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SHORT COMMUNICATION

Restricted movements and high site fidelity in three East African cloud-forest birds

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Abstract: Species with specific habitat requirements often remain within their habitat and are characterized by a very sedentary behaviour. We used radio-tracking during a 3-wk campaign to investigate the home ranges and movements of three East African passerine bird species, all adapted to cloud-forest habitats: montane white-eye *Zosterops poliogaster mbuluensis*, stripe-cheeked greenbul *Andropadus milanjensis* and white-starred robin *Pogonocichla stellata macarthuri*. Individuals were observed in a forest-grassland mosaic on top of Chyulu Hills, south Kenya. Based on 15 individuals with a total of 1041 fixes, we found (1) that all three species show a sedentary behaviour restricted to their home forest patch; (2) least activity during the afternoon; and (3) re-colonization into its home patch after translocation into a nearby forest patch. Our findings underline that forest-specialist bird species of the tropics show high site fidelity despite their potential movement ability.

Key Words: birds, cloud-forest fragments, home range, kernel density estimation, radio-tracking, site fidelity

Dispersal ability and dispersal behaviour are of high relevance when analysing the population structure of a species and potential effects from landscape structures on biota (Jeltsch *et al.* 2013). Studies on the population structure of forest animal species underline the relevance of the size of the forest habitat, which strongly affect the dispersal behaviour of species, as shown for various bird species (Dolman *et al.* 2007, Githiru *et al.* 2007, Spanhove *et al.* 2009). Radio-tracking can give valuable information on movements, home-range sizes, site-fidelity and species-specific habitat demands.

In this study, we conducted a radio-tracking analysis on three cloud-forest bird species, the montane white-eye *Zosterops poliogaster* (nomenclature after Zimmermann *et al.* 1996), stripe-cheeked greenbul *Andropadus milanjensis* and white-starred robin *Pogonocichla stellata macarthuri*. We measured their daily movements during a 3-wk study. Our study was conducted in the centre of the Chyulu Hills National Park, south-eastern Kenya (2°59′S, 37°85′E). This mountain range consists of patches of pristine cloud forest embedded in a grassland matrix. The cloud-forest patches occur at higher altitudes of about 2000 m asl. The three study species occur in syntopy in East African cloud forests (cf. Bennun *et al.* 1996, Mulwa *et al.* 2007), like on top of the Chyulu Hills in south Kenya. *Zosterops poliogaster* forages in flocks consisting of some dozen individuals, while the two other species dwell solitary or in pairs. Based on these radio-tracking data, we analyse home range sizes, dispersal and site fidelity for the three study species. *Pogonocichla stellata macarthuri* is known to perform seasonal altitudinal movements (Zimmerman *et al.* 1996), and research in the Taita Hills (Kenya) showed that the species even ventures outside of forest (Aben *et al.* 2012, 2014; Mulwa *et al.* 2007). *Zosterops poliogaster* in

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the Chyulu Hills is known as *Z. poliogaster mbuluensis* due to its specific morphology (Zimmermann *et al.* 1996).

We conducted mist-netting during 3-wk in September 2010. The three selected study species were equipped with a LB-2X 0.22 g LTM radio transmitter (Holohil Systems Ltd Transmitters, Ontario, Canada). All captured and understorey birds were in adult plumage; sex of the focal individuals were determined exclusively for *P. stellata macarthuri*. Transmitters were fixed with a wing-loop harness made of natural rubber threads around the birds′ wings following the methods provided by Naef-Daenzer (2007). The wing-loop harnesses fitted to the birds′ body weight (Naef-Daenzer 2007), with 10.8 ± 1.3 g for *Z. poliogaster mbuluensis*, 32.8 ± 3.2 g for *A. milanjensis* and 18.2 ± 2.4 g (mean ± SE) for *P. stellata macarthuri* and thus was below 4–5% of the body weight for the respective bird species (cf. Kenward 2001). Individuals were afterwards released at the same place, except for one individual of *P. stellata macarthuri* which was transferred into the adjoining forest patch prior to release to test for potential site fidelity. In total, we radio-tagged 10 individuals of *Z. poliogaster mbuluensis*, two individuals of *A. milanjensis*, and three individuals of *P. stellata macarthuri*. We used three-element Yagi-antennas (Sirtrack, Havelock North, New Zealand) and AOR AR8200 hand-held receivers (AOR Ltd, Tokyo, Japan). Individuals were located every 10 min via synchronized triangulation by two observers from morning until evening (*c.* 8h00–18h00). To analyse potential differences in daily activity we created the following temporal cohorts: morning (8h00–11h00), midday (11h00–14h00) and afternoon (14h00–18h00). Bird fixes were plotted on a 1:25 000 topographic map using GIS ArcMap 10.0 (1999–2010 ESRI Inc.). Individual home range sizes were calculated by minimum convex polygons with 95% of the locations (MCP95) and fixed kernel estimators with 95% probability level (K95) as well as 50% probability level to determine core areas (K50; Worton 1989, 1995). The ad hoc method was used for estimating the smoothing parameter *h* for bivariate normal kernels per individual. Home ranges were calculated first for single individuals, with ~30 locations covering the entire time span of observation, to reliably estimate home-range sizes (Seaman *et al.* 1999). After analysing the dataset of *Z. poliogaster mbuluensis* by individual, we merged all individuals to one large dataset to calculate home range and movements for the entire flock. This calculation was conducted with the R package *adehabitatHR* (Calenge 2006). Furthermore individual movement distances between consecutive locations were calculated using the R package *adehabitatLT* (Calenge 2006). All calculations were done using R version 3.0.2.

We used linear mixed-effects models (Pinheiro & Bates 2000) with a maximized log-likelihood implemented in the R package *nlme* to analyse differences between movement distances: (1) among the three species; (2) among the three different time cohorts; and (3) for interactions between explanatory parameters. To account for repeated measurements from individuals, the factor bird identity was included as random effect. To achieve a normal error distribution and/or to avoid heteroscedasticity, the movement distances were square root-transformed. Model simplification was done by removing the least significant term of the full model starting with the interaction term and comparing both models using an ANOVA until obtaining the minimal adequate model. Significance of explanatory variables was assessed by calculating the F- and P values of an ANOVA table. Contrasts between time cohorts were investigated by re-ordering factor levels. To analyse movement distance of *P. stellata macarthuri* before and after re-colonizing its home patch, during different day times, as well as interaction terms between both parameters, we used a factorial ANOVA. To achieve normal error distribution, the movement distance was square root-transformed. To get the minimal adequate model, an automatic model simplification was obtained using the step command.

We obtained reliable data for 624 fixes from 10 individuals of *Z. poliogaster mbuluensis*, 188 fixes from two individuals of *A. milanjensis*, and 229 fixes from three individuals of *P. stellata macarthuri*. Time of observation ranged from a minimum of 1 h (WE4) to a maximum 7 d (WE8) (details about the period of observation and the number of fixes per individual are given in Table 1). Home ranges were restricted to one forest patch, with mean sizes (MCP95, K95, K50; ± SE, respectively) as follows: *Z. poliogaster mbuluensis* 2.1 ± 0.2 ha; 4.7 ± 0.3 ha; 1.2 ± 0.1 ha (based on eight individuals with ~30 locations); *A. milanjensis* 2.6 ± 0.4 ha; 4.9 ± 0.1 ha; 1.1 ± 0.1 ha (based on two individuals), and *P. stellata* 1.9 ± 0.5 ha; 4.3 ± 1.0 ha; 1.0 ± 0.3 ha (based on three individuals, including the data of one individual after re-colonizing the home patch; Figure 1). Movement distances per 10 min did not differ significantly among the three species analysed (*Z. poliogaster mbuluensis*: 57.8 ± 1.9, *A. milanjensis*: 56.2 ± 3.2, *P. stellata macarthuri*: 57.3 ± 4.0; variable excluded from the minimal adequate model). Bird individuals for all three species showed highest activities during morning (59.8 ± 1.8 m per 10 min) and midday (60.5 ± 4.8 m per 10 min), but comparatively low activities in the afternoon (43.3 ± 2.8 m per 10 min; $F_{2/892} = 7.02$; $P < 0.001$).

One individual of *P. stellata macarthuri* was released in a neighbouring forest patch. After 2 d, the individual migrated back to its home patch, crossing about 120 m of grassland matrix (Figure 1d). Kernel home range sizes (K95, K50) were larger in the translocated patch compared with the home patch (Table 1: WSR2). However, movement distances per 10 min tended to decrease in the new environment after translocation

Table 1. Basis datasets used for home range and movement pattern analyses for montane white-eye *Zosterops poliogaster mbuluensis*, striped-cheeked mountain greenbul *Andropadus milanjensis* and the white starred robin *Pogonocichla stellata macarthuri.* Given are IDs for each individual, date of collection, number of fixes obtained (*N*) and smoothing parameter (*href*) for Kernel home range estimations. Home ranges sizes (MCP 95, K95) and core range (K50) in ha are given.

ID	First–Last observation	*N*	*href*	MCP95	K95	K50
Zosterops poliogaster mbuluensis						
WE1	18 September	63	21.21	1.21	3.30	0.58
WE2	19–21 September	60	26.28	2.47	5.18	1.40
WE4	19 September	7	–	–	–	–
WE5	19–21 September	73	23.71	1.99	4.20	1.29
WE6	22 September	16	–	–	–	–
WE7	22 September	30	33.13	1.63	5.88	1.46
WE8	22–28 September	144	25.88	2.97	5.62	1.46
WE9	22–26 September	117	22.09	2.68	4.37	0.97
WE10	23–25 September	87	22.48	1.95	4.19	0.99
WE11	23 September	27	29.62	1.72	5.00	1.22
All		624	19.40	3.82	4.69	1.38
Andropadus milanjensis						
GB1	22–28 September	115	23.92	3.02	5.00	1.15
GB2	25–28 September	73	25.23	2.14	4.72	0.95
All		188	–	–	–	
Pogonocichla stellata macarthuri						
WSR1	20–21 September	24/0	20.27	0.94	2.53	0.49
WSR2	20–28 September	34/74	43.45/30.37	2.71/2.34	10.02 /5.97	2.82/1.42
WSR3	24–28 September	97	24.45	2.47	4.49	1.01
All		195				
Total		1041				

(53.7 ± 8.3 m; $F_{1,87} = 3.26$; $P = 0.07$) than in its home patch after moving back (79.7 ± 8.4 m). There was no significant difference in daily activity between the individual observed in the new habitat (translocated) (morning: 52.6 ± 10.5 m, midday: NA, afternoon: 54.4 ± 11.7 m) and the individual being back in its home patch (morning: 80.3 ± 8.4 m, midday: 93.4 ± 23.3 m, afternoon: 42.6 ± 9.2 m; variables excluded from the minimal adequate model).

In addition to our telemetry data from radio-tracking, we observed individuals of *Z. poliogaster mbuluensis* migrating between forest patches. A flock consisting of about 30–40 individuals first moved to the southern edge of our main study patch. Individuals concentrated on a large tree at the edge of the forest, grouped, and crossed the matrix (crossing distance about 120 m) to an adjoining forest patch in the east in a very rapid, straight-line flight on the shortest flight path possible and in close proximity to the ground.

Our data indicate restricted movement behaviour for all three understorey forest bird species. The movements detected and observed are restricted to one single forest patch, in which individuals collect food (mostly along forest edges during morning), and roost during the night. This restricted movement behaviour is in congruence with other studies on the dispersal behaviour of these forest bird species (Borghesio & Laiolo 2004), but also for other forest vertebrates (Moore *et al.* 2008, Smith *et al.* 2011). As long as habitat resources are available, individuals may remain in their home patch, as movement is energy consuming and thus only a positive investment if the new patch provides an improved habitat quality (Robles & Ciudad 2012). Various studies have shown that smaller territories usually indicate higher habitat quality, while reduced habitat quality often leads to larger home ranges (Carey *et al.* 1990, Hansbauer *et al.* 2008). In addition, home-range sizes strongly depend on season most probably as a response on the availability of food resources (Wiktander *et al.* 2001). Furthermore, the behavioural ecology of species might affect the mobility of individuals (Githiru *et al.* 2006). The strong restriction to a specific home patch in our study is underlined by the observed homing behaviour of the translocated individual of *P. stellata macarthuri*. This individual returned to its original patch after 1 d. This behaviour can be explained by either (1) strong site-fidelity, (2) high habitat quality in the original forest patch, or (3) the existence of family structures such as the presence of a nest i.e. fledglings in the original forest patch (however, as the understorey individual showed no brood patch, this third scenario can be excluded).

Our data covers only 3 wk of observation. However, movement behaviour in organisms may differ considerably over the year and in different life-stages. For example, adults are mostly residents, juveniles of the same taxon are assumed to show stronger dispersal behaviour to colonize new, unoccupied habitats (cf. Anders *et al.* 1998). Furthermore, our data represent very small territories, which contradicts other findings on tropical cloud-forest bird species observed in the Usambara

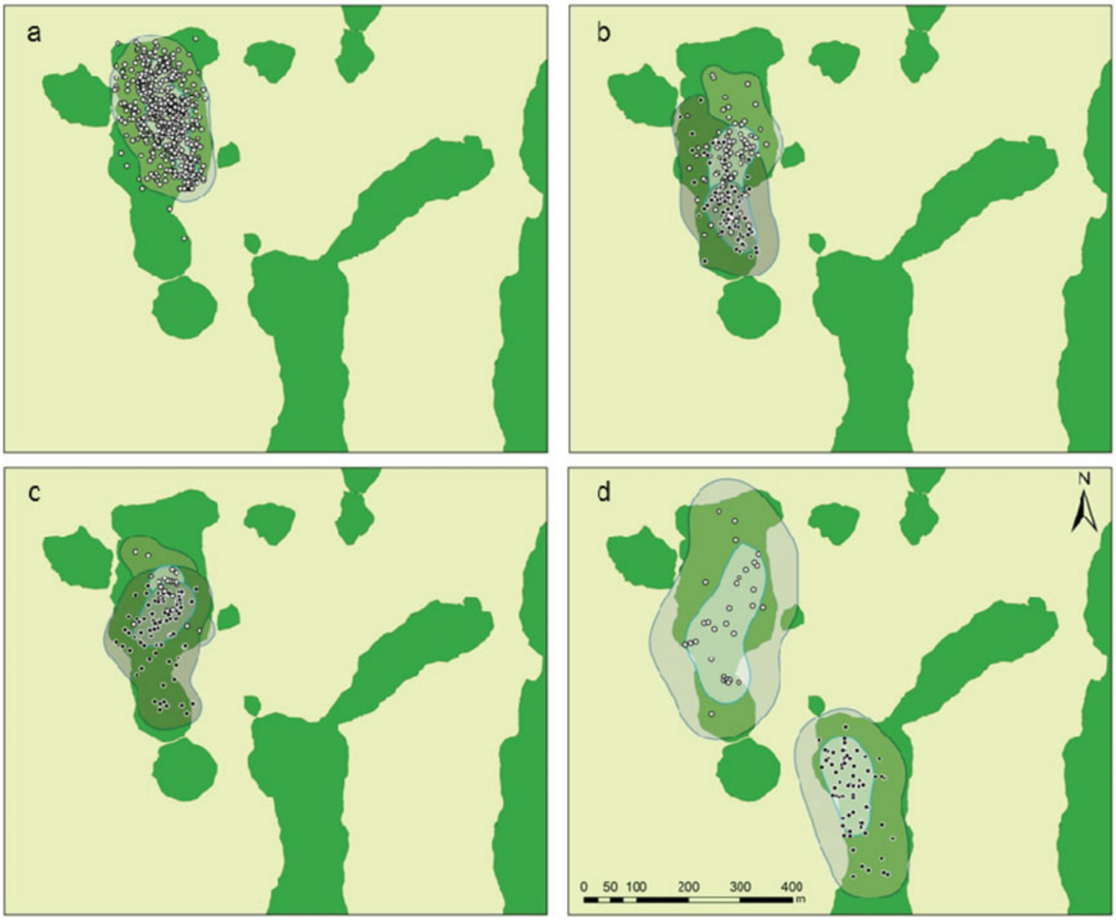

Figure 1. Results obtained from radio-tracking, performed in the forest-grassland mosaic in the Chyulu Hills, south Kenya, shown for the three bird species, montane white-eye *Zosterops poliogaster mbuluensis* (a), striped-cheeked mountain greenbul *Andropadus milanjensis* (b) and white starred robin *Pogonocichla stellata macarthuri* (c). Fixes are shown as white and black dots (for the respective individual), and the 95% Kernels (dark blue line) and the 50% Kernels (light blue line) calculated based on all fixes (for *Z. poliogaster mbuluensis*) and individual-wise (for *A. milanjensis* and *P. stellata macarthuri*). The latter picture (d) indicates the translocation of *P. stellata macarthuri* from the eastern patch into the western patch, and its colonization back to its home-patch. Forest cover is indicated in dark green, grassland is indicated in light green.

Mountains, Tanzania (Newmark *et al.* 2010). However, also in this latter study, most individuals avoided crossing non-forested openings (Newmark *et al.* 2010).

While our short-term ecological data suggest a high site-fidelity of the three study birds, genetic data imply a moderate exchange of individuals, sufficient to equilibrate the genetic structure over local populations, as indicated for *Z. poliogaster mbuluensis* over the Chyulu Hills (Habel *et al.* 2014a, b), as well as for *A. milanjensis* and *P. stellata macarthuri* for the adjoining Taita Hills (Callens *et al.* 2011). Studies showed that only few individuals per generation (as observed for *Z. poliogaster mbuluensis*) are sufficient to balance genetic differentiation (Slatkin 1987). In conclusion, our data have to be interpreted with caution as they were generated (1) during a short period of time, (2) based on adults, i.e. excluding the potentially more mobile juveniles, and (3) without taking various seasonal stages over the year into consideration.

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LITERATURE CITED

ABEN, J., ADRIAENSEN, F., THIJS, K. W., PELLIKKA, P., SILJANDER, M., LENS, L. & MATTHYSEN, E. 2012. Effects of matrix composition and configuration on forest bird movements in a fragmented

Afromontane biodiversity hot spot. *Animal Conservation* 15: 658–668.

ABEN, J., STRUBBE, D., ADRIAENSEN, F., PALMER, S. C. F., TRAVIS, J. M. J., LENS, L. & MATTHYSEN, E. 2014. Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *Journal of Applied Ecology* 51:693–702.

ANDERS, A. D., FAABORG, J. & THOMPSON, F. R. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *The Auk* 115:349–358.

BENNUN, L., DRANZOA, C. & POMEROY, D. 1996. The forest birds of Kenya and Uganda. *Journal of East African Natural History* 85:23–48.

BORGHESIO, L. & LAIOLO, P. 2004. Habitat use and feeding ecology of Kulal White-eye *Zosterops kulalensis*. *Bird Conservation International* 14:11–24.

CALENGE, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516–519.

CALLENS, T., GALBUSERA, P., MATTHYSEN, E., DURAND, E. Y., GITHIRU, M. & LENS, L. 2011. Genetic signature of population fragmentation varies with mobility in seven bird species of a fragmented Kenyan cloud forest. *Molecular Ecology* 20:1829–1844.

CAREY, A. B., REID, J. A. & HORTON, S. P. 1990. Spotted Owl home range and habitat use in Southern Oregon Coast Ranges. *Journal of Wildlife Management* 54:11–17.

DOLMAN, P. M., HINSLEY, S. A., BELLAMY, P. E. & WATTS, K. 2007. Woodland birds in patchy landscapes: the evidence base for strategic networks. *Ibis* 149:146–160.

GITHIRU, M., LENS, L., BENNUN, L. A. & PERRINS, C. 2006. Experimental evidence of “floaters” in two isolated populations of an Afrotropical forest bird. *Ostrich* 77:28–35.

GITHIRU, M., LENS, L. & BENNUN, L. 2007. Ranging behaviour and habitat use by an Afriotropical songbird in a fragmented landscape. *African Journal of Ecology* 45:581–589.

HABEL, J. C., ULRICH, W., PETERS, G., HUSEMANN, M. & LENS, L. 2014a. Lowland panmixia versus highland disjunction: genetic and bioacoustic differentiation in two East African White-eye bird species. *Conservation Genetics* 15:655–664.

HABEL, J. C., MULWA, R. K., GASSERT, F., RÖDDER, D., MEYER, J. & LENS, L. 2014b. Genetic signature of diverging habitat features in the Mountain White-eye *Zosterops poliogaster*. *Heredity* 113:205–214.

HANSBAUER, M. M., STORCH, I., PIMENTEL, R. G. & METZGER, J. P. 2008. Comparative range use by three Atlantic Forest understorey bird species in relation to forest fragmentation. *Journal of Tropical Ecology* 24:291–299.

JELTSCH, F., BONTE, D., PE’ER, G., REINEKING, B., LEIMGRUBER, P., BALKENHOL, N., SCHRÖDER, B., BUCHMANN, C. M., MUELLER, T., BLAUM, N., ZURELL, D., BÖHNING-GAESE, K., WIEGAND, T., ECCARD, J. A., HOFER, H., REEG, J., EGGERS, U. & BAUER, S. 2013. Integrating movement ecology with biodiversity research – exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology* 1:6.

KENWARD, R. 2001. *A manual for wildlife radio tagging*. Academic Press, London. 322 pp.

MOORE, R. P., ROBINSON, W. D., LOVETTE, I. J. & ROBINSON, T. R. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* 11:1–9.

MULWA, R. K., BENNUN, L. A., OGOL, C. P. K. & LENS, L. 2007. Population status and distribution of Taita White-eye *Zosterops silvanus* in the fragmented forests of Taita Hills and Mount Kasigau, Kenya. *Bird Conservation International* 17:141–150.

NAEF-DAENZER, B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology* 38:404–407.

NEWMARK, W. D., MKONGEWA, V. J. & SOBEK, A. D. 2010. Ranging behaviour and habitat selection of terrestrial insectivorous birds in north-east Tanzania: implications for corridor design in Eastern Arc Mountains. *Animal Conservation* 13:474–482.

PINHEIRO, J. C. & BATES, D. M. 2000. *Mixed-effects models in S and S-PLUS*. Springer, New York. 358 pp.

ROBLES, H. & CIUDAD, C. 2012. Influence of habitat quality, population size, patch size, and connectivity on patch-occupancy dynamics of the Middle Spotted Woodpecker. *Conservation Biology* 26:284–293.

SEAMAN, D. E., MILLSPAUGH, J. J., KERNOHAN, B. J., BRUNDIGE, G. C., RAEDEKE, K. J. & GITZEN, R. A. 1999. Effects of sample size on Kernel Home Range Estimates. *Journal of Wildlife Management* 63:739–747.

SLATKIN, M. 1987. Gene flow and the geographic structure of natural populations. *Science* 236:787.

SMITH, M. J., BETTS, M. G., FORBES, G. J., KEHLER, D. G., BOURGEOIS, M. C. & FLEMMING, S. P. 2011. Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landscape Ecology* 26:709–721.

SPANHOVE, T., LEHOUCK, V., BOETS, P. & LENS, L. 2009. Forest fragmentation relaxes natural nest predation in an Afromontane forest. *Animal Conservation* 12:267–275.

WIKTANDER, U., OLSSON, O. & NILSSON, S. G. 2001. Seasonal variation in home-range size, and habitat area requirement of the Lesser Spotted Woodpecker (*Dendrocopos minor*) in southern Sweden. *Biological Conservation* 100:387–395.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168.

WORTON, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794–800.

ZIMMERMANN, D. A., TURNER, D. A. & PERSON, D. J. 1996. *Birds of Kenya and Northern Tanzania*. Christopher Helm, London. 421 pp.