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Managing human disturbance: factors influencing flight-initiation distance of birds in a West African nature reserve

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Escape behaviour in response to perceived predators can be employed as a guide when designating protected areas around sensitive bird species to minimize the impact of human disturbance. A key measure of escape response is flight–initiation distance (FID), the distance at which a prey animal initiates its escape when approached by a potential predator. We tested the predictions of optimal escape theory by determining the factors that influence FID of bird species in a Nigerian reserved area and its surrounding habitats and so the potential utility of FID in managing human disturbance on birds, for the first time within a West African context. We tested how FID varied with group size, proximity to vegetation acting as protective cover, levels of human use, and survival rate, and whether these relationships varied by species. We collected 504 FIDs for seven bird species in Amurum Forest Reserve and its surrounding habitats (Jos, Nigeria). FID was lower in larger groups and when species were closer to protective cover. FID was lower outside of the protected area because animals in sites with higher levels of human presence and use may become habituated. FID was higher for species with higher survival, being consistent with predictions from life history theory. Overall, birds perceived humans as a potential threat and responded in accordance to the predictions of optimal escape theory, with FID increasing with increased cost of staying. Reserve managers in Africa could use species and context specific FIDs to designate buffer distances for the protection of wildlife from human disturbance.

Introduction

Optimal escape theory predicts that prey animals should optimize their escape from an approaching predator by initiating escape as soon as the costs of staying (e.g. being killed or injured) is higher than the costs of escape (e.g. reduced foraging time, energetic costs, lost mating opportunities) (Ydenberg & Dill 1986). A prey animal reduces these costs by first assessing risk and responding to different levels of risk by varying the distance at which it commences escape when approached by the potential predator (Stankowich & Blumstein 2005; Eason et al. 2006); this distance is called flight–initiation distance (FID) (Ydenberg & Dill 1986). Generally, animals increase FID with increased level of risk and reduce FID with reduced level of risk (Ydenberg & Dill 1986). Consequently, factors that influence a prey animal's perception and assessment of risk should typically influence FID, and so it can be used by wildlife managers to quantify how tolerant animals are to human activities (Burger 1981; Frid & Dill 2002; Rodgers & Schwikert 2002; Pease et al. 2005).

FID has been widely studied across different animal taxa (Cooper & Blumstein 2015), e.g. insects (Dill & Ydenberg 1987; Nelson & Formanowicz 2005), fish (Januchowski-Hartley et al. 2011), amphibians (Tidwell & Hayes 2013), reptiles (Cooper 2003, 2008), birds (Blumstein 2003; Thiel et al. 2007; Burger et al. 2010), and mammals (Nyahongo 2007; Reimers et al. 2009; Tarakini et al. 2014). It has been applied in several conservation contexts such as to measure the degree of an animal's fearfulness of humans (Stankowich & Blumstein 2005), delineate buffer zones around sensitive species, habitats and human activities (Rodgers & Smith 1997; Rodgers & Schwikert 2002; Weston et al. 2012; Guay et al. 2016). It has also been used to indicate hunting pressure on animals (Tarakini et al. 2014; Sreekar et al. 2015) and to protect water birds from being disturbed by boats (Burger et al. 2010; Glover et al. 2011). FID has also been extensively studied across different continents of the world (Møller et al. 2014, 2016; Livezey et al. 2016). For instance, FID has been collected for as many as 352 bird species and applied to manage human–induced disturbances (Glover et al. 2011; Weston et al. 2012; Guay et al. 2016). Similarly, several studies focusing on FID has been conducted on European birds across different urbanization and latitudinal gradients in Europe (Díaz et al. 2013; Samia et al. 2017).

However, there are only a few published studies of FID within an African context (Dill 1990a; Nyahongo 2007; Magige et al. 2009; Tarakini et al. 2014) and none that we are aware of in a West

African context. This is particularly relevant because of the very rapidly increasing human populations in the region and the close contact of people with animals, even within reserved areas. We thus investigated the factors that might influence FID in several common bird species in the Amurum Forest reserve in Nigeria, West Africa. Optimal escape theory makes a number of predictions relevant to FID:

1. Group size: FID is expected to decrease because individual risk is diluted in larger groups (Foster & Treherne 1981) or because predators are less likely to make a successful hunt on multiple targets – the confusion effect (Neill & Cullen 1974; Milinski 1977). However, FID might also increase as group size increases because probability of predator detection increases with group size (Pulliam 1973; Siegfried & Underhill 1975; Lazarus 1979; Roberts 1996).
2. Distance to vegetation cover: If prey animals perceive vegetation cover as a place to seek refuge (Dill & Houtman 1989; Dill 1990b), the risk of predation is expected to increase with the distance between the approached bird and vegetation used as a refuge (Cooper 2007; Lagos et al. 2009; Clucas & Marzluff 2012). We predicted that FID should increase with increasing distance from vegetation cover.
3. Degree of human presence and activities (reserve versus outer farmed areas): Animals in sites with high levels of human presence and activities are often reported to become habituated and have lower FIDs (Stankowich & Blumstein 2005; Webb & Blumstein 2005; Møller 2010; Grolle et al. 2014; Tarakini et al. 2014), Likewise, urban birds are known to be more habituated to human activities than are rural ones (Samia et al. 2017). However, it has been reported that in areas where human presence is linked with activities such as hunting, birds respond with longer FIDs (Sreekar et al. 2015). We predicted that FID of birds would be higher in the reserve compared with the surrounding farmed areas, characterised by higher human presence and activities. Although, the reserve experiences a level of human exposure because it is used for research and educational activities, disturbance is much lower than surrounding lands. The reserve is effective as a nature haven for wildlife in the area because it is protected against anthropogenic disturbances such as farming, grazing, hunting, logging and indiscriminate burning and contains several species of birds, plants and mammals, e.g. Tantalus Monkey *Cercopithecus (aethiops) tantalus* and Rock Hyrax *Procavia capensis*

(Abalaka 2009; Daru et al. 2015; Ali et al. 2016), that do not occur outside the reserve because of harvesting. In contrast, the area surrounding the reserve is a settlement area, and exposed to uncontrolled human access, activities such as farming, and feral animals.

4. Life history: A key component to risk evaluation by birds is life history strategy, where longer lived species are expected to take fewer risks than shorter lived species (Bennett & Owens 2002). We therefore, expect differences in basal levels of risk taking between species as a result of differences in life histories between them. For instance, tropical birds differ from temperate ones in several life history traits. Tropical birds live longer (Peach et al. 2001; Lloyd et al. 2014), have smaller clutch sizes (Ghalambor & Martin 2001; Martin 2004) and attempt first breeding at a relatively older age (Martin 2004). Møller & Liang (2013) showed that tropical birds take smaller risks than closely related temperate taxa in order not to jeopardize their prospects of long-term survival. We thus predicted that species with higher survival rates would have larger FIDs i.e. take less risk as an optimal strategy to maximize lifetime reproductive success than would species with lower estimates of survival (Martin 1995, 2002; Ghalambor & Martin 2001).

We also tested whether any of the relationships between FID and group size, distance to vegetation cover or levels of human use depend on species by including species in the model as well as the interaction terms (group size*species, distance to cover*species, site*species) in the analysis. We predict that these relationships are likely to be species-specific, hence our inclusion of the interaction terms in the model.

Finally, we considered “alert distance” and “starting distance” and their interaction as confounding variables. Detection distance, distance at which prey animals detects an approaching predator, is important to the process of making decisions to initiate escape (Lima & Dill 1990; Blumstein 2003). Alert distance, the distance at which an approached animal exhibits alert behaviour in response to the approaching perceived predator is used as a surrogate measure of detection distance (Stankowich & Coss 2005; Samia et al. 2017). This is because it is difficult to know for sure at what point prey animals detect approaching predators (Ydenberg & Dill 1986). The premise on which alert distance can serve as surrogate for detection distance is the fact that, animals are unlikely to respond to stimuli they have not yet become aware of (detected). The fact that an animal shows alert behaviour towards an approaching predator serves as evidence that it has detected the predator, so long as precautions have been taken to ensure that no other external influence such as other predators or loud sounds exist during an approach. The limitation of using alert behaviour as a proxy is that it is restricted to animal species that show alert behaviours to approaching predators (Ydenberg & Dill 1986; Cooper 2008). Since all of the focal species in this study exhibited alert behaviours, we have measured and used alert distance as a surrogate for detection distance. FID increases with alert distance because animals that notice the approaching perceived predator at large distances incur costs associated with prolonged monitoring and are less likely to show a default, surprise, instantaneous escape response (Stankowich & Coss 2005; Cooper et al. 2015; Samia et al. 2017). Starting distance is the distance at which a perceived predator begins its approach towards the prey, and this significantly influences FID in many species with few exceptions (Blumstein 2003; Engelhardt & Weladji 2011; Clucas & Marzluff 2012; Tarakini et al. 2014).

Methods

Study area

This study was conducted in the Amurum Forest Reserve, Laminga (09°53’N, 08°59’E), Laminga, Jos East, Nigeria, West Africa. The reserve holds one of the few remnants of natural vegetation typical of the Jos plateau. The reserve was established in 2001 as an Important Bird and Biodiversity Area partly because it contains the endemic Jos Plateau Indigo Bird *Vidua maryae* and its brood-host the Rock Fire Finch *Lagonosticta sanguinodorsalis* (Ezealor 2002). It consists of three distinct habitat types: dry savannah, rocky outcrops and gallery forests. Observations were made in the rocky outcrop and savannah habitats within the reserve as well as rocky outcrop and savannah habitats in outer farmed areas surrounding the reserve.

Bird species

Study species were selected because they occurred in large numbers within and outside the reserve of the study area. All mass measurements of focal birds were extracted from the ringing database of the A.P. Leventis Ornithological Research Institute (APLORI) and Borrow and Demey (2008). Species chosen were:

1. Rock Firefinch *Lagonosticta sanguinodorsalis*. This species is endemic to the Jos Plateau area of Nigeria. It is a bird of conservation concern belonging to the Estrildidae family (Barshep et al. 2005; Brandt & Cresswell 2008; Abalaka & Hansson 2014). It favours wooded grassland and rocky outcrops having body length of 10cm on average and a body mass of 10.6g. It feeds on small grass seeds and occurs singly, in pairs or in small family groups (Fry & Keith 2004; Borrow & Demey 2008).
2. Red-cheeked Cordon-blue *Uraeginthus bengalus*. This bird species is also a member of the Estrildidae family that is widespread and abundant within the northern Guinea and Sudan zones (Fry & Keith 2004). It favours degraded savannah, gardens as well as farms, and has a body length of 13 cm and mass of 10.1 g (Borrow & Demey 2008). Individuals of this species forage singly, in pairs or in small groups. It feeds on small seeds of annual grasses and termites (Fry & Keith 2004).
3. Familiar Chat *Cercomela familiaris.* This species belongs to the Muscicapidae family, it favours rocky areas in savannah, notably over much of Jos Plateau (Elgood et al. 1994). It has an average body length of 14 cm and mass of 17.3 g (Keith et al. 1992; Borrow & Demey 2008). Individuals are often seen singly, in pairs or larger groups and forage on insects and other invertebrates on the ground.
4. Common Bulbul *Pycnonotus barbatus.* This species belongs to the Pycnonotidae family, and it is Africa's ubiquitous, quite conspicuous and familiar bird found in almost all habitat types except closed forest and treeless desert (Borrow & Demey 2008). It has a mean body length of 18–20cm and mass of 38.2 g (Keith et al. 1992). Individuals are usually found in pairs or small groups (Keith et al. 1992). Food includes wild and cultivated fruits, nectar, seeds and insects.
5. Laughing Dove *Streptopelia senegalensis.* This species belongs to the Columbidae family. It is abundant and ubiquitous throughout most of sub-Saharan Africa (Urban et al. 1986). It inhabits open woodland and all kinds of human settlements, has an average body length of 24 cm and mass of 93 g (Urban et al. 1986; Borrow & Demey 2008). Individuals often form flocks of 3–4 or more, and feed primarily on seeds and insects (Urban et al. 1986).

The five species above, used in the main analysis, belong to two distinct avian orders: Passeriformes (Rock Firefinch, Red–cheeked Cordon bleu, Familiar Chat, Common Bulbul) and Columbiformes

(Laughing Dove). There was no survival estimate found for Laughing Dove in Stevens et al. (2013) or elsewhere in the literature. Hence, to increase the number of species for the survival analysis, FID data were taken from two additional common bird species for which survival estimates were available: sample sizes, however, were not sufficient to include these species in the main analysis. The two additional species below belongs to the avian order Coliiformes (Speckled Mousebird *Colius striatus*) and Passeriformes (African Thrush *Turdus pelios*).

6. Speckled Mousebird *Colius striatus*: This species belongs to the Coliidae family, it is highly gregarious, occurring usually in small, noisy parties. It is found in various open and wooded habitats, feeds mainly on leaves and fruits. It has a body length of 30–36 cm and an average body mass of 52.8 g (Borrow & Demey 2008).

7. African Thrush *Turdus pelios:* This species belongs to the Turdidae family. It is a ground feeding species, occurring solitarily or in small groups, that mostly feeds on plant matter, earthworms and terrestrial arthropods. It has a body length of about 23 cm and mass of 65.2 g on average (Akinpelu & Oyedipe 2004; Borrow & Demey 2008).

Field methods

Field observations were made using binoculars (8 x 42 mm) to identify focal species between 06:30 – 09:30 hrs and 16:00 – 18:00 hrs from 5th May to 27th June 2014. The observer (BB) walked slowly through existing paths within the study area searching for focal species, as has been done in other FID studies (Blumstein 2003; Cooper 2003; Fernández-Juricic et al. 2006). To eliminate possible effects of observer size, and observer bias as well as to avoid variation that might occur through different colours of clothes (Eason et al. 2006), only one observer conducted all trials, wearing the same colour of clothes throughout the survey period. Observations were only made when there was no other person or other confounding factors such as a flying aerial predator or other flying birds between the observer and the focal bird (Pease et al. 2005; Eason et al. 2006; Weston et al. 2012) . Approaches were made only on individuals at positions where no obstructing vegetation prevented the observer and focal bird from seeing each other (Fernández-Juricic et al. 2006; Fernández-Juricic & Rodriguez-prieto 2008). Individuals perched above six meters were excluded, because during a preliminary survey it was discovered that individuals perched at such heights do not usually respond to the observer’s approach. Birds that were alert already were excluded regardless of starting distance.

Most approached birds were not individually marked; however, re-sampling individuals was avoided by focusing on birds in different locations and not re-sampling the same location more than once per species on each visit. Some individuals of focal species had colour rings on them as part of previous and ongoing studies, and so the colour combinations of the colour ringed individual were noted during this study. We did not encounter any ringed individual twice during this study further suggesting that it is unlikely that we repeatedly sampled the same individuals. Furthermore, data collection was alternated daily between the reserve and outer farmed areas outside the reserve (Webb & Blumstein 2005).

On locating an individual of a focal bird species, FID measurements, the predictors (group size, distance to vegetation cover and position in or outside of the reserve), and several potential confounding variables (habitat, species, activity, orientation, social status, position, time of day, and perch height) were recorded. Group size was determined by counting the number of individuals within 10m radius of the focal individual (Clucas & Marzluff 2012), before beginning the approach and at the end of each approach. Distance to the nearest vegetation cover (cover was defined as any cluster of trees, shrubs or bushes into which the focal bird can escape) was measured as the distance between the position of the bird and the nearest vegetation cover to it (Cooper 2003); initially by eye to the nearest meter and then checked where necessary by pacing after the response was concluded. Habitat was recorded as either rocky outcrop or savannah, species, as was activity (preening, resting, foraging or calling) and orientation (facing, backing, having side view to the left, side view to the right) of the focal bird in respect to the observer as well as flock type (social status; either conspecifics or hetero–specifics), position of the birds (on ground, rock, grass, shrub or tree), time of day (morning or evening) and perch height to the nearest 0.2 m (measured using a calibrated range pole). The point at which approach was initiated was marked before observer commenced the approach at a slow, steady speed of ~0.5 ms^{-1} (Blumstein 2003; Fernández-Juricic et al. 2006) while maintaining a direct gaze at the focal bird (Blumstein 2003; Eason et al. 2006; Clucas & Marzluff 2012). The points at which focal bird detected the observer and began to exhibit alert behaviour such as increased head-ups, alarm calls, body movements or tail flicks were marked by the observer by dropping a marker on the ground (Eason et al. 2006). The approach continued until the focal bird escaped. The observer stopped when the bird escaped and measured the FID as the distance between the position of the observer and the position of the bird (Blumstein 2003; Eason et al. 2006; Fernández-Juricic et al. 2006; Bregnballe et al. 2009). Starting distance was measured as the distance between the first marked point, where the observer initiated the approach and the position of the focal individual (Blumstein 2003). Alert distance was measured as the distance between the position of bird and the second marked point, at which bird detected the observer and began to exhibit alert behaviour (Fernández-Juricic et al. 2001; Eason et al. 2006).

All distance measurements were taken in meters using a laser range finder (Nikon Laser-800; Nikon, Tokyo, Japan with measuring range of 10 – 730 meters) by pointing the laser beam at the position (point) from which focal bird escaped (Fernández-Juricic et al. 2001; Clucas & Marzluff 2012). Since the laser range finder used could not take distance measurements of less than 10m, all such distances were measured directly with a meter length stick.

Data analysis

All data collected were analysed using general linear mixed models with a normal error distribution in R statistical package version 3.0.2 (2013-09-25) using the lme4 and lmertest libraries (R Development Core Team 2013). An individual based approach was used, using multiple measurements from a species and then controlling for the repeated measures using a mixed model. Starting distance, distance to cover, group size, perch height and alert distance were entered as covariates; while species (five levels), habitat type (two levels), site (two levels), time of day (two levels), flock type (two levels), position (six levels), activity (four levels) and orientation (four levels) were entered as categorical variables alongside all the two-way interactions among the above mentioned explanatory variables. Random effects of species nested in family nested in order were included to control for phylogenetic effects. Following examples of Thiel et al. 2007; Reimers et al. 2009; Clucas & Marzluff 2012; Tarakini et al. 2014, variables were selected using backward elimination as recommended in Crawley (2005) by starting with full models containing all biologically plausible main effects and interaction terms. Variables with the highest p-values were removed starting with the non–significant interactions and procedure repeated until the final model was attained. The final model was selected using Akaike's Information Criterion (AIC), as the model with the lowest AIC value, and with all terms retained being statistically significant. Final models were checked by reinsertion of all variables removed, singly back into the model. All the variables reintroduced back into the final model remained non–significant and the variables that were significant in the final model remained significant. We present both starting models and final models to demonstrate that model simplification did not change the overall biological significance of the results. FID measurements were square–root transformed prior to the analysis to improve the normal distribution of the residuals of the model: final models were visually checked for not significantly violating assumptions according to criteria in Crawley (2005). All FID data were back transformed when illustrating predicted results from the final model. Interactions between species and the predictors were also added to the model.

A further species based General Linear model assuming a normal distribution was tested to investigate the relationship between survival and FID. This model only contained six data points (one for each species) and so was deliberately kept simply as FID ~ survival. This was an priori hypothesis of interest and limited power prevented the addition of other variables to the model. Note also, limited power prevented phylogenetic control within the analysis and so any trends revealed may largely reflect traits within Passerines, because 5/6 species belonged to this order. Mean values of variables are presented as mean ± SE.

Results

At the end of the survey, a total of 465 approaches to focal birds were recorded for use in the analyses. Of these, 133 approaches were conducted on Common Bulbul, 122 were on Red-cheeked Cordon-bleu, 92 on Familiar Chat, 77 on Laughing Dove, 41 on Rock Firefinch, 20 on African Thrush and 19 for Speckled Mousebird. Responses to 193 approaches were recorded inside the reserve and 272 recorded outside the reserve. Approaches were initiated at distances ranging from 15 to 94 m (32.0 ± 0.5). Focal individuals exhibited alert behaviour at distances ranging from 5 to 54 m (18.3 ± 0.3) while FID ranged from 2 to 41 m (14.2 ± 0.3). Individuals of focal species approached occurred in groups ranging from a single individual to 22 individuals (2.5 ± 0.1) and on average focal species were 4.8 ± 0.3 m away from cover. Species specific summaries are included in Appendix Table 1.

The model with the lowest AIC value, hence best model, retained time of day, site, habitat type, species, position, group size, starting distance, alert distance, distance to cover and the interaction term starting distance * alert distance (Table 1). FID significantly decreased with increasing group size in all species (Table 1, Figure 1). Meanwhile, FID increased significantly with increasing distance to cover (Table 1, Figure 2). FID was significantly higher in the reserve than outside (Table 1). FID varied little depending on taxonomy (i.e. between species and families); marginal R^2 for the final model in Table 1 was 0.64, overall R^2 accounting for phylogeny was 0.65 (Table 1; Appendix Table 2), i.e. only 0.01 of the total variance was accounted for by taxonomic differences. The relationship between FID and group size, FID and distance to cover as well as FID by sites did not differ by species because the interaction terms species*group size, species*distance to cover and species*site were not significant in any cases (Table 1). Activity, orientation, flock type and perch height were not significantly related to FID in this study.

The model testing the relationship between survival estimates and FID indicated that FID in focal species significantly increased with survival ($F_{1,\ 4} = 13.4$, $p < 0.02$, $B = 23.47$, Adj. $R^2 = 0.71$; or Spearman's rank correlation coefficient rho = 0.89, $p = 0.033$; Figure 3); see Appendix Table 2 for species specific survival and FID values used.

Discussion

The result from the study generally confirmed all our predictions although there was little variation found across the species we sampled. FID decreased with increasing group size, confirming that FID is likely to decrease because individual risk is diluted in larger groups and the fact that predators are less likely to make a successful hunt on multiple targets due to confusion effect (Neill & Cullen 1974; Milinski 1977). Our finding therefore, agrees with Foster and Treherne (1981) and Pulliam (1973) that individuals in a group may benefit through risk dilution, and so perceive a lower risk when in larger groups. However, positive relationships have been reported between FID and group size in Dark-bellied Brent Geese *Branta bernicla bernicla* (Owens 1977), shorebirds (Glover et al. 2011) and fish (Januchowski-Hartley et al. 2011). .

We found a positive linear relationship between FID and distance to cover indicating that focal birds perceived higher levels of threat with increasing distance from refuge (Dear et al. 2015; Monclús et al. 2015). Refuge could vary depending on species involved; for example, some birds use water as refuge and thus have longer FIDs when further from water (Guay et al. 2013; Dear et al. 2015). For animals that utilize vegetation cover during escape from their predators, risk increases with distance to vegetation cover (Dill & Houtman 1989) and so animals far from vegetation cover usually have longer FIDs than those closer to it (Ydenberg & Dill 1986). This finding is consistent across many different taxa: e.g. reptiles (Cooper 2007), birds (Clucas & Marzluff 2012) and mammals (Dill & Houtman 1989; Lagos et al. 2009). However, vegetation might have inhibitory effects on visibility and thus may prevent accurate processing of visual information from the environment thereby decreasing the probability of early detection (Javůrková et al. 2012). Furthermore, predation risk can increase with proximity to cover for prey animals whose predators attack from cover rather than open (Cresswell 1994). The relationship between FID and distance to cover may thus be confounded by these factors.

We recorded a significantly higher FID in areas with lower human presence (reserve) compared with areas characterised by higher human presence (outside the reserve). This suggests at least to some degree a higher level of habituation in birds that occur outside the reserve of the study area. Habituation and experience with humans significantly influences the escape response of animals during animal – human interactions (Stankowich & Blumstein 2005). Generally, animals are able to habituate to the level of human presence in two ways, depending on the behaviour of humans toward them (Cooper & Blumstein 2013). In areas where human presence is frequent and non-threatening, animals lose their fear of humans and respond with shorter FIDs (Stankowich & Blumstein 2005; Webb & Blumstein 2005; Grolle et al. 2014; Tarakini et al. 2014; Samia et al. 2017). On the other hand, in areas where human presence is associated with threatening or discouraging behaviour such as hunting, animals respond with exaggerated FIDs (Januchowski-Hartley et al. 2011; Clucas & Marzluff 2012; Sreekar et al. 2015). In certain cases, habituation to humans can cause problems through also affecting habituation to natural predators and because of dietary shifts as animals feed in close proximity to humans (Hines 2011; Geffroy et al. 2015). Since the focal species observed in this study are not under any hunting pressure in the study sites, the significantly lowered mean FID in settlement area outside the reserve compared with that observed inside the reserve may perhaps be attributed to habituation of focal bird species to nonlethal, repeated exposure to humans.

We found a strong positive linear correlation between mean FID and survival estimates across the focal bird species we sampled. Although our sample size is small, it was nonetheless a strong relationship, confirming our prediction that species with higher survival rates (and/or life history traits which correlate with this) would have larger FIDs. Species that initiate flight early when approached by a predator are assumed to take less risk, while those that delay escape are held to take more risk (Møller & Liang 2013). Life history theory proposes that longer living species take fewer risks compared with shorter-lived ones in order to optimize their overall fitness (Martin 1995, 2002; Ghalambor & Martin 2001; Bennett & Owens 2002) This then implies that longer living species increase their probability of future breeding by taking less risk while shorter-lived ones take more risk to boost their current reproductive output. Our focal species differed in their mean FID, indicating that they associated different levels of risk to the observer. This could possibly be attributed to differences in ecology and life history traits between them. For example, variation in size among species have been shown to drive avian interspecific differences in FID and body size is one of the best predictors of survival rate (Blumstein et al. 2005; Fernández-Juricic et al. 2006; Bregnballe et al. 2009). Larger species are known to have higher visual acuity (Brooke et al. 1999; Kiltie 2000) and higher wing loading (Burns & Ydenberg 2002), both of which influence flight manoeuvrability and possibly escape strategy (Fernández-Juricic et al. 2001). These imply that, under comparable risk of predation, the benefits of early escape will be higher for larger species than for smaller ones. Furthermore, differences in other ecology and life history traits (Bregnballe et al. 2009) such as foraging habits (Blumstein et al. 2005), energy requirements (Blumstein et al. 2005), escape strategy (Cresswell 1993), levels of exposure and so habituation to humans (Burger 1981) are the probable explanations for the interspecific variation in FID among bird species.

Although there were species differences in the absolute levels of FID as stated above, we found no strong evidence for any of the relationships between FID and group size or distance to cover to depend on species, nor for the difference in FID between the reserve and outside of the reserve to depend on species. This suggests that, for at least the limited range of species we tested, that FID is broadly affected in the same way by group size, proximity to vegetation cover acting as a refuge and habituation to humans. Furthermore, this suggests the generality of the FID approach, despite ecological and life history differences, at least for the species we sampled.

Other results with respect to the confounding variables are also consistent with predictions of optimal escape theory. Starting distance was related to FID consistent with the findings of Blumstein (2003) and confirms that starting distances should be included in FID studies as a covariate. FID increased with alert distance consistent with the many other studies that have reported strong positive correlations between FID and alert distance (Stankowich & Coss 2005; Eason et al. 2006; Lagos et al. 2009) probably because prey animals that detect approaching predators at greater distances may initiate escape at longer distances to minimize the costs associated with monitoring. There was also evidence that the relationship between FID and starting distance depends on alert distance. This can be best explained by incorporating the perceptual limit hypothesis which states that escape from an approaching predator is constrained by the prey animal's ability to detect predators and assumes that prey animals flee as soon as predators are detected (Ydenberg & Dill 1986) and the economic escape theory which predicts that individuals do not usually flee as soon as potential predators are detected, but delay their decision until the costs of staying outweighs the benefit of staying (Ydenberg & Dill 1986). Both hypotheses may be true depending on the distance at which the approached individual initially detects the approaching predator.

In conclusion, this study provides the first empirical data for testing the predictions of optimal escape theory in West Africa. Overall, the focal birds perceived humans as a potential threat and responded in accordance to the predictions of optimal escape theory. We show that bird species differ in FID, probably because of life history traits and their ecology. Consequently, some species are expected to be less able to deal with human disturbance (that does not actually have immediate fitness costs) than others and so identification of these through FID on a case by case basis will allow reserve managers to manage human access and viewing of wildlife in nature reserves. For instance, the endemic Rock Firefinch that showed greater sensitivity will require more management attention than would the Red-cheeked Cordon-bleu. Safe buffer zones may be built using the highest mean FID so the need of the less demanding species, and likely species where FID is unknown, are also met. However, care must be taken to avoid excessively long buffers that threaten birdwatching, educational activities and research. Hence, alternatives like formed path buffers around human access routes can be used to manage disturbance. Furthermore, larger buffers may be built round certain sensitive habitats for the conservation of birds with special habitat needs.

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Table 1: The relationship between square–root transformed FID and explanatory variables in five bird species within Amurum Forest Reserve and outside. The full model (marginal R^2 = 0.52, overall R^2 = 0.74) and the model with the lowest AIC (final) (marginal R^2 = 0.64, overall R^2 = 0.65) are shown. Random effects of species nested in family nested in order were included to control for phylogenetic effects. Reserve and Common Bulbul take the value of the intercept. Significant p values and variables in bold.

	Full model					**Final model**				
	Est	**SE**	**df**	**t**	**p**	**Est**	**SE**	**df**	**T**	**P**
(Intercept)	1.370	0.495	427	2.8	<0.001	1.258	0.198	191	6.4	**<0.001**
Time of day morning	-0.059	0.046	427	-1.3	0.208	-	-	-	-	-
Outside reserve	-0.121	0.089	427	-1.4	0.177	-0.115	0.048	404	-2.4	**0.018**
Habitat type savannah	-0.074	0.051	427	-1.4	0.151	-	-	-	-	-
Position ground	-0.080	0.119	427	-0.7	0.504	-	-	-	-	-
Position rock	-0.027	0.110	427	-0.2	0.803	-	-	-	-	-
Position shrub	0.001	0.081	427	0.0	0.991	-	-	-	-	-
Position thicket	0.118	0.112	427	1.0	0.296	-	-	-	-	-
Position tree	-0.107	0.093	427	-1.1	0.254	-	-	-	-	-
Activity foraging	0.101	0.104	427	1.0	0.335	-	-	-	-	-
Activity preening	0.135	0.112	427	1.2	0.228	-	-	-	-	-
Activity resting	0.127	0.082	427	1.5	0.125	-	-	-	-	-
Orientation facing	-0.019	0.060	427	-0.3	0.754	-	-	-	-	-
Orientation side-view-left	-0.013	0.080	427	-0.2	0.869	-	-	-	-	-
Orientation side-view-right	0.053	0.068	427	0.8	0.439	-	-	-	-	-
Flock type	0.029	0.062	427	0.5	0.645	-	-	-	-	-
Group size	-0.016	0.016	427	-1.0	0.321	-0.031	0.012	457	-2.7	**0.008**
Starting distance	0.020	0.006	427	3.4	**0.001**	0.019	0.006	449	3.5	**<0.001**
Alert distance	0.147	0.010	427	13.4	**<0.001**	0.147	0.010	434	14.3	**<0.001**
Distance to cover	0.010	0.007	427	1.4	0.151	0.014	0.004	458	3.5	**<0.001**
Perch height	-0.012	0.020	427	-0.6	0.551	-	-	-	-	-
Familiar Chat	-0.140	0.606	0	-0.2	1.000	-	-	-	-	-
Laughing Dove	-0.176	0.618	0	-0.3	1.000	-	-	-	-	-
Red-cheeked Cordon-bleu	-0.075	0.608	0	-0.1	1.000	-	-	-	-	-
Rock Firefinch	-0.151	0.617	0	-0.2	1.000	-	-	-	-	-
Familiar chat: group size	-0.049	0.039	427	-1.3	0.211	-	-	-	-	-
Laughing Dove: group size	-0.043	0.032	427	-1.3	0.184	-	-	-	-	-
RC Cordon-bleu: group size	-0.055	0.031	427	-1.7	0.086	-	-	-	-	-
Rock Firefinch: group size	-0.052	0.061	427	-0.8	0.401	-	-	-	-	-
Familiar Chat: Dist to cover	0.015	0.015	427	1.0	0.334	-	-	-	-	-
Laughing Dove: Dist to cover	0.017	0.011	427	1.5	0.123	-	-	-	-	-
RC Cordon-bleu: Dist to cover	0.003	0.010	427	0.3	0.752	-	-	-	-	-
Rock Firefinch:Dist to cover	0.018	0.032	427	0.6	0.574	-	-	-	-	-
Outside: Familiar Chat	-0.053	0.154	427	-0.3	0.729	-	-	-	-	-
Outside: Laughing Dove	-0.040	0.154	427	-0.3	0.798	-	-	-	-	-
Outside: RC Cordon-bleu	0.067	0.148	427	0.5	0.649	-	-	-	-	-
Outside: Rock Firefinch	0.093	0.198	427	0.5	0.641	-	-	-	-	-
Starting distance: Alert distance	-0.001	0.0003	427	-5.1	**<0.001**	0.001	0.0002	455	-5.3	**<0.001**

Figure legends:

Figure 1: The predicted relationship between FID and group size plotted from the final model (shaded area indicates 1 standard error). Circles Common Bulbul, triangles Familiar Chat, + symbols Laughing Dove, x symbols Red-cheeked Cordon Bleu and diamonds Rock Firefinch.

Figure 2: The predicted relationship between FID and distance to cover plotted from the final model (shaded area indicates 1 standard error). Circles Common Bulbul, triangles Familiar Chat, + symbols Laughing Dove, x symbols Red-cheeked Cordon Bleu and diamonds Rock Firefinch.

Figure 3: The predicted relationship between mean FID of six bird species and mean adult survival estimated for each species.

Figure 1:

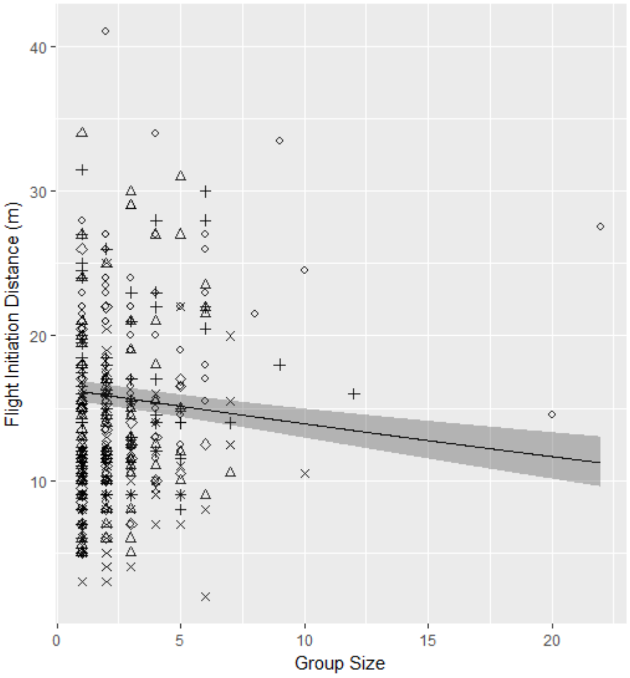

Flight Initiation Distance (m)
40
30
20
10
0
5
10
15
20
Group Size

Figure 2:

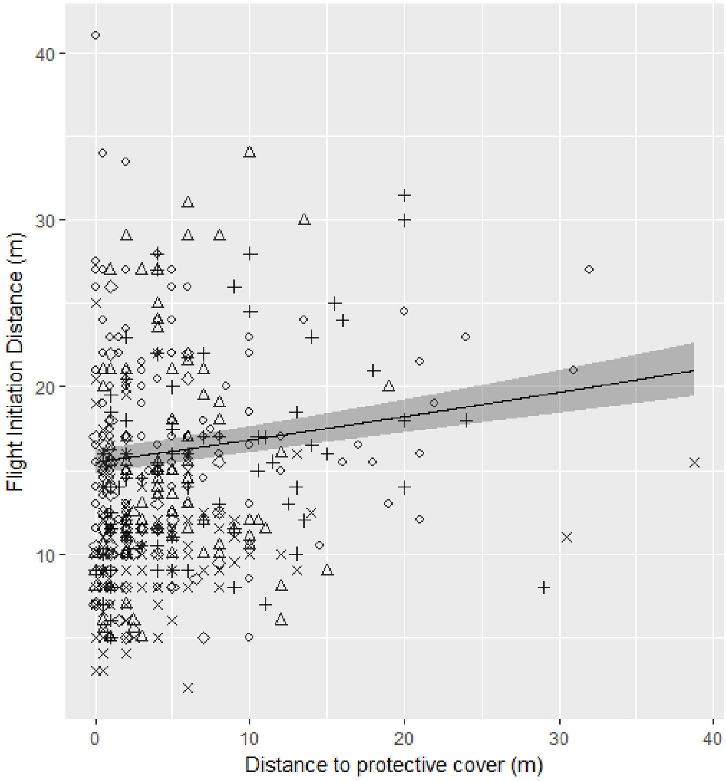
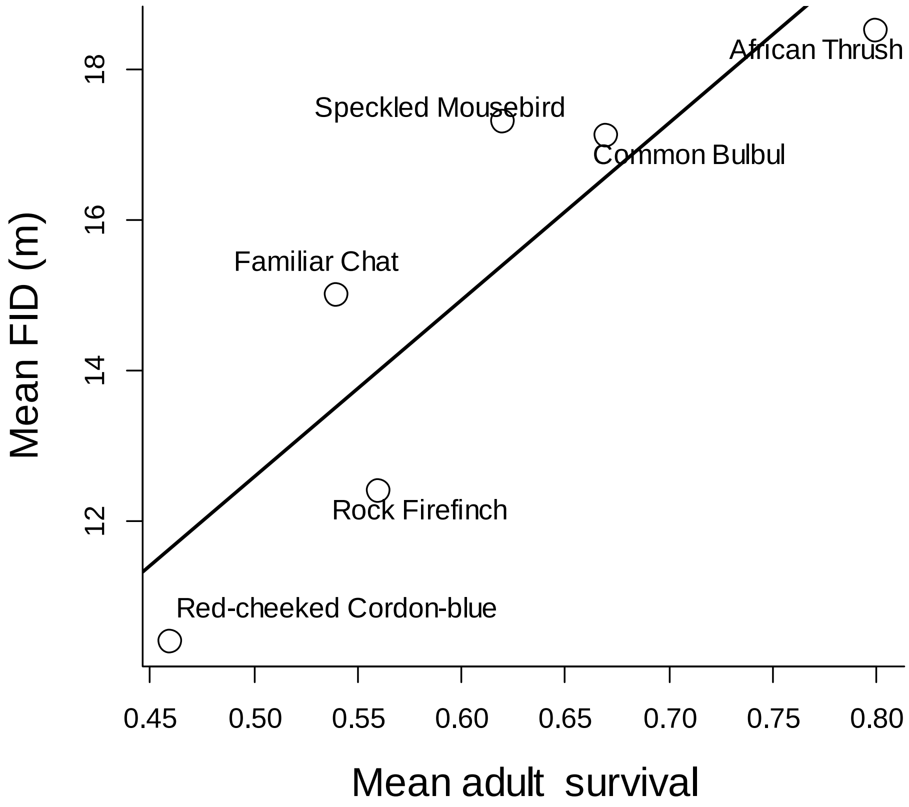

Flight Initiation Distance (m)
40
30
20
10
Distance to protective cover (m)
0
10
20
30
40

Figure 3:


Mean FID (m)
12
14
16
18
Mean adult survival
0.45
0.50
0.55
0.60
0.65
0.70
0.75
0.80
African Thrush
Speckled Mousebird
Common Bulbul
Familiar Chat
Rock Firefinch
Red-cheeked Cordon-blue

Appendix

Appendix Table 1: Species specific summaries of main variable for the five species used in the main FID analysis.

Continuous variables										
	Common Bulbul: N=133		**Familiar Chat: N=92**		**Laughing Dove=77**		**RC Cordon-bleu=122**		**Rock Firefinch=41**	
	Mean	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**
FID	17±0.5	5-41	15±0.7	5–34	15±0.7	531.5	10±0.4	2–25	12±0.7	5–26
Alert distance	21±0.5	6–45	20±0.7	7–36	21±0.8	7.5–54	14±0.4	5–25	16±0.9	6–29.5
Starting Distance	35±0.9	20–71	33±1.2	16–94	36±1.3	20.5–75	26±0.7	15–55	27±1.2	16–46
Group size	3±0.3	1–22	2±0.16	1–7	3±0.2	1–12	2±0.2	1–10	2±0.2	1–6
Distance to cover	5±0.6	0–32	5±0.4	0–19	7±0.7	0–29	4±0.5	0–38	3±0.4	0–8
Perch height	3± 0.2	0–6	5±0.2	0–6	2±0.2	0–6	1±0.1	0–6	1±2.1	0–5
Categorical variables										
Time section	**Morning**	**Evening**	**Morning**	**Evening**	**Morning**	**Evening**	**Morning**	**Evening**	**Morning**	**Evening**
	N=60	N=73	N=34	N=58	N=31	N=46	N=52	N=70	N=15	N=26
Habitat	**Rock**	**Savannah**	**Rock**	**Savannah**	**Rock**	**Savannah**	**Rock**	**Savannah**	**Rock**	**Savannah**
	N=49	N=84	N=76	N=16	N=46	N=31	N=47	N=75	N=35	N=6
Site	**Reserve**	**Outside**	**Reserve**	**Outside**	**Reserve**	**Outside**	**Reserve**	**Outside**	**Reserve**	**Outside**
	N=48	N=85	N=73	N=19	N=21	N=56	N=21	N=101	N=30	N=11

Appendix Table 2: Mean survival and mean FID for each bird species used in the survival analysis

Species*	**Scientific name**	**Mean survival ± SE**	**Number of captures**	**Number of recaptures**	**95% CI of survival estimates**	**Mean FID ± SE(m)**
FCHAT	*Cercomela familiaris*	0.54±0.06	45	37	0.41–0.66	15.0 ± 0.8
RECCB	*Uraeginthus bengalus*	0.46±0.04	498	226	0.38–0.54	10.4 ± 0.7
ROCFF	*Lagonosticta sanguinodorsalis*	0.56±0.04	305	300	0.48–0.63	12.4 ± 1.0
COMBU	*Pycnonotus barbatus*	0.67±0.05	311	111	0.56–0.76	17.1 ± 0.5
AFRTH	*Turdus pelios*	0.80±0.06	190	87	0.66–0.89	18.5 ± 2.8
SPEMO	*Colius striatus*	0.62±0.05	223	95	0.51–0.72	17.25 ± 2.1

*FCHAT=Familiar Chat, RECCB=Red-cheeked Cordon–bleu, ROCFF=Rock Firefinch, COMBU=Common Bulbul, AFRTH=African Thrush, SPEMO=Speckled Mousebird. All survival estimates, number of captures and recaptures as well as 95% CI were extracted from Stevens et al. (2013)