University of Groningen

Common Cuckoo home ranges are larger in the breeding season than in the non-breeding season and in regions of sparse forest cover

Williams, Heather M.; Willemoes, Mikkel; Klaassen, Raymond H. G.; Strandberg, Roine; Thorup, Kasper

[Link to publication in University of Groningen/UMCG research database](Link)

CrossMark

ORIGINAL ARTICLE

Common Cuckoo home ranges are larger in the breeding season than in the non-breeding season and in regions of sparse forest cover

Heather M. Williams[1,2] · Mikkel Willemoes[1] · Raymond H. G. Klaassen[3,4] · Roine Strandberg[3] · Kasper Thorup[1]

Abstract Knowledge of species' habitat requirements can be gained from studying individual variation in home range size, under the assumption that larger home ranges reflect increased resource needs or decreased habitat quality. We used satellite telemetry to delineate home ranges of South Scandinavian Common Cuckoos (*Cuculus canorus*) throughout their annual cycle. Annual stage (breeding or non-breeding period) and percentage of forest cover were good predictors of home range size. Average breeding season home ranges were ten times as large as those of non-breeding home ranges, suggesting strong temporal variation in the birds' resource needs, and perhaps lower habitat quality in the breeding range compared to the African part of their annual range. Furthermore, although the Cuckoos rarely chose a home range with complete forest cover, we found a significant negative relationship between forest cover and home range area. This suggests that heterogeneous landscapes which include some dense forest cover constitute important habitat for Cuckoos, and that the continuing trend of forest loss in tropical Africa could reduce habitat quality for the Cuckoo in the non-breeding season.

Keywords *Cuculus canorus* · Common Cuckoo · Home range · Migration · Forest loss · Satellite telemetry

✉ Heather M. Williams
hmwilliams85@gmail.com

1 Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark

2 Graduate Program in Evolution, Ecology and Behavior, University at Buffalo, 411 Cooke Hall, Buffalo, NY, USA

3 Department of Biology, Lund University, Ecology Building, 22362 Lund, Sweden

4 Dutch Montagu's Harrier Foundation and Animal Ecology Group, Centre for Ecological and Evolutionary Studies, Groningen University, P.O. Box 11103, 9700 CC Groningen, The Netherlands

Zusammenfassung

Die Streifgebiete von Kuckucken sind größer zur Brutzeit als außerhalb und in Regionen mit spärlicher Waldbedeckung

Kenntnisse zu Habitatansprüchen von Arten können durch Untersuchung individueller Variationen in den Reviergrößen erlangt werden unter der Annahme, dass größere Reviere einen gesteigerten Ressourcenbedarf oder eine verringerte Habitatqualität widerspiegeln. Mit Hilfe der Satellitentelemetrie ermittelten wir die 'home ranges' südskandinavischer Kuckucke (*Cuculus canorus*) im Jahresverlauf. Jahresperiode (Brut- oder Nicht-Brutzeit) und der Anteil der Waldbedeckung waren gute Prädiktoren für die Größe von Revieren. Die durchschnittlichen Reviergrößen in der Brutzeit waren zehnmal größer als die Reviere außerhalb der Brutzeit, was auf eine starke zeitliche Variation des Ressourcenbedarfs der Vögel hindeutet und möglicherweise auch auf eine geringere Habitatqualität im Brutgebiet verglichen mit dem afrikanischen Teil ihres Jahreslebensraumes. Darüber hinaus, obwohl die Kuckucke selten ein Revier mit kompletter Waldbedeckung besetzten, fanden wir einen signifikant negativen Zusammenhang zwischen Waldbedeckung und 'home

range'-Fläche. Dies lässt vermuten, dass heterogene Landschaften inklusive einiger dichter Waldbereiche ein wichtiges Habitat für Kuckucke darstellen und dass der anhaltende Trend des Waldverlustes im tropischen Afrika die Habitatqualität für Kuckucke außerhalb der Brutzeit verringern könnte.

Introduction

Populations of sub-Saharan migrant birds have declined over the past 30 years, making them a conservation priority (Sanderson et al. 2006). A recent review highlighted human-induced habitat change as the leading cause of these declines (Vickery et al. 2014). However, our limited knowledge of the resource needs of migrant birds beyond their European breeding grounds is hindering our ability to pinpoint drivers of species decline and to make specific suggestions for more effective conservation policy (Vickery et al. 2014; Heldbjerg and Fox 2010). This study aims to respond to this need by studying the spatial behaviour of South Scandinavian Common Cuckoos (*Cuculus canorus*) (henceforth 'Cuckoos') to better understand what constitutes habitat quality throughout their complete annual range.

Home range size is predicted to correlate with resource availability, with animals occupying the smallest area which meets their resource needs (Harestad and Bunnell 1979). This prediction has been confirmed empirically in many taxa [e.g. Tufto et al. (1996) in Roe Deer (*Capreolus capreolus*); Stenger (1958) in Ovenbirds (*Seiurus aurocapillus*); Holmes (1967) in Dunlin (*Calidris alpine*); Simon (1975) in the Mountain Spiny Lizard (*Sceloporus jarrovi*)]. As resource availability essentially determines habitat quality, home range size is considered predictive of habitat quality. Under this assumption, we use satellite-tracking data of the Common Cuckoo (Willemoes et al. 2014) to test the effect of environmental and biological variables on Cuckoo spatial behaviour throughout their entire annual range.

As Cuckoos are dietary specialists, feeding primarily on forest caterpillars (Payne 2005), we predict a negative relationship between forest cover and home range area. Similarly, as studies have previously found that the Normalised Difference Vegetation Index (NDVI) and precipitation rate correlate with invertebrate abundance (Pettorelli et al. 2011; Frampton et al. 2000; Ockendon et al. 2014), we will test the effect of these parameters on home range, with the expectation of a negative relationship. Home range may also vary due to different individual resource needs. As home range size is known to vary by sex in some avian species (Weaving et al. 2014; Small et al. 2007;

Cardador et al. 2009), we will also test for a gender difference. Finally, we expect Cuckoo spatial behaviour to change during the breeding season, when Cuckoos must not only forage and find shelter but must also locate host species to support their brood parasitic life history. For this reason, we will also test for an effect of annual stage (breeding vs. non-breeding) on home range area.

Methods

Satellite telemetry

This study uses the dataset described by Willemoes et al. (2014) of seven satellite-tracked South Scandinavian Cuckoos (four males, three females). Birds were caught in mist nets and tagged with satellite transmitters (5-g solar PTT-100, Microwave Telemetry, Inc., Columbia, MD, USA) using backpack harnesses. Transmitters functioned on a 10-h on/48-h off duty cycle, with multiple location points sometimes recorded within a single duty cycle. Data were collected between May 2010 and June 2013. Previous analysis of satellite tracks highlighted eight major stationary periods in the Cuckoo annual cycle (breeding area in South Scandinavia, stopover in Central Europe, stopover in South-east Europe, stopover in East Sahel, first wintering area in South-west-central Africa, second wintering area in North-west-central Africa, stopover in West Africa and stopover in Italy), where at least half of the tracked Cuckoos spent a minimum of 5 days (Willemoes et al. 2014).

Calculation of home range areas

The full dataset included Argos location quality classes between 3–0 and A–B, where 3 denotes the highest location accuracy (<250 m), and A and B are of lower quality (Argos 2011). This dataset was pruned by deleting all lower Argos location quality classes (A, B, and 0), leaving the remaining data points accurate to within 1.5 km (Argos 2011). Data points obtained during migration steps between major stop locations were also removed from the data set. Latitude and longitude were plotted over time to manually determine home ranges as a series of points showing relative locational stability and a lack of directionality. Home ranges consisting of fewer than ten points were removed from the analysis, as were home ranges with a minimum duration of less than 48 h. Finally, a small number of data points (<5 %) were deleted due to a lack of corresponding environmental data. Unfortunately, this process left insufficient data to analyse home ranges from Central Europe, South-east Europe or Italy. Data pruning resulted in a remaining dataset of 74 home ranges spread

between the South Scandinavian breeding range and four stopover locations in the non-breeding range (East Sahel, South-west-central Africa, North-west-central Africa and West Africa), each with between 10 and 115 data points (Table S1).

We defined three different home range area estimates—100 % minimum convex polygon (MCP100), kernel density 95 % utilisation (KD95), and kernel density 50 % utilisation (KD50)—using the adehabitatHR package (Calenge 2006). As a least-squares cross-validation function did not converge on an error, we used the ad hoc method to estimate the smoothing parameter for each kernel density estimate (Worton 1989). We also calculated the average distance between points and the MCP100 centre of mass (DCoM) using the SDMTools package (VanDerWal et al. 2014). The use of multiple measures of home range area provides an opportunity to check the robustness of models across each methodology and to assess how predictor variables affect core-range (KD50) and full-range (KD95 and MCP100) spatial behaviours differently.

Home ranges (MCP100) from each major stop location were overlaid with maps showing land cover categories (Global Land Cover 2000 database 2003). The area of each land cover category was calculated per home range, then summed within each major stop region (Table S2), to provide a quantification of changes in land cover over the Cuckoo's migration. Home ranges from each major stop location were also plotted in Google Earth (v. 7.1.2.2041) and visually examined to assess changes in habitat type and structure (Fig. S1a–f).

R version 3.1.2 software (R Core Team 2014) was used in all analyses, and Pearson's r was used in all correlation tests.

Explanatory variables

Six explanatory variables were selected following a priori hypotheses (Table 1). All possible pairs of these parameters were tested for collinearity, but as all combinations showed only weak correlations ($|r| < 0.3$, $n = 74$, $p > 0.05$), all parameters were retained for further analysis.

Argos location quality was found to be significantly correlated with home range size, with higher-quality data consistently resulting in smaller home range estimates in both the breeding and non-breeding seasons and across all home range metrics (Fig. S2a) (Argos location quality—MCP100 $r = -0.62$, $n = 74$, $p < 0.001$; KD95 $r = -0.68$, $n = 74$, $p < 0.001$; KD50 $r = -0.68$, $n = 74$, $p < 0.001$; DCoM $r = -0.75$, $n = 74$, $p < 0.001$). Similarly, a significant correlation was found between sample size and MCP100 home range measures, in which a larger sample size was linked with a larger home range area

(Sample size—MCP100 $r = 0.46$, $n = 74$, $p < 0.001$; KD95 $r = 0.20$, $n = 74$, $p = 0.084$; KD50 $r = -0.12$, $n = 74$, $p = 0.283$; DCoM $r = 0.22$, $n = 74$, $p = 0.053$) (Fig. S2b). Argos location quality and sample size were thus included as nuisance parameters in all models.

To rule out the possibility that the nuisance parameters interacted with the other explanatory variables in an unforeseen way, the full dataset was randomly sampled to produce a secondary dataset of 62 home ranges of equal sample size ($n = 15$) and equal average Argos location score (2). As the two datasets produced qualitatively similar results (Table S3), analysis was based on the full dataset due to its larger sample size and lack of repeated points.

Model fitting

As the dataset included repeated measures for some of the individuals, data were analysed using a general linear mixed model (GLMM) with ID as a random intercept. Response variables were log-transformed (natural logarithm) to improve their adherence to the normal distribution.

All possible subsets of the explanatory variables in Table 1 and the four interaction terms between annual stage and NDVI, precipitation rate, forest cover and sex were fitted to the data and ranked with AICc (second-order Akaike information criterion) using the lme4 (Bates et al. 2014) and MuMIn (Barton 2014) packages. AICc is a suitable measurement for this analysis, as it ranks the fit of multiple models whilst including penalties for use of additional parameters and low sample size relative to parameter number (Burnham and Anderson 2002). The nuisance parameters 'Argos location quality' and 'Sample size' were included in all models to reduce the potential for bias, and a null model was evaluated which considered only the effect of Argos location quality, sample size and Cuckoo ID. Averaging of all subset models was used to produce a ranking of the relative importance of parameters independent of Argos location quality and sample size (Table 2).

This process was repeated with breeding season data excluded to check for an effect of major stop region (East Sahel, South-west-central Africa, North-west-central Africa or West Africa) within the African non-breeding season (Table S4). As major stop region was not a well-supported parameter in this model, the non-breeding season data were grouped for all subsequent analyses.

Inference from the sum of weights can be misleading, as even predictor variables totally uncorrelated to the response variable can assume a wide distribution of expected values (Galipaud et al. 2014). To aid inference, a baseline sum-of-weights distribution for each predictor

Table 1 Definitions of parameters tested in analysis

Parameter	Data description	Data source	Prediction
Annual stage	Either 'breeding' (in South Scandinavia) or 'non-breeding' (in E. Sahel, South-west-central Africa, North-west-central Africa or West Africa)	Willemoes et al. (2014)	Larger breeding than non-breeding home ranges
NDVI	Normalised Difference Vegetation Index (NDVI) of each occurrence point, averaged per home range	TERRA MODIS 16-day (NASA LP DAAC)	Higher NDVI results in smaller home ranges
Precipitation rate	Maximum precipitation rate ($kg/m^2/s$) at occurrence points per home range	NCEP Reanalysis dataset (Kalnay et al. 1996; Kemp et al. 2012)	Higher precipitation rate results in smaller home ranges
Forest cover	Percentage of tree cover (vegetation >5 m height) for each occurrence point, averaged per home range	Global Forest Watch (Hansen et al. 2013)	Greater forest cover results in smaller home ranges
Sex	Cuckoo gender	Willemoes et al. (2014)	
ID	Individual Cuckoo identity	Willemoes et al. (2014)	Included in all models as a random factor
Sample size	Number of occurrence points per home range		
Argos quality	Mean Argos location quality score per home range ('3' is accurate to within 250 m, '2' to within 500 m and '1' to within 1.5 km)	Argos User's Manual, Argos (2011)	

variable was calculated from 1000 random permutations of the kernel density 95 % utilisation estimates (Fig. S3). Where the distribution of baseline mean sum of weights is wide-ranging (or has a relatively high median value), interpretation of the GLMM sum of weights should be treated with caution (Galipaud et al. 2014). As the randomised permutation test showed a moderate spread of possible sums of weights with a median value of up to 0.30 (Fig. S3), predictors with a relative importance of less than 0.5 were not interpreted so as to maintain a conservative analysis.

Marginal and conditional R^2 statistics were then calculated for each model with a ΔAICc <4 as an indicator of goodness of fit (Nakagawa and Schielzeth 2013), and an overall weighted average marginal R^2 was calculated by adjusting individual model R^2 statistics by their AICc weights. Best models (ΔAICc <4) resulted in a GLMM explaining up to 86 % of home range size variation [Average weighted marginal R^2 DCoM = 0.795; MCP100 = 0.861; KD95 = 0.779; KD50 = 0.790 (Table 3, Table S5)]. Parameter estimates and their standard errors were obtained for all variables with a relative importance greater than 0.5 and for the nuisance parameters (Table 4).

Results

Averaging of all subset models found strong support for a relationship between home range size and annual stage (relative parameter importance of 1 in all home range

metrics) and moderate support for a relationship with forest cover (relative parameter importance of between 0.59 and 0.97 in all home range metrics) after accounting for the effect of Argos location quality and sample size (Table 2). The null model was not amongst the best-supported models for any of the home range metrics (Table S5).

Mean home range area in the breeding season is approximately ten times as large as that in the non-breeding season for both male and female Cuckoos (Breeding season mean home range area = 135 ± 70 km^2; Non-breeding season mean home range area = 12 ± 8 km^2) (Fig. 1; Table S6), and home range area decreases as forest cover increases (Fig. 2). This relationship between forest and home range size is consistent between the breeding and non-breeding seasons. Negative trends were also consistent within each of the four individual non-breeding major stops, but reached statistical significance only in North-west-central Africa (KD95—East Sahel $r = -0.437$, $n = 19$, $p = 0.06$; South-west-central Africa $r = -0.335$, $n = 31$, $p = 0.07$; North-west-central Africa $r = -0.816$, $n = 6$, $p = 0.05$; West Africa $r = -0.326$, $n = 7$, $p = 0.48$).

As expected with a study of such large spatial scale, there were significant differences in land cover among the major stop regions (Fig. S1a–f). The breeding region was dominated by cultivation and artificial surfaces, and East Sahel was characterised as a mosaic of cropland, shrubs and grasses. South-west-central Africa and North-west-central Africa were both relatively forested, whereas West Africa was relatively diverse in its land

Table 2 Relative importance of parameters represented in GLMM after accounting for the effect of Argos location quality and sample size

	Annual stage	Forest	Sex	Precipitation	NDVI	Forest*annual stage	Sex*annual stage	NDVI*annual stage	Precipitation*annual stage
DCoM	1 (Br > NBr)	0.6 (−)	0.38 (M > F)	0.3 (−)	0.03 (+)	0.28	0.12	0.1	0.07
MCP100	1 (Br > NBr)	0.97 (−)	0.28 (M > F)	0.28 (+)	0.33 (+)	0.74	0.06	0.08	0.08
KD95	1 (Br > NBr)	0.76 (−)	0.3 (M > F)	0.27 (−)	0.31 (+)	0.36	0.08	0.09	0.06
KD50	1 (Br > NBr)	0.59 (−)	0.4 (M > F)	0.33 (−)	0.30 (+)	0.24	0.16	0.1	0.08

Direction of effect is shown in brackets

Br breeding season, *NBr* non-breeding season, *M* males, *F* females

* Denotes an interaction term

cover, with forested areas, crops, shrubs and grasses (Table S2).

Discussion

We found a strong effect of annual stage on home range, with breeding season home ranges being, on average, ten times larger than in the non-breeding season. This could suggest seasonal variation in the Cuckoos' resource needs, with larger areas required during the breeding season. Although larger home ranges in breeding birds have been demonstrated in previous studies (e.g. Anich et al. 2010; Stenger 1958), these increases were linked to the increased energy requirements associated with the incubation and feeding of young—factors that do not apply to the Cuckoo as an obligate brood parasite. Rather, it is likely that the breeding season home ranges for the Cuckoo are larger because they must encompass both forested areas for foraging *and* reed-bed/open areas for access to hosts, in this region primarily Reed Warblers (*Acrocephalus scirpaceus*), but also Meadow Pipits (*Anthus pratensis*) and Dunnocks (*Prunella modularis*). The use of two distinct habitats during the breeding season has previously been described in the Common Cuckoo, where individual home ranges were structured into areas for reproductive behaviours and for feeding/roosting behaviours (Vogl et al. 2004; Nakamura et al. 2005). Furthermore, the breeding home range areas calculated here are very large in comparison to other similarly sized (partially or completely) insectivorous species such as the Green Woodpecker (*Picus viridis*) (Rolstad et al. 2000) or Song Thrush (*Turdus philomelos*) (Peach et al. 2004). As the Cuckoo is known to lay up to 25 eggs per season (Payne 2005), the female's breeding home ranges should ideally be large enough to encompass sufficient host territories that they can lay just one egg per host nest, in temporal synchrony with the female hosts' own laying schedules (Moskàt et al. 2006). A wide-ranging 'searching' habit needed to support this strategy could explain the very large home ranges observed here, at least for female Cuckoos. Those in male Cuckoos may be explained by the need for their territories to encompass at least part of several female territories.

Alternatively, the larger home ranges in the breeding season could reflect lower habitat quality and resource density relative to that in the non-breeding season. We found substantial variation in land cover between the breeding and non-breeding regions, and the ecology and productivity of a tropical forest in the African wintering grounds is clearly different from that of a human-managed temperate woodland in the breeding zone. Indeed, habitat type is known to affect home range area in other avian

Table 3 Full data GLMM models with ΔAICc <4 for KD95

Model parameters	df	Δ AICc	AICc weight	R^2 marginal	R^2 conditional
Kernel density 95 % utilisation					
Forest + annual stage	7	0	0.136	0.778	0.778
Forest + annual stage + forest*annual stage	8	0.190	0.124	0.785	0.785
Annual stage	6	0.965	0.084	0.768	0.768
Forest + annual stage + NDVI	8	2.002	0.050	0.780	0.780
Forest − annual stage + sex	8	2.225	0.045	0.779	0.779
Forest + annual stage + sex + forest*annual stage	9	2.263	0.044	0.787	0.787
Forest + annual stage + NDVI + forest*annual stage	9	2.290	0.043	0.787	0.787
Forest + annual stage + precipitation	8	2.449	0.040	0.779	0.779
Forest + annual stage + precipitation + forest*annual stage	9	2.786	0.034	0.785	0.785
Annual stage + precipitation	7	3.237	0.027	0.768	0.768
Annual stage + sex	7	3.239	0.027	0.768	0.768
Annual stage + NDVI	7	3.386	0.025	0.768	0.768
Forest + annual stage + NDVI + annual stage*NDVI	9	3.708	0.021	0.783	0.783
Weighted average marginal R^2	0.779				

Annual stage = breeding or non-breeding. In addition to listed model parameters, all models include the effect of sample size and Argos location quality and ID as a random factor

* Denotes an interaction term

Table 4 Full model averaged parameter estimates with shrinkage

	Intercept	Annual stage	Forest	Argos	Sample
DCoM	9.96 (0.84)	−0.91 (0.44)	−0.01 (0.01)	−0.80 (0.15)	0.00 (0.00)
MCP100	22.02 (1.58)	−2.24 (0.84)	−0.06 (0.04)	−1.60 (0.33)	0.04 (0.00)
KD95	22.70 (1.61)	−1.77 (0.85)	−0.02 (0.03)	−1.60 (0.33)	0.01 (0.00)
KD50	21.08 (1.73)	−1.73 (0.90)	−0.01 (0.02)	−1.60 (0.29)	0.00 (0.00)

Standard error is shown in parentheses. Only parameters that were well supported by AIC rankings are shown

species (e.g. Cardador et al. 2009). We do, however, consider it very unlikely that a habitat quality difference alone could cause the tenfold increase in home range area between the non-breeding and breeding seasons that we observed here.

This study also demonstrated a negative relationship between forest cover and home range area which is consistent between the breeding and non-breeding regions. The Cuckoo is a dietary specialist, feeding on hairy caterpillars in woodland (Payne 2005). As such, areas of high forest cover provide increased density of food resources, allowing Cuckoos to be supported by a smaller home range. Increased forest cover is also considered to improve avian habitat quality because of decreased predation risk in dense cover (Anich et al. 2010). Therefore, the availability of dense forest cover in the home range may reduce the need for nightly movement to other areas for protected roosting opportunities. However, even in the highly forested winter

range, the Cuckoos rarely select a home range with complete forest cover, pointing to a possible preference for a semi-open landscape. These two observations (high forest cover indicating high habitat quality and potential avoidance of complete forest cover) could be reconciled by considering the Cuckoo as a possible forest edge specialist. A high percentage of forest cover within a heterogeneous landscape will most likely lead to a large amount of forest edge. Thus, we may consider dense forest with a mosaic of open patches to be the highest-quality habitat for the Cuckoo.

Although we consider the decline in home range size with increased percentage of forest cover to indicate that forest cover is a good predictor of habitat quality, we are unable to completely exclude other possible explanations. In the breeding season, varying host density could cause the observed negative correlation between home range size and forest cover. At lower host density, the
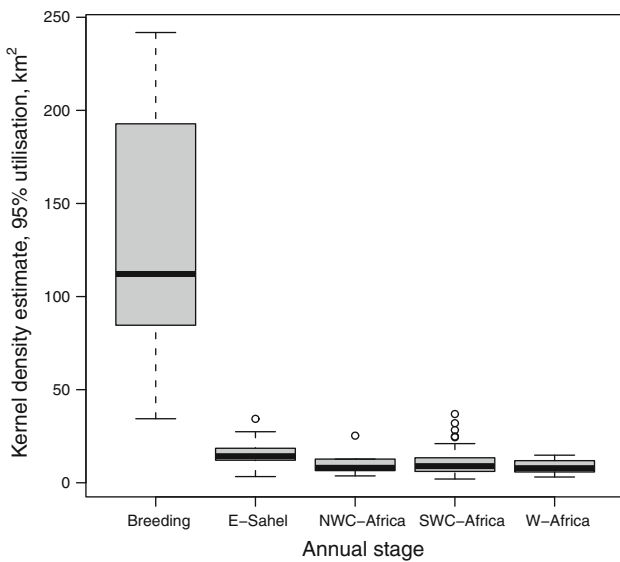
Fig. 1 Home range sizes (shown here by kernel density 95 % utilisation) by major stop location

proportion of the relatively open habitat of the hosts should increase within the home range, thus 'diluting' the percentage of forest cover. In the non-breeding season, we cannot exclude the possible effect of changing habitat type between different major stop regions on home range area. These regions do have different levels of forest cover, and it is possible that other (unmeasured) parameters could both cause this pattern with forest cover and independently affect habitat

quality. However, of the parameters we considered likely to explain habitat quality, percentage of forest cover was the only one that varied accordingly. Furthermore, correlations between forest cover and home range size within each major stop region showed consistently negative trends, although these do not always reach statistical significance in our limited dataset. Finer-scale comparison of habitat types within each major stop region may help to confirm this finding.

Between 1980 and 2009, populations of Common Cuckoos in Europe declined by over 20 % (Vickery et al. 2014). This study has indicated different resource needs and spatial behaviour in the Cuckoo between the breeding and non-breeding ranges, implying the need for a dual-aspect conservation strategy. In the breeding season, the species' success depends on easy access to both its hosts and to woodland for foraging and cover. Ensuring connectivity of these habitats and minimising urban fragmentation could reduce commuting distance and, thus, energy cost for the Cuckoo in the breeding season. Meanwhile, deforestation is continuing at an alarming rate in West and Central Africa (the Cuckoo's main wintering regions), with a net forest loss of 0.49 % per year between 2000 and 2010 (FAO 2010). As relatively dense forest cover constitutes high habitat quality for the Cuckoo, the species appears to be one of the many at risk from human-induced habitat change in the non-breeding range (Vickery et al. 2014). Conservation measures for the Cuckoo should include maintaining relatively high forest cover density in its known migratory stopover sites.
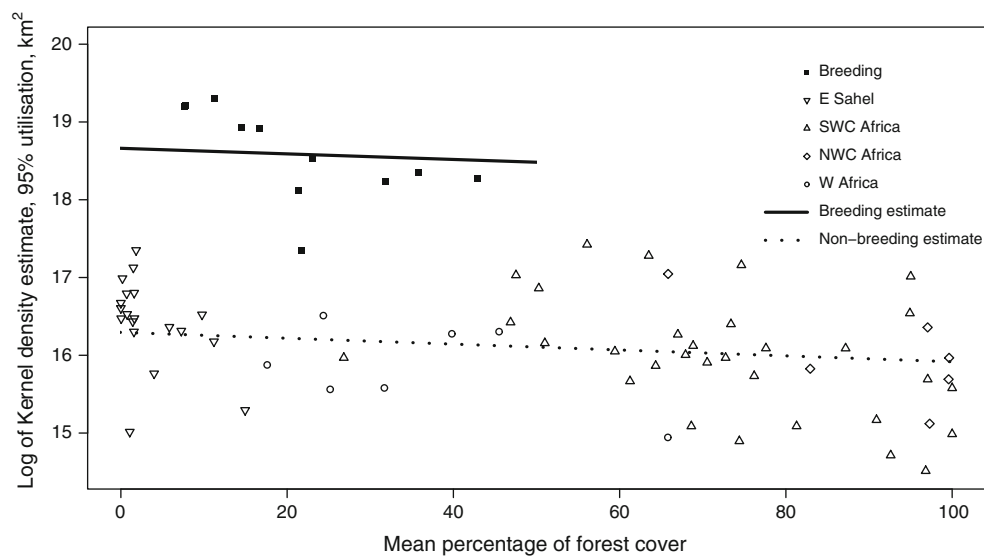

Fig. 2 Relationship between home range area (measured here by kernel density 95 % utilisation) and mean home range percentage of forest cover. *Trendlines* show model predictions of the effect of forest cover from the best-supported model (Annual stage + Forest cover + Argos + Sample)

References

Anich NM, Benson TJ, Bednarz JC (2010) Factors influencing home-range size of Swainson's Warblers in Eastern Arkansas. Condor 112:149–158

Argos (2011) Argos User's Manual. http://www.argos-system.org/web/en/76-user-s-manual.php. Accessed 29 May 2015

Bartoń K (2014) MuMIn: Multi-model inference. R package version 1.10.0. http://CRAN.R-project.org/package=MuMIn. Accessed 29 May 2015

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4. Accessed 29 May 2015

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol Model 197:516–519

Cardador L, Manosa S, Varea A, Bertolero A (2009) Ranging behaviour of Marsh Harriers *Circus aeruginosus* in agricultural landscapes. Ibis 151:766–770

FAO (2010) Global forest resources assessment, main report, 2010. FAO Forestry Paper 163

Frampton GK, Van Den Brink PJ, Gould PJL (2000) Effects of spring drought and irrigation on farmland arthropods in Southern Britain. J Appl Ecol 37:865–883

Galipaud M, Gillingham MAF, David M, Dechaume-Moncharmont FX (2014) Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. Methods Ecol Evol 5:983–991

Global Land Cover 2000 database (2003). European Commission, Joint Research Centre. http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php. Accessed 29 May 2015

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend LRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Harestad AS, Bunnell FL (1979) Home range and body weight—a re-evaluation. Ecology 60:389–402

Heldbjerg H, Fox T (2010) Long-term population declines in Danish trans-Saharan migrant birds: capsule Long-distance migrant birds show less favourable trends than sedentary/short-distance species. Bird Study 55:267–279

Holmes RT (1967) Differences in population density, territoriality, and food supply of Dunlin on arctic and subarctic tundra. In: Watson A (ed) Animal populations in relation to their food resources: A symposium of the British Ecological Society. Blackwell, Oxford and Edinburgh, pp 303–319

Kalnay E, Kanamitsu M, Kistler R, Collins W, Deaven D, Gandin L, Iredell M, Saha S, White G, Woollen J, Zhu Y, Leetmaa A, Reynolds R, Chelliah M, Ebisuzaki W, Higgins W, Janowiak J, Mo KC, Ropelewski C, Wang J, Jenne R, Joseph D (1996) The NCEP/NCAR 40-year reanalysis project. Bull Amer Meteor Soc 77:437–470

Kemp MU, van Loon EE, Shamoun-Baranes J, Bouten W (2012) RNCEP: global weather and climate data at your fingertips. Methods Ecol Evol 3:65–70

Moskàt C, Barta Z, Haber ME, Honza M (2006) High synchrony of egg laying in Common Cuckoos (*Cuculus canorus*) and their great reed warbler (*Acrocephalus arundinaceus*) hosts. Ethol Ecol Evolut 18:159–167

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Nakamura H, Miyazawa Y, Kashiwagi K (2005) Behaviour of radio-tracked Common Cuckoo females during the breeding season in Japan. Ornithol Sci 4:31–41

NASA Land Processes Distributed Active Archive Center (LP DAAC). MODIS/Terra Vegetation Indices 16-Day L3 Global 1 km SIN Grid. http://reverb.echo.nasa.gov. Accessed 29 May 2015

Ockendon N, Johnston A, Baillie SR (2014) Rainfall on wintering grounds affects population change in many species of Afro-Palaearctic migrants. J Ornithol 155:905–917

Payne RD (2005) The Cuckoos. Oxford University, Oxford, p 515

Peach WJ, Denny M, Cotton PA, Hill IF, Gruar D, Barritt D, Impey A, Mallord J (2004) Habitat selection by song thrushes in stable and declining farmland populations. J Appl Ecol 41:275–293

Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewsja B, Lima M, Kausrud K (2011) The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. Clim Res 46:25–27

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. Accessed 29 May 2015

Rolstad J, Løken B, Rolstad E (2000) Habitat selection as a hierarchical spatial process: the green woodpecker at the northern edge of its distribution range. Oecologia 124:116–129

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, Van Bommel FP (2006) Long-term population declines in Afro-Palearctic migrant birds. Biol Conserv 131:93–105

Simon CA (1975) The influence of food availability on territory size in the Iguanid lizard *Sclerroporus jerrovi*. Ecology 56:993–998

Small MF, Taylor ES, Baccus JT, Schaefer CL, Simpson TR, Robertson JA (2007) Nesting home range and movements of an urban white-winged dove population. Wilson J Ornithol 119:467–471

Stenger J (1958) Food habits and available food of Ovenbirds in relation to territory size. Auk 75:335–346

Tufto J, Andersen R, Linnell J (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. J Anim Ecol 65:715–724

VanDerWal J, Falconi L, Januchowski J, Shoo L, Storlie C (2014) SDMTools: species distribution modelling tools: tools for processing data associated with species distribution modelling exercises. R package version 1.1-20. http://CRAN.R-project.org/package=SDMTools. Accessed 29 May 2015

Vickery JA, Ewing SR, Smith KW, Pain DJ, Bairlein F, Skorpilova J, Gregory RD, Fox T (2014) The decline of afro-palearctic migrants and an assessment of potential causes. Ibis 156:1–22

Vogl W, Taborsky B, Taborsky M, Teuschl Y, Honza M (2004) Habitat and space use of European Cuckoo females during the egg laying period. Behaviour 141:881–898

Weaving MJ, White JG, Hower K, Isaac B, Cooke R (2014) Sex-biased space-use response to urbanization in an endemic urban adapter. Landsc Urban Plan 130:73–80

Willemoes M, Strandberg R, Klassen RHG, Tøttrup AP, Vardanis Y, Howey PW, Thorup K, Mikelski M, Alerstam T (2014) Narrow-front loop migration in a population of the Common Cuckoo as revealed by satellite telemetry. PLoS One 9(1):e83515. doi:10.1371/journal.pone.0083515

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168