Received: 20 November 2018 | Revised: 28 June 2019 | Accepted: 19 July 2019
DOI: 10.1111/btp.12702

ORIGINAL ARTICLE

WILEY bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

Movement ecology of Afrotropical birds: Functional traits provide complementary insights to species identity

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Associate Editor: Emilio Bruna
Handling Editor: Edward Webb

Abstract

Effects of anthropogenic activities on habitats and species communities and populations are complex and vary across species depending on their ecological traits. Movement ecology may provide important insights into species' responses to habitat structures and quality. We investigated how movement behavior across a human-modified landscape depends on species identity and species traits, with particular focus on habitat specialization, feeding guilds, and dispersal behavior. We tracked 34 individuals of nine Afrotropical bird species during three years in an anthropogenic riparian landscape of East Africa. We investigated whether species' functional traits predicted their habitat use and movement behavior better than species' identities. Our results indicate that habitat specialists mainly occur in dense riparian thickets, while habitat generalists do occur in agricultural land. Home-ranges of omnivorous habitat generalists are larger than of frugivorous and insectivorous generalists and omnivorous and insectivorous specialists. Movement speed was highest in settlement areas for all species, with activity peaks during morning and afternoon for habitat specialists. Our results reveal that functional traits and species identity provide complementary insights into responses of organisms to habitat structures and habitat quality.

KEYWORDS
habitat use, home-range, Kenya, land use, movement behavior, movement speed, niche breadth, riparian vegetation

1 | INTRODUCTION

Increasing human demographic pressure and rising living standards are driving ever-higher demand for resources, which has caused intense pressure on pristine habitats (Maxwell, Fuller, Brooks & Watson, 2016; Sala et al., 2000). Many natural habitats have been transformed into agricultural land and settlements, and thus today exist as small and degraded habitat remnants, with negative effects on the biota and associated ecological functions (Gaston et al., 2018; Pereira, Navarro & Martins, 2012). Such changes at the landscape scale may strongly influence species richness and abundance, as well as population structures and species behavior (Fahrig, 2003; Newbold et al., 2015), such as movement behavior (Jeltsch et al., 2013).

Birds offer an excellent model to study potential effects of environmental change on individual behavior (Schulze et al., 2004). Bird species vary in a wide range of traits, including resource preferences, habitat use, feeding strategy, and social behavior (Wilman et al., 2014). However, how habitat use and movement influence responses to habitat degradation remain unclear. Studies on birds showed that habitat degradation may affect movement behavior. Birds have larger home-ranges in disturbed and fragmented environments, and smaller home-ranges in intact and interconnected habitats (Carey, Reid & Horton, 1990; Godet, Hamange, Marquet, Joyeux & Fournier, 2017; Hansbauer, Storch, Pimentel & Metzger, 2008). Such effects can reduce population density and, thus, negatively impact the long-term viability of populations (Estrada, Morales-Castilla, Caplat & Early, 2016). Species with more specific habitat demands (in the following termed specialists) are assumed to suffer more from environmental changes, than species that can use a broad range of ecological resources and habitats types (in the following termed generalists; Becker, Fonseca, Haddad, Batista & Prado, 2007). Previous studies have shown that ground-foraging species are especially sensitive to habitat degradation and fragmentation (Barlow, Peres, Henriques, Stouffer & Wunderle, 2006). Further, microhabitat variables such as shallow leaf litter and low tree densities impede the movement behavior of insectivorous birds (Stratford & Stouffer, 2013). Other functional traits, such as dietary niche, dispersal ability and social structure, may also shape habitat use and movement behavior of species (Lundberg & Moberg, 2003). While many trait-based studies have described the correlates of species responses to land-use across large spatial scales (Bregman et al., 2016; Estrada et al., 2016; Newbold et al., 2013), few studies have assessed how habitat structures at a local scale may influence habitat use and movement behavior of bird species (Da Silveira, Niebuhr, de Lara Muylaert, Ribeiro, & Pizo, 2016).

In this study, we radio-tracked nine Afrotropical bird species to analyze their habitat use, home-range size, movement speed, and diurnal movement patterns across an anthropogenic riparian landscape. We categorized each species by habitat specialization, feeding preference, and dispersal ability, functional traits that are known to influence species' responses to environmental changes (Laurance, Stouffer, & Laurance, 2004; Lees & Peres, 2009; Neuschulz, Brown, & Farwig, 2012; Newbold et al., 2013; Van Houtan, Pimm, Halley, Bierregaard, & Lovejoy, 2007). Based on these data, we test the following hypotheses:

1. Habitat use and movement behavior differ among bird species and functional traits, with reduced movement and stronger restriction to dense riparian thickets for specialists.
2. Functional traits provide complementary insights into the habitat use and movement behavior if compared with species identity.

2 | METHODS

2.1 | Study area

We collected data in a semiarid landscape near Kitui city in southeastern Kenya (1°23′S; 38°00′E). Field work was conducted during four field seasons, during August 2014 and 2015 and Löschen March 2015 and 2016. The region is characterized by two short and distinct rainy seasons (a short rainy season from end of March to beginning of June, and a longer rainy season from end of October till January; Jaetzold, Schmidt, Hornetz & Shisanya, 2006). To minimize the effect of seasonal variation, all our fieldwork was conducted at the end of the respective dry seasons. Our study area is characterized by fast human population growth (KNBS Kenyan Bureau of Statistics, 2010) and subsequent destruction and degradation of pristine riparian habitats (Habel, Teucher, Ulrich & Schmitt, 2018). Today, the landscape consists of a mosaic of riparian thickets, agricultural land, small settlements, and the riverbed of Nzeeu river.

We manually mapped the land surface of 148.2 ha along the river and classified the land cover into the following habitat types using a GPS Garmin Etrex 60SCP device and a tablet computer with QGIS: riparian thicket (46.8 ha, 22.8%), agricultural land (94.9 ha, 74.6%), and settlement (6.4 ha, 2.7%). The mean size of riparian thickets was 1.1 ha (ranging from 0.02 to 5.4 ha), with 80 percent of the patches smaller than 2.0 ha. The 43 riparian thicket patches consist of mainly low stature (<5 m) stands of small trees, with a few taller trees (>5 m) as well as lower shrubs, including the invasive exotic shrub *Lantana camara*. The mean size of the 141 agricultural patches was 0.7 ha (0.001–7.4 ha). The settlements occur clustered in four areas, but single households are spread across the entire study area. The riverbed consists of open sand during the dry seasons. We processed these data with QGIS 2.4.0 (QGIS Development Team 2014), corrected the topology and merged neighboring geometries. A detailed map of our study region showing the landscape configuration and composition is displayed in Figure S1.

2.2 | Study species

We tracked 34 individuals of the following nine bird species: Bare-eyed Thrush *Turdus tephronotus*, African Black-headed Oriole *Oriolus larvatus*, Northern Brownbul *Phyllastrephus strepitans*, Common Bulbul *Pycnonotus barbatus*, Hinde's Babbler *Turdoides hindei*, Rüppell's Robin-Chat *Cossypha semirufa*, Rufous Chatterer *Turdoides rubiginosa*, Tropical Boubou *Laniarius aethiopicus*, and Sombre Greenbul *Andropadus importunes*. Species were categorized as either habitat specialists or habitat generalists. Generalists use a variety of habitat types according to the literature, whereas specialists are mainly restricted to one habitat type, here only species exclusively found in riparian thickets are considered (according to Zimmerman, Turner & Pearson, 1996). Furthermore, we classified all species according to their dietary niche based on Wilman et al. (2014) as follows: (a) insectivores (>50 percent invertebrates in diet), (b) frugivores (>50 percent fruits and nectar in diet), and (c) omnivores (≤50 percent in all diet categories). Feeding preference of a species may strongly shape its behavior and habitat use (see Monsarrat et al., 2013). Thus, we classified foraging behavior based on the estimated percentage time spent foraging on the ground (hereafter referred as "extent of ground-foraging behavior"; Wilman et al., 2014). To estimate dispersal ability, we compiled biometric data from museum specimens to calculate the hand-wing index (HWI), a standard proxy for flight strength and dispersal ability in birds, which may influence the ability of species to adapt to changes in habitat structure and habitat quality at the landscape scale (Claramunt, Derryberry, Remsen & Brumfield, 2011). HWI is calculated as Kipp's distance (the distance between the wing tip and the tip of the first secondary on the folded wing) divided by wing length (the distance from the wing tip to the carpal joint measured on the folded wing), multiplied by

TABLE 1 Ecological classification of the nine study species. Data shown are number of individuals under observation (*N*), mean number of fixes per species ± *SE* and range (minimum – maximum), followed by four functional traits: habitat specialization, feeding guild, extent of ground-foraging behavior (according to Wilman et al., 2014), hand-wing-index (HWI; Claramunt et al., 2011), and body weight ± *SE* (own records per individual)

Common name	Scientific name	N	Mean No. fixes (Min. to Max.)	Habitat specialization	Feeding guild	Ground-foraging behavior (%)	Hand-wing index	Weight (g)
Bare-eyed Thrush	*Turdus tephronotus*	8	296.6 ± 68.1 (125–628)	Generalist	Insectivores	100	18.31	47 ± 1
Black-headed Oriole	*Oriolus larvatus rolleti*	2	296.5 ± 52.5 (244–349)	Generalist	Omnivores	10	28.54	75 ± 0
Northern Brownbul	*Phyllastrephus strepitans*	2	151.0 ± 15.0 (136–166)	Generalist	Omnivores	50	9.54	28 ± 2
Common Bulbul	*Pycnonotus barbatus*	3	429.0 ± 49.1 (360–524)	Generalist	Frugivores	20	14.12	29 ± 1
Hinde's Babbler	*Turdoides hindei*	5	463.6 ± 124.7 (136–819)	Specialist	Omnivores	100	6.90	70 ± 3
Rueppell's Robin-Chat	*Cossypha semirufa*	5	272.6 ± 49.8 (98–395)	Specialist	Insectivores	50	9.49	29 ± 2
Rufous Chatterer	*Turdoides rubiginosa*	4	386.8 ± 63.7 (231–527)	Generalist	Insectivores	100	8.71	54 ± 4
Tropical Boubou	*Laniarius aethiopicus*	2	184.5 ± 45.5 (139–230)	Specialist	Omnivores	40	9.41	49 ± 9
Zanzibar Sombre Greenbul	*Andropadus importunus insularis*	3	216.3 ± 40.5 (149–289)	Specialist	Frugivores	10	13.19	54 ± 19

100 (Claramunt et al., 2011). There was no significant correlation between any combination of these different traits, or with mean body weight per species, which are known to influence animals' movement behavior (Harestad & Bunnel, 1979; Haskell, Ritchie & Olff, 2002; $p > .05$; for test statistics see Table S2). Trait data are provided in Table 1.

2.3 | Radio tracking

We trapped individual birds with mist nets, ringed them with numbered metal rings, and equipped them with a Pip Ag376 backpack tag (Biotrack Ltd) sending 25 ms signals at a pulse rate of 55 ppm, with a predicted life span of 32 days. Tags were attached with underwing loops of rubber band. Trapping and telemetry were conducted with members of the Ornithology Section of the National Museums of Kenya, Nairobi. Signals were received with a four-element Yagi antenna (HB9CV; Wagener Telemetrieanlagen) and a tracking receiver R1000 with a 148–174 MHz band width (Communication Specialists Inc.). Birds were tracked by triangulating the tag's position using bearings recorded by two observers standing at least 150 m apart from each other, mainly at open and elevated points. Both observers took a bearing every 10 min simultaneously from 07:00 hr to 17:30 hr using a compass and recorded their own position with a GPS device (Garmin International Inc.). We started collecting data on the day after tags were attached to allow individuals to adapt to the transmitter and to avoid short-term behavioral changes (Kenward, 2001). Positions located more than 1,000 m distant from the averaged observer positions were not taken into consideration for further analyses due to potential tracking errors, as a compromise between line of sight tag range (up to 3 km) and tag range above ground (up to 600 m; see Biotrack product information http://www.biotrack.co.uk, downloaded at 08 July 2015). On average, individuals were tracked for 10.8 ± 0.8 days (mean ± *SE*), ranging from 3.2 to 21.4 days (number of fixes for each species are provided in Table 1).

2.4 | Habitat use, home-range estimates and movement speeds

Habitat use was calculated by intersecting the birds' locations with our land-cover map using QGIS. Then proportional use of each habitat type (riparian thicket, agricultural land, riverbed, settlement) was calculated as the number of locations within a certain land-use category divided by the total number of locations × 100 for each bird individual separately. Here, we analyzed the use of the different habitat types in a spatial context (percentage habitat used per habitat type over the study period).

Individual home-range sizes were estimated using autocorrelated kernel density estimation (AKDE) in the ctmm R package (Fleming & Calabrese, 2017b) for 95%, 75%, and 50% levels. The AKDE method was chosen as it corrects for temporal autocorrelation bias and is more accurate than the conventional kernel density estimation (KDE) with frequent fixes (here 10 min interval; Fleming and Calabrese, 2017a, 2017b, Noonan et al., 2019). Therefore, continuous time movement models (ctmm) were used to separate the continuous-time movement process of an individual from the discrete-time sampling process (Fleming et al., 2014). We visually inspected individual variograms (function: "variogram.fit") to assess the autocorrelation structure of the movement data. The asymptote of the variogram and the array of autocorrelation timescales were then estimated automatically. These estimates were used to fit the ctmm, from which the *akde* utilization distribution and home-range estimates were calculated (Fleming & Calabrese, 2017a). A common problem with home-range estimates is that results are sensitive to sampling depth, that is the number of data points per individual (Harris et al., 1990). Thus, we correlated home-range estimates of all individuals (n = 34) with the number of spatial data points per individual. Home-range estimates were not positively correlated with the number of data points per individual (AKDE 95: $r = .16$, $p = .36$; AKDE 75: $r = -.15$; $p = .38$; AKDE 50: $r = -.26$; $p = .14$; Spearman's rank correlation due to non-normality of parameters; for correlations per species with >3 individuals see Table S3). Therefore, we assume that our home-range estimates are not biased by variation in sampling depth.

Movement speed was calculated from movement distances between subsequent locations of individuals (in m/s) using the R package adehabitatLT (Calenge, 2006). Individual movement speeds in relation to the different habitat types were determined by the QGIS "Point-in-polygon-function." Speed was calculated based on consecutive fixes (measured every 10 min) and the distance between those fixes. Furthermore, we referred each bearing point to one of the four habitat types (see above). Habitat type specific speed was than analyzed for all events, when subsequent fixes were in the same habitat type. In cases where birds moved between different habitat types, we excluded the data.

2.5 | Statistics

We used linear mixed-effects models ("lme"; Pinheiro & Bates, 2000) with a maximized log-likelihood implemented in the nlme R package (Pinheiro, Bates, DebRoy & Sarkar, 2012) to analyze the proportional use of each habitat type in relation to species' traits, as well as the interaction between the two categorical trait variables (habitat specialization × diet). Due to limited sample size, we used separate models for each habitat type. Habitat use was arcsine–square–root transformed (function: asin(sqrt(habitat use)) to achieve a normal error distribution and/or to avoid heteroscedasticity. To account for differences between the different years and study periods within one year, the factors "year" (n = 3) and "study period" nested within year (n = 2) were included as random effects. To avoid heteroscedasticity (see Pinheiro & Bates, 2000), a constant variance function for species identity available in the nlme package was used. Original models and models with the variance function were compared by choosing the lowest Akaike Information Criterion (AIC) value from an ANOVA table (Pinheiro & Bates, 2000). Model simplification was undertaken in an automatic backward model selection procedure by AIC using a stepwise algorithm. Therefore, we used the "stepAIC" function implemented in the R package MASS (Venables & Ripley, 2002), removing variables until the minimal adequate model (MAM) with the smallest AIC was obtained. Contrasts between factor levels were investigated by least-squares means from the MAM using the R package lsmeans (Lenth, 2016).

Home-range estimates (AKDE 95, 75, 50; log(x + 1)-transformed) and movement speed (log(x + 1)-transformed) per habitat type were analyzed in relation to bird traits using the same modeling procedure described above. In the case of movement speed, we included the factor "birdID" (n = 34) nested in study period as an additional random factor to account for repeated measurements of the same time of day per individual. Further, we compared diurnal movement activity for habitat generalists and specialists by testing the effects of time of day (numeric variable, in hours) in relation to the movement speeds within the same hour, in riparian thickets and agricultural land, separately. Since a non-linear relationship between movement speed and time of day was expected with at least one activity peak, polynomials until the 7th order were used to model the data (Schai-Braun, Rödel & Hackländer, 2012). Therefore, we applied "lmes" and the same modeling procedure described for habitat use. For all response variables, we also tested the relationship with species identity for all birds together. Significance of terms in the best model was assessed by calculating the F- and p-values of an ANOVA table. Non-transformed means and standard errors are presented throughout in text and figures. All analyses were conducted in R version 3.4.1 (R Core Team 2017).

3 | RESULTS

3.1 | Habitat use

Overall, individual birds used riparian thicket (44.74 ± 2.13%) and agricultural land (44.54 ± 1.79%) more than the riverbed (4.69 ± 0.57%) and settlements (0.43 ± 0.10%; riparian thicket = agricultural land > riverbed > settlement; $F_{3,129} = 821.89$, $p < .001$; missing fraction were fixes that were unassignable to any habitat type). For differences among habitat types for species with different habitat specialization and feeding guild, see Figure S4aS4a. There was no effect of habitat specialization on the use of riparian thickets (Figure 1a), whereas specialized species were less associated with agricultural land compared with generalists, independently of the feeding guild (Figure 1b, Table 2). Omnivorous generalists were less associated with the riverbed than were frugivorous generalists, as well as insectivorous and omnivorous specialists (interaction specialization × diet, Figure 1c). Omnivorous specialists were less associated with settlements than omnivorous generalists (interaction specialization × diet; Figure 1d). There was no association between HWI and the use of any habitat type (Table 2). We found no effects of the extent of ground-foraging behavior on the use of agricultural land, the riverbed, or settlements, whereas the use of riparian thicket decreased with increasing extent of ground-foraging behavior (Table 2). Habitat use of riparian thickets, agricultural land, and settlements did not differ among the bird species (thicket and agriculture: removed from MAM; settlements: $F_{8,22} = 2.04$, $p = .09$).

However, we found species-specific differences in the use of the riverbed ($F_{8,22}$ = 9.35, p < .001; Table S4b).

3.2 | Movement behavior

On average and across all individuals observed, birds occupied home-ranges of 49 ± 4 ha (AKDE 95), or more conservatively 13 ± 1 ha (AKDE 75), with a core area covering 5 ± 1 ha (AKDE 50). AKDE 95, 75, and 50 home-range estimates of frugivorous and insectivorous generalists were smaller than those of omnivorous generalists, which in turn had larger home-ranges than omnivorous and insectivorous specialists (interaction of habitat specialization × diet: Figure 2a–c). There was no effect of the extent of ground-foraging behavior on home-ranges for all home-range estimators and HWI for AKDE 95 and 50, whereas AKDE 75 decreased with increasing HWI (Table 2). AKDE 95, 75, and 50 home-range estimates differed between the different bird species (AKDE 95: $F_{8,22}$ = 23.53, p < .001; AKDE 75: $F_{8,22}$ = 24.80, p < .001; AKDE 50: $F_{8,22}$ = 15.49, p < .001; Table S5).

On average, birds moved more slowly in the riverbed (0.21 ± 0.01 m/s) and in the riparian thicket (0.24 ± 0.01 m/s) than across agricultural land (0.31 ± 0.01 m/s) and settlements (0.97 ± 0.10 m/s; riverbed = riparian thicket < agricultural land < settlement; $F_{3,8322}$ = 79.24, p < .001). For differences among habitat types for species with different habitat specialization and feeding guild, see Figure S6a. In riparian thickets, generalists moved faster than specialists. In agricultural land, omnivorous generalists moved faster than frugivorous generalists (interaction specialization × diet). There was no further effect of feeding guild or the extent of ground-foraging behavior on movement speed in any of the habitat types (Table 2). In addition, there was no effect of HWI on movement speeds in riparian thickets, agricultural land, and the riverbed, whereas movement speed of individual birds decreased in settlements with increasing HWI (Table 2). Movement speed did not differ between different bird species when moving through the riverbed or settlements (removed from MAM) but showed differences when moving through riparian thickets ($F_{8,22}$ = 3.79, p < .01) and agricultural land ($F_{8,22}$ = 2.92, p < .05; Table S6b).

There was no difference in diurnal movement speed of generalists in riparian thickets and agricultural land (for all remaining polynomials in the MAM p > .05; see Figure S7a,b). In contrast, diurnal movement speed of specialists in riparian thickets was explained by a 5th order polynomial, was lowest during the afternoon (12:00 hr until 17:00 hr) and peaked during the morning (09:00 hr until 10:00 hr; $F_{1,1833}$ = 4.40, p < .01; see Figure S7c). Diurnal movement speed of specialists across agricultural land peaked during the morning around 11:00 hr (explained by a 5th order polynomial; $F_{1,1619}$ = 8.30, p < .01; see Figure S7d).

4 | DISCUSSION

4.1 | Habitat use and movement behavior

Our analyses confirm that the same fragmented landscape impacts Afrotropical bird species differently according to their functional traits. The relationship between traits and movement responses was complex, with attributes such as habitat specialization, dietary specialization and, to a lesser extent dispersal ability, all influencing

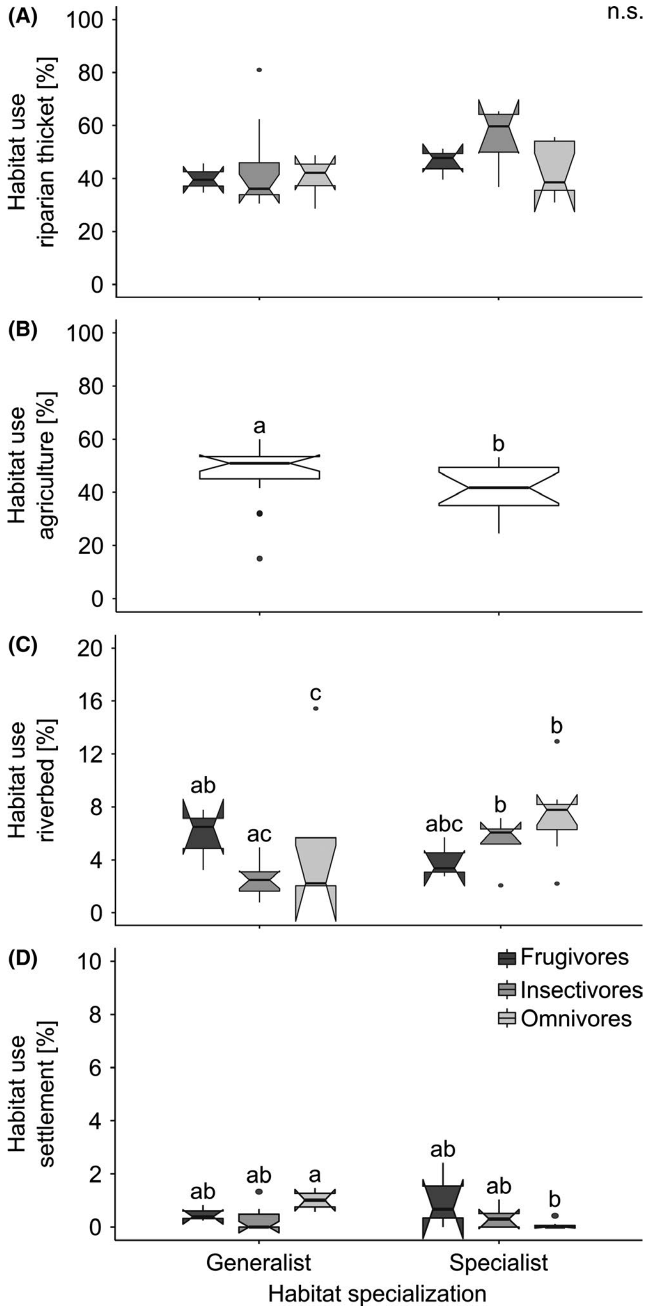

FIGURE 1 Boxplots showing birds' use of (A) riparian thicket, (C) riverbed, (D) settlement subdivided by habitat specialization and feeding guild, and (B) agricultural land subdivided by habitat specialization. Whiskers extend to the most extreme data point which is no further than 1.5 times the interquartile range from the box. Notches give a 95 percent confidence interval for comparing medians. Significance between factor levels was assessed by least-squares means from the Minimum Adequate Model. Boxes sharing the same letter are not significantly different. Non-significant difference is indicted by "n.s." Note: different scaling of the y-axis was used due to different range of predictor variables. Raw data are shown for clarity

TABLE 2 Results of linear mixed-effects models, after an automatic backward stepwise model selection, showing effects of habitat specialization (habitat generalists vs. specialists), feeding guilds (insectivores vs. frugivores vs. omnivores), extent of ground-foraging behavior (estimated percentage time spent foraging on the ground), hand-wing index, and two-way interaction between habitat specialization and feeding guild on birds' habitat use (split by habitat type), home-range size (estimated by autocorrelated kernel density estimation (AKDE) for 95%, 75% and 50% levels), and movement speed (split by habitat type). *F*- and *p*-values from and ANOVA table are given. Bold values indicate those predictor variables which significantly affect response variables at $p < .05$. Variables indicated by "–" were removed from the minimal adequate model

	Habitat specialization		Feeding guild		Ground-foraging behavior (%)		Hand-wing index		Habitat specialization × feeding guild	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Habitat use										
Riparian thicket	–	–	–	–	6.40	**.02**	–	–	–	–
Agricultural land	26.42	**<.001**	2.86	.08	0.47	.50	–	–	2.85	.08
Riverbed	40.72	**<.001**	1.13	.34	–	–	–	–	7.27	**.003**
Settlement	1.19	.29	2.30	.12	–	–	0.03	.87	5.59	**.01**
Home-range size										
AKDE 95	68.26	**<.001**	46.19	**<.001**	2.37	.14	–	–	15.87	**<.001**
AKDE 75	49.91	**<.001**	66.28	**<.001**	–	–	8.30	**.01**	10.81	**<.001**
AKDE 50	50.56	**<.001**	33.38	**<.001**	–	–	0.75	.40	8.47	**.001**
Movement speed										
Riparian thicket	5.99	**.02**	3.05	.07	–	–	–	–	2.87	.08
Agricultural land	1.73	.20	2.49	.10	0.02	.90	–	–	6.41	**.01**
Riverbed	3.36	.08	–	–	4.19	.05	–	–	–	–
Settlement	0.23	.64	0.49	.63	–	–	6.15	**.04**	2.15	.19

habitat use, home-range size, movement speed, and activity patterns. For example, we found that omnivorous habitat generalists have larger home-ranges, use settlements more frequently, and move at similar speeds in both riparian thickets and agricultural land. This contrasted with habitat specialists, as well as habitat generalists with specialized diets, all of which tended to have more restricted home-ranges and move more rapidly in unsuitable terrain, such as agricultural land and settlements.

Previous studies have shown that habitat or diet generalists use a broader variety of habitats and resources than specialists do and, thus, may adapt more readily to environmental changes (Devictor et al., 2008; Gray, Baldauf, Mayhew & Hill, 2007). Conversely, bird species specialized on dense habitats typically have high site fidelity and remain within their favored habitat patches (Shaw & Musina, 2003; Shaw, Njoroge, Otieno & Mlamba, 2014), as long as sufficient resources are available (Wiktander, Olsson & Nilsson, 2001). However, increasing habitat degradation and fragmentation might cause increased overall home-range size in both generalist and specialist bird species (Carey et al., 1990; Hansbauer et al., 2008). Our results confirm that specialized birds move slowly in natural habitats in a highly fragmented landscape, but are forced to move more frequently among small habitat patches, and that they do so by moving much more rapidly in unsuitable terrain, such as agricultural land and settlements. This is presumably because these species are not adapted to exist in open terrain and attempt to cross such gaps as rapidly as possible.

Our data also revealed that specialists varied in their movement activity throughout the day (with activity peaks in riparian thickets during morning and afternoon), while generalists were more consistent in their movement patterns. Small birds typically have two main diurnal activity peaks, one in the morning and again in the afternoon, particularly in tropical regions (Brandt & Cresswell, 2009; Manu & Cresswell, 2013, but see Taylor & Paul, 2006). This might arise from higher temperatures or increased predation by raptors during the middle of the day (Bonter, Zuckerberg, Sedgwick & Hochachka, 2013). The bimodal activity pattern of specialists in riparian thickets fits with this general pattern, perhaps as a result of balancing trade-offs between starvation and predation risk (Houston, McNamara & Hutchinson, 1993; Polo & Bautista, 2006, but see Brandt & Cresswell, 2009). In contrast, generalists do not show any significant temporal activity peaks, perhaps because they have an increased energy budget and are better adapted to high temperatures and more effective avoidance of predation in open areas throughout the day than specialists.

4.2 | The value of functional traits

Our analyses revealed that functional traits yield complementary insights into behavioral responses to habitat quality together with data based on species identities. In particular, variation in home-range size and movement behavior was best explained by habitat specialization and feeding guild, but less by dispersal ability and

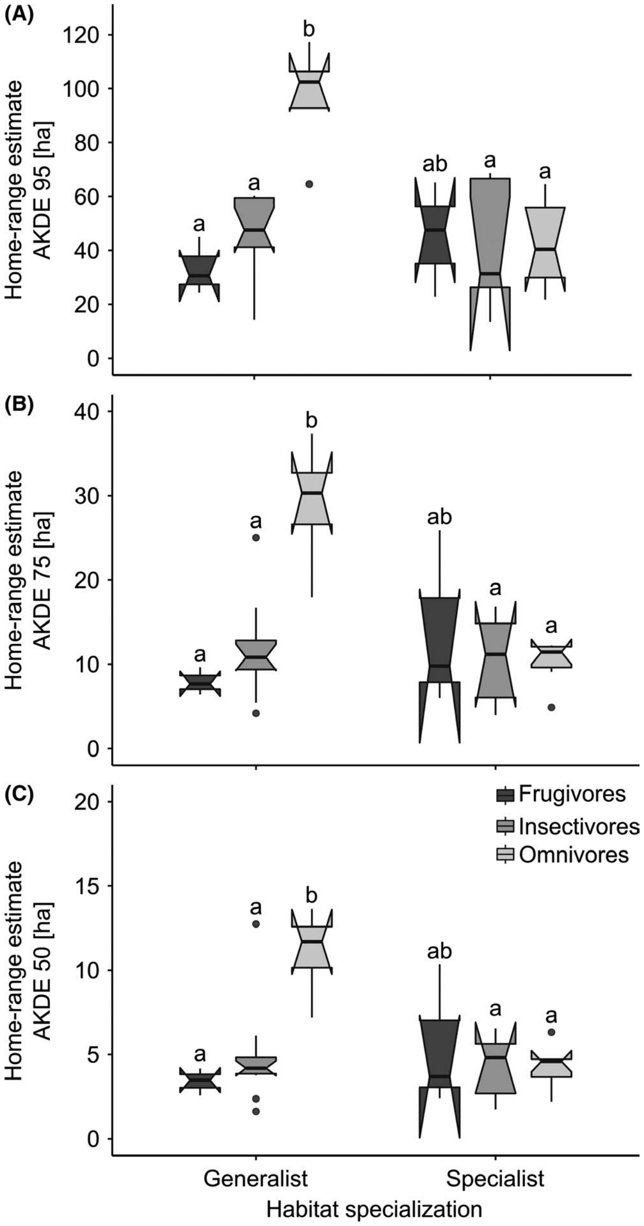

FIGURE 2 Boxplots of (A) AKDE 95, (B) AKDE 75, and (C) AKDE 50 home-range estimates, subdivided by habitat specialization and feeding guild. Whiskers extend to the most extreme data point which is no further than 1.5 times the interquartile range from the box. Notches give a 95 percent confidence interval for comparing medians. Significance between factor levels was assessed by least-squares means from the Minimum Adequate Model. Boxes sharing the same letter are not significantly different. Note: different scaling of the *y*-axis was used due to different range of predictor variables. Raw data are shown for clarity

ground-foraging behavior. These effects may explain variations in population structure and persistence following land-use change, particularly as increased spatial requirements per individual may reduce population density and viability (Jeltsch et al., 2013), while increased movement across unsuitable terrain carries energetic costs and mortality risks (Cattarino, McAlpine & Rhodes, 2016). In addition, trait-based differences in movement patterns may influence ecological processes such as seed dispersal by frugivorous species, and the effectiveness of birds as "mobile links" in ecosystems (Lundberg & Moberg, 2003; Şekercioğlu, Wenny & Whelan, 2016). Thus, our findings add to a growing body of work supporting the use of functional traits in assessing the impact of land-use change on the structure and functioning of ecological communities (Hillebrand & Matthiessen, 2009; Bregman et al. 2014, 2016; Gagic et al., 2015), with particular relevance to understanding individual movements at local scales (Cattarino et al., 2016).

4.3 | Caveats of our study

We would like to close our discussion by mentioning some shortcomings of our study, with respect to study design and data quality. VHF telemetry provides only limited accuracy, which might be a problem especially in such fine-structured landscape mosaics as provided by our study area. Thus, fixes apparently located inside a thicket patch might, in reality, be located outside the patch (or vice versa). If frequent, such errors might significantly impact the explanatory power of our data with respect to habitat use (see Fischer & Habel, 2018). Furthermore, comparative work in disturbed and undisturbed landscapes would provide relevant information of potential responses of species to environmental changes and habitat destruction. Thus, further studies would contribute to a better understanding of the generality of the relationships between traits, movement behavior, and habitat use, and how species respond to environmental changes.

ACKNOWLEDGMENTS

We thank Marie Therese Bleicher, Ivon Cuadros, Claudia Dieckow, Jana Holler, Esam Ishaq, Dominik Meier, Sandra Pschonny, Esther Reith, Simone Rost, Anja Wiese, Camilo Zamora (Freising, Germany), and Onesmus Kioko (Nairobi, Kenya) for their help in the field and Mike Teucher for his support in GIS and the production of a map of our study area. This study was conducted in collaboration with members of the Section Ornithology of the National Museums of Kenya, Nairobi. We thank the Technical University Munich and the German Academic Exchange Service for financial support. We are grateful to two anonymous referees for providing valuable comments on previous versions of this study.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.22mq8g2 (Habel, Tobias & Fischer, 2019).

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How to cite this article: Habel JC, Tobias JA, Fischer C. Movement ecology of Afrotropical birds: Functional traits provide complementary insights to species identity. *Biotropica*. 2019;00:1–9. https://doi.org/10.1111/btp.12702