 30.5±7.4 |
| Marabou stork | *Leptoptilos crumeniferus* | 1 | 8.0±0.0 | 32.0±0.0 |
| Marico sunbird | *Nectarinia mariquensis* | 1 | 8.0±0.0 | 12.0±0.0 |
| Marsh sandpiper | *Tringa stagnatilis* | 21 | 45.0±5.0 | 128.6±13.0 |
| Mouse-coloured sunbird | *Nectarinia veroxii* | 2 | 4.0±0.0 | 5.5±0.5 |
| Northern brown-throated weaver | *Ploceus castanops* | 1 | 12.0±0.0 | 20.0±0.0 |
| Northern brownbul | *Phyllastrephus strepitans* | 3 | 16.0±2.3 | 28.7±5.2 |
| Northern white-crowned shrike | *Eurocephalus rueppelli* | 7 | 19.4±3.3 | 51.6±9.7 |
| Olive sunbird | *Nectarinia olivacea* | 1 | 33.0±0.0 | 62.0±0.0 |
| Olive thrush | *Turdus olivaceus* | 2 | 4.0±0.0 | 19.0±4.0 |
| Open-billed stork | *Anastomus lamelligerus* | 4 | 39.8±8.5 | 81.8±11.4 |
| Orange-winged ptylia | *Pytilia afra* | 1 | 11.0±0.0 | 32.0±0.0 |
| Pale flycatcher | *Bradornis pallidus* | 15 | 7.2±1.2 | 22.3±3.0 |
| Palm-nut vulture | *Gypohierax angolensis* | 1 | 29.0±0.0 | 97.0±0.0 |
| Papyrus canary | *Serinus koliensis* | 2 | 10.0±1.0 | 17.5±1.5 |
| Parrot-billed sparrow | *Passer gongonensis* | 3 | 10.0±2.5 | 29.7±6.6 |
| Peter's twinspot | *Hypargos niveoguttatus* | 1 | 4.0±0.0 | 6.0±0.0 |
| Pied crow | *Corvus albus* | 4 | 7.0±3.8 | 81.0±33.5 |
| Pied kingfisher | *Ceryle rudis* | 8 | 7.6±1.5 | 16.6±2.8 |
| Pin-tailed whydah | *Vidua macroura* | 15 | 12.9±1.3 | 35.8±5.5 |
| Pink-backed pelican | *Pelecanus rufescens* | 2 | 39.0±16.0 | 81.5±27.5 |
| Rattling cisticola | *Cisticola chiniana* | 1 | 10.0±0.0 | 27.0±0.0 |
| Red-fronted tinkerbird | *Pogoniulus pusillus* | 1 | 3.0±0.0 | 13.0±0.0 |
| Red-and-yellow barbet | *Trachyphonus erythrocephalus* | 1 | 13.0±0.0 | 28.0±0.0 |
| Red-billed firefinch | *Lagonosticta senegala* | 17 | 6.0±0.6 | 15.7±1.6 |
| Red-billed quelea | *Quelea quelea* | 4 | 17.0±3.4 | 47.8±10.3 |
| Red-cheeked cordon-bleu | *Uraeginthus bengalus* | 17 | 7.6±1.2 | 21.1±4.4 |
| Red-chested sunbird | *Nectarinia erythrocerca* | 9 | 7.7±1.0 | 22.7±4.6 |
| Red-eyed dove | *Streptopelia semitorquata* | 10 | 9.2±1.7 | 27.9±3.8 |
| Red-faced cisticola | *Cisticola erythrops* | 1 | 5.0±0.0 | 19.0±0.0 |
| Red-headed quelea | *Quelea erythrops* | 1 | 19.0±0.0 | 33.0±0.0 |
| Red-rumped swallow | *Hirundo daurica* | 2 | 10.0±2.0 | 18.0±3.0 |
| Red-winged starling | *Onychognathus morio* | 3 | 1.0±0.0 | 10.3±1.2 |

**Table A2** (*continued*)

| Common name | Scientific name | *N* | FID (m) | SD (m) |
|---|---|---|---|---|
| Ring-necked dove | *Streptopelia capicola* | 8 | 10.8±2.6 | 28.1±3.8 |
| Ringed plover | *Charadrius hiaticula* | 12 | 7.8±0.8 | 33.8±3.9 |
| Roseate tern | *Sterna dougallii* | 1 | 44.0±0.0 | 99.0±0.0 |
| Rosy-breasted longclaw | *Macronyx ameliae* | 1 | 4.0±0.0 | 9.0±0.0 |
| Ruddy turnstone | *Arenaria interpres* | 52 | 16.8±1.3 | 35.7±2.4 |
| Rufous chatterer | *Turdoides rubiginosa* | 4 | 10.0±2.9 | 18.3±3.6 |
| Rufus-naped lark | *Mirafra africana* | 1 | 9.0±0.0 | 36.0±0.0 |
| Sacred ibis | *Threskiornis aethiopicus* | 4 | 19.8±5.9 | 93.5±31.9 |
| Sanderling | *Calidris alba* | 8 | 27.1±3.7 | 50.3±4.5 |
| Saunder's tern | *Sterna saundersi* | 4 | 24.5±7.1 | 62.8±17.3 |
| Scaly babbler | *Turdoides squamulata* | 9 | 9.9±1.7 | 27.6±5.8 |
| Silverbird | *Empidornis semipartitus* | 13 | 7.5±1.8 | 27.7±3.6 |
| Slate-coloured boubou | *Laniarius funebris* | 3 | 11.7±3.2 | 29.3±3.4 |
| Slender-billed weaver | *Ploceus pelzelni* | 9 | 6.0±1.0 | 18.8±1.6 |
| Sooty gull | *Larus hemprichii* | 4 | 30.0±2.3 | 72.3±9.2 |
| Southern red bishop | *Euplectes orix* | 1 | 2.0±0.0 | 26.0±0.0 |
| Speckled mousebird | *Colius striatus* | 24 | 6.4±0.8 | 22.4±2.1 |
| Spectacled weaver | *Ploceus ocularis* | 4 | 4.8±0.8 | 21.3±3.4 |
| Spotted mourning thrush | *Cichladusa guttata* | 1 | 16.0±0.0 | 41.0±0.0 |
| Spur-winged plover | *Vanellus spinosus* | 7 | 16.4±2.1 | 44.9±4.7 |
| Striped kingfisher | *Halcyon chelicuti* | 2 | 14.5±1.5 | 25.0±3.0 |
| Superb starling | *Lamprotornis superbus* | 13 | 13.3±2.6 | 37.9±5.3 |
| Swamp flycatcher | *Muscicapa aquatica* | 4 | 6±1.8 | 16.0±1.5 |
| Tambourine dove | *Turtur tympanistria* | 3 | 8.7±3.2 | 18.0±4.0 |
| Tawny-flanked prinia | *Prinia subflava* | 15 | 12.1±1.3 | 24.5±1.9 |
| Terek sandpiper | *Xenus cinereus* | 3 | 27.3±7.7 | 66.0±4.2 |
| Three-banded plover | *Charadrius tricollaris* | 4 | 12.5±2.6 | 30.5±11.7 |
| Trilling cisticola | *Cisticola woosnami* | 2 | 9.5±5.5 | 18.0±8.0 |
| Tropical boubou | *Laniarius aethiopicus* | 4 | 7.5±2.6 | 19.3±1.9 |
| Trumpeter hornbill | *Bycanistes bucinator* | 4 | 11.8±5.3 | 87.6±23.6 |
| Village indigobird | *Vidua chalybeata* | 2 | 7.5±0.5 | 37.0±14.0 |
| Village weaver | *Ploceus cucullatus* | 24 | 8.5±0.8 | 22.5±2.6 |
| Violet-backed starling | *Cinnyricinclus leucogaster* | 5 | 15.4±3.8 | 32.8±6.6 |
| Von der Decken's hornbill | *Tockus deckeni* | 1 | 20.0±0.0 | 82.0±0.0 |
| Wahlberg's eagle | *Aquila wahlbergi* | 1 | 7.0±0.0 | 79.0±0.0 |
| Water thick-knee | *Burhinus vermiculatus* | 1 | 14.0±0.0 | 46.0±0.0 |
| Wattled starling | *Creatophora cinerea* | 1 | 26.0±0.0 | 49.0±0.0 |
| Whimbrel | *Numenius phaeopus* | 21 | 57.2±6.9 | 131.8±19.1 |
| White-bellied go-away-bird | *Corythaixoides leucogaster* | 2 | 6.5±0.5 | 45.0±24.0 |
| White-browed coucal | *Centropus superciliosus* | 17 | 14.1±2.3 | 33.2±4.3 |
| White-browed robin chat | *Cossypha heuglini* | 1 | 18.0±0.0 | 51.0±0.0 |
| White-browed scrub robin | *Erythropygia leucophrys* | 2 | 5.0±1.0 | 14.5±2.5 |
| White-browed sparrow-weaver | *Plocepasser mahali* | 1 | 4.0±0.0 | 16.0±0.0 |
| White-faced whistling duck | *Dendrocygna viduata* | 5 | 27.4±1.9 | 64.0±8.9 |
| White-fronted plover | *Charadrius marginatus* | 1 | 11.0±0.0 | 46.0±0.0 |
| White-winged black tern | *Chlidonias leucopterus* | 2 | 33.0±5.0 | 84.0±6.0 |
| Wire-tailed swallow | *Hirundo smithii* | 5 | 12.8±2.6 | 23.8±4.5 |
| Woodland kingfisher | *Halcyon senegalensis* | 4 | 9.8±2.0 | 33.5±4.3 |
| Woolly-necked stork | *Ciconia episcopus* | 2 | 13.0±1.0 | 100.5±39.5 |
| Yellow billed stork | *Mycteria ibis* | 6 | 17.0±3.6 | 85.5±14.1 |
| Yellow-throated long claw | *Macronyx croceus* | 1 | 10.0±0.0 | 34.0±0.0 |
| Yellow wagtail | *Motacilla flava* | 1 | 23.0±0.0 | 48.0±0.0 |
| Yellow-backed weaver | *Ploceus melanocephalus* | 3 | 9.0±2.6 | 27.3±3.3 |
| Yellow-bellied greenbul | *Chlorocichla flaviventris* | 5 | 12.8±2.5 | 44.4±12.0 |
| Yellow-bellied waxbill | *Estrilda quartinia* | 1 | 8.0±0.0 | 21.0±0.0 |
| Yellow-crowned canary | *Serinus flavivertex* | 3 | 7.3±1.9 | 31.0±9.2 |
| Yellow-fronted canary | *Serinus mozambicus* | 9 | 12.1±3.3 | 21.3±3.8 |
| Yellow-rumped seedeater | *Serinus xanthopygius* | 4 | 10±2.2 | 24.8±2.9 |
| Yellowbill | *Ceuthmochares aereus* | 1 | 11.0±0.0 | 36.0±0.0 |
| Zanzibar red bishop | *Euplectes nigroventris* | 11 | 13.5±2.7 | 32.1±4.3 |
| Zanzibar sombre greenbul | *Andropadus importunus* | 8 | 15.3±3.1 | 27.3±3.3 |

Australian data are presented in Guay et al. (2016).

**Table A3**
AIC values of global models predicting flight initiation distance, comparing models that do and do not control for phylogeny and sample size weighting

| Model | AIC | ΔAIC | Akaike weight |
|---|---|---|---|
| OLS (no phylogeny or weights) | −443.74 | 0 | 0.5 |
| PGLS (no weights)[1] | −443.74 | 0 | 0.5 |
| PGLS with weights | −360.68 | 83.06 | 0 |
| OLS with weights | −350.62 | 93.11 | 0 |

[1] The PGLS and OLS models are effectively identical because the maximum likelihood estimate of Pagel's λ is 0, indicating no phylogenetic effect in the data.