

Bird flight initiation distances in relation to distance from human settlements in a Tanzanian floodplain habitat

Linn M. Bjørvik · Svein Dale · Gudmund H. Hermansen ·
Pantaleo K. T. Munishi · Stein R. Moe

Received: 27 March 2014 / Revised: 8 August 2014 / Accepted: 15 September 2014 / Published online: 26 September 2014
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Abstract Human activity affects wildlife in many ways, but there have been few studies of how wildlife behavioural responses to human disturbance vary with distance from centres of human activity. Theory suggests that fear responses may be either higher in areas with high disturbance (disturbance avoidance) or lower in such areas (e.g. due to habituation). We used flight initiation distance (FID) to study how fear responses of 16 bird species varied with distance from villages (range 0.1–11.6 km) within the Ramsar site of Kilombero Valley, Tanzania. A linear model indicated that FID was not related to distance from villages, but varied between habitats. However, a piecewise linear model (linear response up to 2 km, flat response >2 km from villages) provided a better fit and suggested that there may be a small decrease in FID close to human settlements, in particular for the Common Bulbul (*Pycnonotus barbatus*) and a few other species, although the

majority of species still showed little change in FID with distance from human settlements. Our results suggest that a few species may respond to human disturbance with a decreased FID, whereas the majority of species showed little variation in FID in relation to distance from human settlements, and may therefore be negatively affected by increasing frequency of human disturbance.

Keywords Birds · Fear response · Flight initiation distance · Habituation · Human disturbance

Zusammenfassung

Fluchtdistanzen von Vögeln in Beziehung zum Abstand von menschlichen Siedlungen in einer Überschwemmungsebene in Tansania

Menschliches Handeln beeinflusst Tiere auf vielerlei Arten, aber es gab nur wenige Untersuchungen, wie sich die Verhaltensantworten der Tiere auf Störung durch Menschen unterscheiden in Abhängigkeit vom Abstand zum Zentrum menschlichen Handelns. Die Theorie sagt, dass Angstreaktionen entweder höher sind in Gegenden mit viel Störungen (Störungsmeidung) oder niedriger (z.B. aufgrund von Habituation). Wir betrachteten Fluchtdistanzen von 16 Vogelarten im Kilombero-Tal, einem Ramsar-Gebiet in Tansania, um zu untersuchen, wie sich deren Angstreaktionen unterschieden in Abhängigkeit ihrer Distanz zu Ortschaften (im Bereich von 0.1 bis 11.6 km). Ein lineares Modell zeigte, dass es zwischen Fluchtdistanz und Abstand von Ortschaften keinen Zusammenhang gab, sondern sie sich mit dem Habitat änderte. Allerdings ergab ein piecewise linear Modell (linear bis zu 2 km, flach >2 km zu Ortschaften) eine bessere Anpassung und deutete darauf hin, dass es eine kleine Verringerung der

Communicated by A. Hedenström.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-014-1121-1) contains supplementary material, which is available to authorized users.

L. M. Bjørvik · S. Dale (✉) · S. R. Moe
Department of Ecology and Natural Resource Management,
Norwegian University of Life Sciences, P.O. Box 5003,
1432 Ås, Norway
e-mail: svein.dale@nmbu.no

G. H. Hermansen
Departement of Mathematics, University of Oslo, Blindern,
P.O. Box 1053, 0316 Oslo, Norway

P. K. T. Munishi
Department of Forest Biology, Faculty of Forestry and Nature
Conservation, Sokoine University of Agriculture, Morogoro,
Tanzania

Fluchtdistanz geben könnte in der Nähe von menschlichen Siedlungen, insbesondere für den Graubülbul (*Pycnonotus barbatus*) und für andere Arten, wobei die meisten Arten in Abhängigkeit vom Abstand zu menschlichen Siedlungen jedoch nur eine geringe Änderung in der Fluchtdistanz zeigten. Unsere Ergebnisse deuten darauf hin, dass einige wenige Arten auf menschliche Störungen mit einer Verringerung ihrer Fluchtdistanz reagieren, während der Großteil der Arten nur geringe Unterschiede in ihrer Fluchtdistanz zeigten, und daher negativ beeinflusst werden könnten durch eine Zunahme der Häufigkeit menschlicher Störungen.

Introduction

Human disturbance affects large proportions of wildlife worldwide, and it is important to understand how disturbance effects vary between and within species and how disturbance effects can be mitigated. Animals often respond to humans in the same way as to predators (Frid and Dill 2002) and move away when approached according to trade-offs between costs and benefits of fleeing versus staying (Ydenberg and Dill 1986; Lima and Dill 1990; Cooper and Frederick 2007). Studies of responses to human disturbance have often used flight initiation distance (FID) as a measure of the strength of the fear response (Tarlow and Blumstein 2007), and FID can give an indication of ability to coexist with humans (Møller 2008). There is considerable variation between and within species in behavioural responses to disturbance, related to, for example, body size, body condition, social structure and habitat (Fernández-Juricic et al. 2001; Beale and Monaghan 2004; Blumstein 2006; Stankowich 2008).

From a conservation viewpoint, studies of how different levels of human activity affect wildlife are needed. There are relatively few studies which have addressed how flight responses of multiple species vary along gradients of human disturbance (Blumstein et al. 2005). A priori, one might expect that fear responses should be strongest in areas with most human disturbance, similar to areas with high predation risk (disturbance avoidance; Ydenberg and Dill 1986; Lima and Dill 1990; Frid and Dill 2002; Valcarcel and Fernández-Juricic 2009). However, human disturbance is often non-lethal, and animals may habituate to disturbance (Stankowich and Blumstein 2005; Bisson et al. 2009; Rodríguez-Prieto et al. 2009; Vennesland 2010), or individuals with low fear responses may successfully exploit areas with high disturbance (non-random assortment of individuals; Carrete and Tella 2010, 2011), or individuals may decrease their allocation of anti-predator effort in high-risk areas (Lima and Bednekoff 1999;

Rodríguez-Prieto et al. 2009). Thus, fear responses may be lower in areas with more human disturbance (Cooke 1980; Webb and Blumstein 2005; Stankowich 2008; Fernández-Juricic et al. 2009; Evans et al. 2010; Keeley and Bechard 2011; Li et al. 2011; Scales et al. 2011; Clucas and Marzluff 2012; Lin et al. 2012; McGiffin et al. 2013). However, no change in response in relation to level of human disturbance has also been found (Sunde et al. 2009), or lowest response at intermediate disturbance (Fernández-Juricic et al. 2003). Thus, theoretical considerations suggest that responses may vary from disturbance avoidance to disturbance tolerance. Although most evidence indicates that some degree of tolerance may be found close to humans, previous studies have usually looked at only a few levels of disturbance (e.g. urban vs. rural; Cooke 1980; Valcarcel and Fernández-Juricic 2009; Keeley and Bechard 2011), and very few have looked at continuous gradients and then only in single species (Webb and Blumstein 2005; Carrete and Tella 2010). More data from a variety of species are therefore needed to assess how fear responses vary with distance from sources of disturbance.

We studied how flight initiation distance of 16 widespread bird species varied in relation to distance from human settlements in the Kilombero Valley flood plain in Central Tanzania. The area is a protected wetland (Ramsar site), but increasing human pressure causes more frequent interactions between wildlife and people (Starkey et al. 2002). Trapping of birds in snares or nets occurs, but levels of direct persecution such as shooting are low. Thus, avian responses to human disturbance such as an approaching person could potentially range from fear to tolerance. We measured FID along a continuous gradient up to 11.6 km from villages. We also recorded habitat in order to take into account other factors that may influence FID. We asked whether FID was shorter close to human settlements (which could indicate habituation, or use of areas close to people by disturbance-tolerant individuals), or longer close to humans (disturbance-avoidance).

Methods

Study area

The study was conducted in the Kilombero Valley (henceforth termed Kilombero), Morogoro region, south-central Tanzania. Kilombero is the largest low-altitude freshwater wetland in East Africa with a flood area of 6650 km² at high water. The valley is about 40 km wide and 175 km long, and is situated at an altitude of about 300 m. The central point coordinates are 8°40'S, 36°10'E. The habitat types of the floodplain vary according to the extent of seasonal inundation. The riverside area is dominated by perennial grasses that can form swards more than

3 m tall, while the low lying valley grassland consists mostly of a mosaic of short and long grasses (Starkey et al. 2002). Wooded grassland occurs on higher ground.

Kilombero is of national importance for the high density of mammals and for the diversity of plants and birds (Starkey et al. 2002; Jenkins et al. 2003). The valley has protection status as a game-controlled area where licensed hunting of large mammals is permitted. Kilombero was declared Tanzania's third Ramsar site in 2002, and ornithological values include large numbers of waterbirds and three endemic species (Starkey et al. 2002). However, current legislation does not protect from changes in land use (Haule et al. 2002). At least 200,000 people live in Kilombero with the majority being agriculturalists cultivating rice in the floodplain during the wet season and maize in the upland during the dry season (Starkey et al. 2002). A total of 75 registered villages are located within the borders of the valley. In addition, there are numerous smaller villages, hamlets and fishing camps in the area (Haule et al. 2002). Outside the villages, pastoralists of diverse ethnic groups have bomas (small settlements) in the marginal woodland and short-grass areas of the floodplain (Bonnington et al. 2007). However, in the parts of the area used in this study, there were few bomas and they had minimal activity, and distance to bomas was therefore not included in analyses because bomas were considered to have a negligible potential disturbance effect compared to that of villages.

The human settlement has expanded significantly in Kilombero during recent years, leading to an increasing amount of livestock grazing, poaching, agriculture, commercial forestry, overfishing and extensive annual burnings (Jenkins et al. 2002). Bird damage to crops is regarded by farmers to be one of the biggest agricultural problems in Kilombero (Kangalawe and Liwenga 2005), and hunting of birds is quite common. However, most of the hunting methods used for birds involve traps, snares and nets (personal communications from villagers), which do not engage humans directly in the capture such as in the case of shooting. Because of that, birds probably do not associate these dangers with people and hence may not regard a human approach as a lethal threat.

Field methods

The field work was carried out during 26 days in July and August 2009, in what is the dry season in Kilombero (Starkey et al. 2002). Thus, most birds were not breeding at this time. The data were gathered in the morning between 0700 and 1130 hours when the birds were most active. A minor number of observations were also made in the afternoon ($n = 14$, around 1700 hours). The observations were made in areas surrounding ten villages along the northwestern and southeastern side of the Ramsar site.

In the beginning of the study, we recorded FID from a wide variety of different species. When we discovered a pattern in which species that occurred most commonly both close to and far from human settlements we focused on recording these. We made 572 observations from 16 species (range 23–51 observations per species). To record FID, a focal bird was identified and approached on foot at a steady pace in a direct line. Only birds that seemed relaxed and were engaged in behaviour such as feeding, resting or preening were approached (Blumstein et al. 2004). The FID was recorded as the distance between the observer and the bird when it flew away as a response to being approached, and was determined with the use of a laser distance measurer for longer distances (Nikon Laser 500) or a measuring tape to the nearest 0.5 m for shorter distances. In addition to the horizontal FID, the perching height of the bird was recorded. The distance from every observation point to the edge of the closest village was found using GPS positions and a geographical information system (GIS; ArcView 3.3). In addition, we recorded the habitat in which observations were made and divided the habitat types into four different categories: wooded grassland (grassland with scattered trees), short grassland (<1 m tall), tall grassland (≥ 1 m tall) and cultivated areas (cf. Starkey et al. 2002). Individual observation sites could have one or more habitats, and occurrence of each habitat type was recorded as present or absent within a 25-m radius.

The same areas were not sampled twice to ensure that sample sizes generally represented different individuals. However, a modest degree of pseudoreplication does not affect the results in FID studies (Runyan and Blumstein 2004). Birds were studied at different distances from the ten villages, both close to where there was a higher level of human disturbance and further away where there was less disturbance (maximum distance of 11.6 km from a village). The number of people observed during each morning of fieldwork varied roughly from >10 close to villages (<1–2 km), often around 3–5 at intermediate distances, and few or none far from villages (>5 km). The ten villages were separated from each other by 2–25 km (distance to closest neighbour) and had a size of approximately 10–50 ha.

Statistical analyses

Our analyses aimed to assess the relationship between distance from closest village and FID while controlling for the effects of habitat and perching height. From inspections of boxplots of the selected species, six outlier observations were identified and excluded from further analyses. Thus, the final dataset consisted of 566 observations. Linear models were used to test for linear effects of explanatory

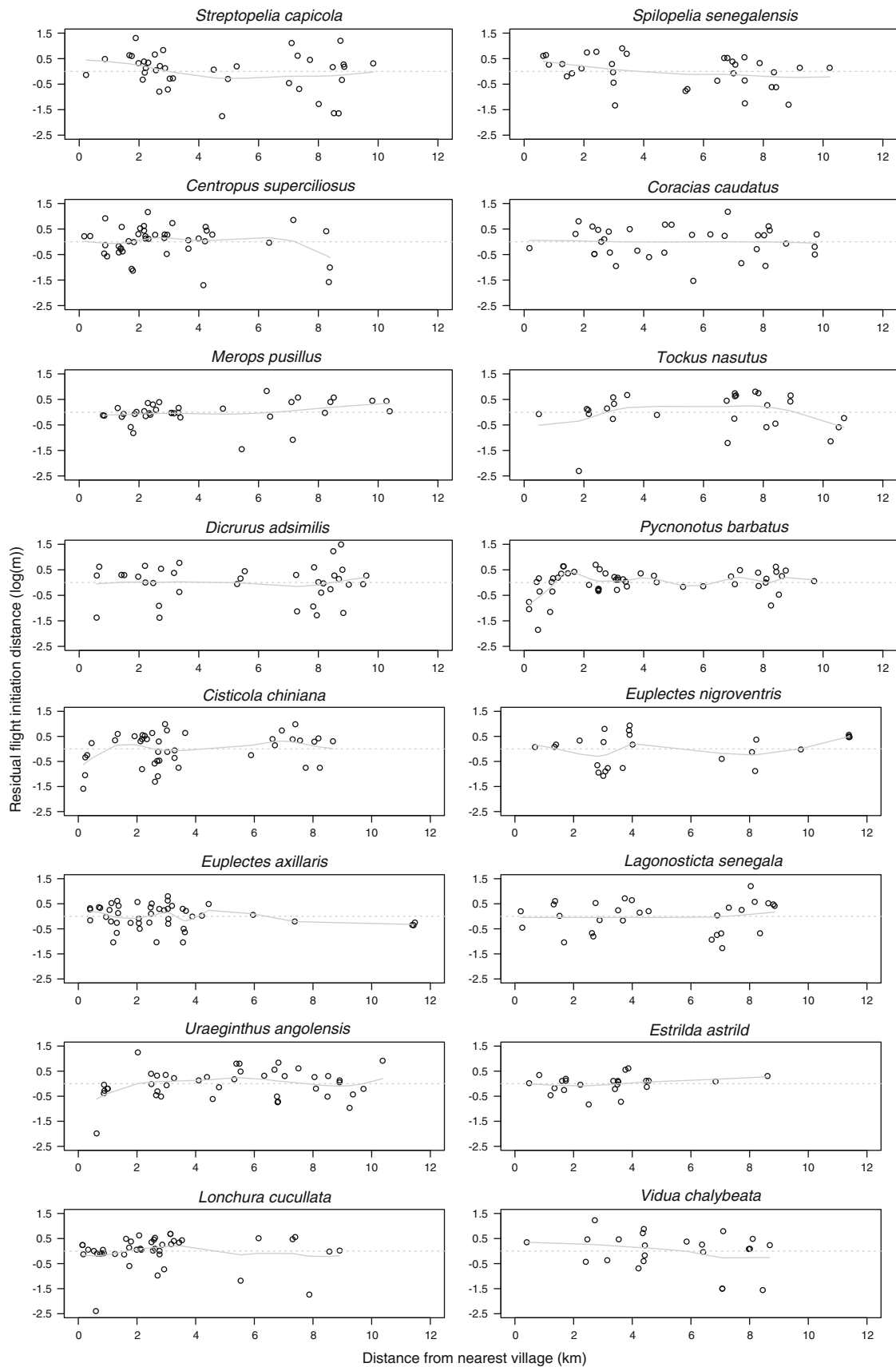


Fig. 1 Residual flight initiation distances in relation to distance from closest village for 16 bird species in the Kilombero Valley, Tanzania. Residuals were from a model of the effects of habitat, perching height and species on flight initiation distance. The lines were fitted using the spline function in R

variables [distance to nearest village, habitat (four variables coded as present/absent) and perching height] on FID (log-transformed). Species was included as a fixed factor. Models including species were compared with models replacing species with family or body mass to assess whether this affected conclusions. Species, family and body mass could not be analysed together in one model because the information in family and body mass becomes redundant when species is included in the model. The models providing the best fit (based on AIC values) are presented in the “Results”, with alternative models in the Electronic Supplementary Material (Online Resources, Tables S2–S8). We also performed single-species analyses of the effects of distance on FID with habitat and perching height as covariates. The use of the multi-species approach in addition to the single-species approach was done to capture overall effects which might be weak and non-significant in single-species analyses. Information on body mass was taken from Urban et al. (1986, 1997), Fry et al. (1988), Keith et al. (1992), and Fry and Keith (2000, 2004). Information on taxonomy was taken from IOC World Bird List version 2.11 (www.worldbirdnames.org/names.html). Information on the 16 species included is given in Online Resources, Table S1. Because recordings of the four habitat variables were made as present/absent, and each observation site had variable numbers of habitats present, all tests involving habitat compare sites where one specific habitat was present with all sites which lacked this habitat, regardless of which other habitat(s) were present instead. Linear models were compared to piecewise linear models which had a linear response up to 2 km from the nearest village and a flat response from 2 km and upwards (choice of 2 km was based on results shown in Fig. 1; see “Results” for further explanation). Analyses were done using R v. 2.14.0 (<http://www.r-project.org/>), and the smooth splines in Fig. 1 were calculated with the spline function using smoothing parameter = 1. We used a significance level of $\alpha = 0.05$.

Results

A linear model including all the 16 species showed that FID was related mostly to habitat (longest FID in short grassland), whereas FID was not related to distance from closest village (Table 1). There were also significant differences between species with some of the larger species

Table 1 Linear model of factors affecting flight initiation distance (ln-transformed, 566 observations) in 16 bird species in Kilombero wetlands, Tanzania ($R^2 = 0.18$)

Source of variation	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	2.63	0.15	17.48	<0.0001
Distance from closest village	0.002	0.01	0.15	0.88
Perching height	0.0003	0.005	0.08	0.94
Habitat (present versus absent)				
Woodland	0.06	0.07	0.84	0.40
Short grassland	0.30	0.08	3.72	0.0002
Long grassland	0.21	0.08	2.61	0.009
Cultivation	0.22	0.08	2.77	0.006
Species (vs. <i>Tockus nasutus</i>)				
<i>Streptopelia capicola</i>	−0.14	0.15	−0.93	0.36
<i>Spilopelia senegalensis</i>	−0.47	0.15	−3.10	0.002
<i>Centropus superciliosus</i>	−0.24	0.15	−1.57	0.12
<i>Coracias caudatus</i>	0.12	0.15	0.79	0.43
<i>Merops pusillus</i>	−0.34	0.15	−2.22	0.027
<i>Dicrurus adsimilis</i>	−0.32	0.15	−2.19	0.029
<i>Pycnonotus barbatus</i>	−0.23	0.14	−1.60	0.11
<i>Cisticola chiniana</i>	−0.84	0.15	−5.51	<0.0001
<i>Euplectes nigroventris</i>	−0.58	0.17	−3.38	0.0008
<i>Euplectes axillaris</i>	−0.21	0.15	−1.37	0.17
<i>Lagonosticta senegala</i>	−0.84	0.16	−5.26	<0.0001
<i>Uraeginthus angolensis</i>	−0.76	0.15	−5.11	<0.0001
<i>Estrilda astrild</i>	−0.51	0.18	−2.91	0.004
<i>Lonchura cucullata</i>	−0.32	0.15	−2.10	0.036
<i>Vidua chalybeata</i>	−0.52	0.17	−3.14	0.002

(*Streptopelia capicola*, *Coracias caudatus*, *Tockus nasutus*) having the longest FIDs (Table 1). The linear model with species provided a better fit to data (AIC = 998.37) than alternative models with family (AIC = 1017.61), body mass (AIC = 1043.75) or family and body mass (AIC = 1009.50). The models including body mass showed that larger species had longer FIDs (Tables S3, S4). All alternative models indicated an effect of habitat, but no effect of distance (Tables S2–S4). Parameter estimates from the linear model suggested that FID for all 16 species was 13.8 m at a distance of 0 km and 14.0 m at 10 km from closest village.

After correcting for all covariates except distance from closest village, a smooth spline as a function of distance from closest village was fitted to the residual FID values for each species, which suggested that a piecewise linear structure provided a reasonable approximation because some species had a reduced FID at short distances (Fig. 1). Hence, for further analyses, we chose a piecewise linear model with a linear response up to 2 km from villages, and a flat response from 2 km and farther from villages. Such a piecewise linear model provided a better fit with data

Table 2 Piecewise linear model of factors affecting flight initiation distance (ln-transformed, 566 observations) in 16 bird species in Kilombero wetlands, Tanzania

Source of variation	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	2.42	0.18	13.65	<0.0001
Distance from closest village	0.11	0.06	1.98	0.049
Perching height	0.0004	0.005	0.10	0.92
Habitat (present versus absent)				
Woodland	0.04	0.07	0.65	0.51
Short grassland	0.29	0.08	3.71	0.0002
Long grassland	0.20	0.08	2.54	0.011
Cultivation	0.23	0.08	3.00	0.003
Species (vs. <i>Tockus nasutus</i>)				
<i>Streptopelia capicola</i>	−0.13	0.15	−0.91	0.36
<i>Spilopelia senegalensis</i>	−0.46	0.15	−3.04	0.002
<i>Centropus superciliosus</i>	−0.22	0.15	−1.48	0.14
<i>Coracias caudatus</i>	0.12	0.15	0.81	0.42
<i>Merops pusillus</i>	−0.33	0.15	−2.22	0.027
<i>Dicrurus adsimilis</i>	−0.31	0.15	−2.10	0.037
<i>Pycnonotus barbatus</i>	−0.20	0.14	−1.43	0.15
<i>Cisticola chiniana</i>	−0.83	0.15	−5.43	<0.0001
<i>Euplectes nigroventris</i>	−0.57	0.17	−3.37	0.0008
<i>Euplectes axillaris</i>	−0.19	0.15	−1.25	0.21
<i>Lagonosticta senegala</i>	−0.83	0.16	−5.20	<0.0001
<i>Uraeginthus angolensis</i>	−0.75	0.15	−5.08	<0.0001
<i>Estrilda astrild</i>	−0.49	0.17	−2.84	0.005
<i>Lonchura cucullata</i>	−0.29	0.15	−1.93	0.054
<i>Vidua chalybeata</i>	−0.51	0.17	−3.10	0.002

The model had a linear response up to 2 km from villages, and a flat response from 2 km and farther from villages. $R^2 = 0.18$

(AIC = 994.34) than the linear model (AIC = 998.37), or a linear model without distance (AIC = 996.39). The piecewise linear model indicated that both habitat (longest FID in short grassland) and distance from closest village (shorter FID close to villages) had significant effects (Table 2). Species effects were highly similar in both the linear and piecewise linear models in that the relative order of species' parameter estimates was unchanged (Tables 1, 2). The piecewise linear model with species was again better than alternative models with family (AIC = 1015.77), body mass (AIC = 1041.07) or family and body mass (AIC = 1007.35). The models including body mass showed that larger species had longer FIDs (Tables S6, S7). Alternative models indicated an effect of habitat, but no longer of distance (Tables S5–S7).

The relationship between distance from nearest village and FID in the piecewise linear model with species was mainly driven by *Pycnonotus barbatus*, *Cisticola chiniana* and *Uraeginthus angolensis* (cf. Fig. 1; Table S8), whereas other species showed little or no response. Without these

three species, the relationship between distance and FID in the piecewise linear model was not significant ($P = 0.75$). Parameter estimates from the piecewise linear model suggested that FID for all 16 species changed from 11.3 m at a distance of 0 km up to 14.1 m at 2 km from closest village. For the species with the largest responses, FID for the interval 0–2 km was estimated to increase from 7.3 to 14.4 m for *Pycnonotus barbatus*, from 2.9 to 5.7 m for *Cisticola chiniana*, and from 4.0 to 13.7 m for *Uraeginthus angolensis* (based on 16, 8 and 6 observations for the interval 0–2 km, respectively; Fig. 1).

Discussion

In general, our results indicated that flight initiation distance was not related to distance from closest village. However, using a threshold of 2 km (based on results shown in Fig. 1), we found that some species appeared to have shorter FIDs close to villages, in particular the Common Bulbul (*Pycnonotus barbatus*) which was one of the most synanthropic species in our dataset (Keith et al. 1992). The latter finding is in line with several previous studies which have found reduced responses in areas with higher human disturbance (see “Introduction” for references). Shorter FID close to humans could indicate habituation or that areas close to humans are used preferentially by individuals with low FIDs. The case of the Common Bulbul argues against the latter hypothesis, because FIDs close to villages seemed to be shorter than for most individuals of this species at longer distances (cf. Carrete and Tella 2011), but we do not have sufficient material to conduct a thorough analysis of this question.

However, given previous findings of reduced responses close to humans in a number of species, it is actually more striking that most of the species we studied did not show any such response. Only a few previous studies of FID have looked at disturbance as a continuous distance gradient from areas with high human activity. Webb and Blumstein (2005) found that FIDs of Western Gulls (*Larus occidentalis*) were shortest in an area with more people, and more than doubled over a distance of 2 km with decreasing disturbance. Carrete and Tella (2010) found that Burrowing Owls (*Athene cunicularia*) doubled their FID along a gradient of 2–170 m between their nests and roads. Our study covered a much larger span in distances which made it likely that observations were made on a range of individuals varying from frequently or continuously exposed to human disturbance to individuals encountering humans infrequently. This would likely encompass a broad range of behavioural responses shown within each species, but FID was in general not related to distance from

humans. For species in our dataset which had positive slopes for FID on distance (i.e. shorter FID close to humans; *Pycnonotus barbatus*, *Cisticola chiniana*, and *Uraeginthus angolensis*), the rate of change in FID as a function of distance approached those reported by Webb and Blumstein (2005) and Carrete and Tella (2010). For the Common Bulbul, which showed the strongest response, FID approximately doubled for the first 2 km from a village according to the piecewise linear model. However, across all species, there was an increase in FID of only 0.02 m/km in the linear model (not significant), and 0.8 m for the first 2 km from villages in the piecewise linear model (significant). Considering that FID was on average about 14 m, such changes seem to have little biological significance.

On the other hand, we caution that our sample of species studied was biased towards those that were common and distributed both close to and further from villages. Thus, there may be a number of other species which show different patterns. In the study area, there were few if any species exclusively distributed close to humans (Starkey et al. 2002), but there may be many species avoiding villages and other areas with disturbance. The latter type of species are likely to have generally long FIDs, and use of areas with frequent disturbance may therefore become uneconomical. Documenting that absence of some species close to humans is due to disturbance is not possible using FID, but would require other methods such as analyses of occupancy rates or comparisons of distributions before and after introduction or removal of human disturbance. Nevertheless, it is striking that even the more common species generally lacked a behavioural response to disturbance.

Our results indicated that habitat was much more strongly related to FID than distance from villages. Habitats differed strongly in both perceptual range and cover, with birds on ground in long grassland having the strongest limitations on detecting approaches but better cover. This may have contributed to the contrast in FID between long and short grassland. Finally, we note that we also found the well-documented relationship between body size and FID; larger birds had longer FIDs, whereas there was apparently no effect of perching height in our dataset.

In conclusion, our results suggest that although some species may be able to adapt to human disturbance, most species did not adjust their behavioural response to human disturbance (i.e. no shortening of FID close to humans). A lack of adjustment may indicate that use of areas close to humans may be less profitable due to higher response costs because such birds will be forced to take flight more often than in less disturbed areas. One may speculate that individuals close to humans have lowered fitness, and that these areas could represent population sinks. This may call for a restrictive attitude towards human activity in the

Kilombero Valley Ramsar site including buffer zones with limitations on human use, and similar considerations may also be needed in other conservation areas. It is likely that, in areas which have a recent history of large human use, many species may still lack behavioural adaptations or adjustments so that disturbance may have stronger negative impacts than in areas with a longer history of coexistence between humans and wildlife.

Acknowledgments We thank Wilbard Ntongani and John Mchetto for great assistance in the field, Michael Grover for all his help with GIS. Tore Slagsvold commented on a previous draft of the manuscript. Financial support was provided by the NUFU project 'Integrating Livelihoods and Multiple Biodiversity Values in Wetland Management in Tanzania'.

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