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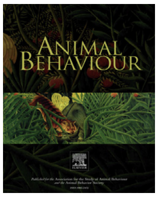

Drivers of home range characteristics across spatiotemporal scales in a Neotropical primate, *Cebus capucinus*

Fernando A. Campos [a,b,*], Mackenzie L. Bergstrom [a], Andrew Childers [c], Jeremy D. Hogan [a], Katharine M. Jack [c], Amanda D. Melin [a,d], Krisztina N. Mosdossy [a], Monica S. Myers [a], Nigel A. Parr [a], Elizabeth Sargeant [a], Valérie A. M. Schoof [c,e], Linda M. Fedigan [a]

[a] *Department of Anthropology, University of Calgary, Calgary, AB, Canada*
[b] *Department of Integrated Biosciences, University of Tokyo, Tokyo, Japan*
[c] *Department of Anthropology, Tulane University, New Orleans, LA, U.S.A.*
[d] *Department of Anthropology, Washington University, St Louis, MO, U.S.A.*
[e] *Department of Anthropology, McGill University, Montreal, QC, Canada*

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The factors that drive within-species variation in animal space use remain poorly understood. A growing body of evidence suggests that both home range attributes and biological interpretations of the home range may depend fundamentally on the scale of analysis. We utilize a multiscale mixed effects modelling framework to examine how seasonal fluctuations in climate, food resource abundance and group mass affect variance in home range area and the maturity stage of forest used by a group-living Neotropical primate, the white-faced capuchin, *Cebus capucinus*. Using an 8-year data set representing over 20 000 contact hours, we estimated home ranges for seven social groups at four nested temporal scales and three nested spatial scales using a movement-based kernel method. Group mass was consistently the most important predictor of home range size in our models, and its effects were relatively insensitive to spatial or temporal scale. Mean daily maximum temperature was an influential factor in shaping monthly range area and composition, with hotter weather favouring smaller home range size and increased use of mature evergreen forest. Greater fruit availability was also associated with smaller monthly range area. The effects of temperature and fruit availability were both scale dependent: the impact of both variables was greatest on the core zone. The different study groups showed marked variation in the habitat composition of their home ranges, but in all groups, higher-use zones consisted of older, more evergreen forest. Our study illustrates the complex ecological processes that affect movement behaviour in a Neotropical primate across a range of spatial and temporal scales, highlighting the importance of group mass, climatic seasonality, landscape heterogeneity and dietary shifts in shaping the home range.

Recent technological and analytical advances have stimulated a renewed interest in understanding the factors that drive variation in animal home ranges (Börger, Dalziel, & Fryxell, 2008; Fryxell et al., 2008; Kie et al., 2010; Smouse et al., 2010). Improvements in GPS technology (Cagnacci, Boitani, Powell, & Boyce, 2010; Tomkiewicz, Fuller, Kie, & Bates, 2010) coupled with new home range estimation methods that explicitly account for autocorrelation in temporally dense location data (Benhamou, 2011; Benhamou & Cornélis, 2010; Downs, Horner, & Tucker, 2011; Horne, Garton, Krone, & Lewis, 2007; Kranstauber, Kays, LaPoint, Wikelski, & Safi, 2012; Long & Nelson, 2012; Lyons, Turner, & Getz, 2013; Steiniger & Hunter, 2013) enable researchers to examine the spatiotemporal dynamics of home ranges with unprecedented precision and detail (Kie et al., 2010). Broad between-species variation in space use patterns are largely explained by body size and trophic level (Harestad & Bunnell, 1979; Jetz, Carbone, Fulford, & Brown, 2004; Kelt & Van Vuren, 2001; Lindstedt, Miller, & Buskirk, 1986; Pearce, Carbone, Cowlishaw, & Isaac, 2013), but the factors that drive within-species variation in space use remain poorly understood and may change depending on the spatial and temporal scales of analysis (Börger et al., 2006). This topic is particularly important for animals living in environments with high spatial and temporal variability because they may face pronounced intra-annual fluctuations in food and water

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* Correspondence: F. A. Campos, Department of Anthropology, University of Calgary, 2500 University Drive NW, Calgary, AB T2N1N4, Canada.
E-mail address: facampos@ucalgary.ca (F. A. Campos).

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availability, thermal stress, and vegetation characteristics (Morellet et al., 2013; Naidoo et al., 2012; Rivrud, Loe, & Mysterud, 2010). The insights gained from such studies can be used to build a vital knowledge base for predicting how animals will respond behaviourally to a variety of disturbance and climate change scenarios.

Understanding the drivers of variation in home range characteristics remains a fundamental question in behavioural ecology (Börger et al., 2008). Multi-individual, multiscale approaches have made significant progress toward understanding the spatiotemporal dynamics of home ranges in several ungulate species (van Beest, Rivrud, Loe, Milner, & Mysterud, 2011; Börger et al., 2006; Morellet et al., 2013; Naidoo et al., 2012; Rivrud et al., 2010), but this analytical framework has only rarely been applied to other animal taxa. Among nonhuman primates, such approaches have provided insights into the factors that influence home range overlap (Markham, Guttal, Alberts, & Altmann, 2013) and daily path length (Pebsworth, MacIntosh, Morgan, & Huffman, 2012) in African savanna-dwelling baboons (*Papio* spp.) and core areas in Neotropical spider monkeys (*Ateles geoffroyi*) (Asensio, Schaffner, & Aureli, 2012). We use a mixed effects modelling approach to explore space use patterns in an arboreal Neotropical primate living in an acutely seasonal tropical dry forest, which is one of the world's most imperilled ecosystems (Portillo-Quintero & Sánchez-Azofeifa, 2010). We frame our research questions and analytical methods around three prominent ecological processes that characterize the study system: strong climatic seasonality, landscape heterogeneity comprising a wide forest age gradient and temporal fluctuations in food resource availability. Our objectives are to characterize the home ranges of white-faced capuchins, *Cebus capucinus*, and to determine which factors are associated with variance in home range attributes. We focus specifically on home range area and the maturity stage of the forest utilized. By analysing the same data set from a range of commonly used spatial and temporal scales, we also aimed to determine how varying definitions of the home range may alter biological inferences about space use behaviour.

Predictions

In many primate species, larger groups tend to have larger home ranges than smaller groups (Clutton-Brock & Harvey, 1977; Di Bitetti, 2001; Dietz, Peres, & Pinder, 1997; Ganas & Robbins, 2005; Isbell, 1991; Janson & Goldsmith, 1995; van Schaik & van Noordwijk, 1989). This pattern can be understood as an extension of the allometric scaling relationship between home range area and body mass among primates (Pearce et al., 2013). These studies support the hypothesis that, all else being equal, individuals in larger groups will need to travel farther and expend more energy to meet their food requirements because of greater within-group feeding competition (Janson & Goldsmith, 1995). Thus, we predicted that home range size would increase with group mass, irrespective of spatial or temporal scale. In addition, we predicted that larger groups would occupy home ranges consisting of more mature evergreen forest, which have greater diversity and density of fruit trees (Asensio, Lusseau, Schaffner, & Aureli, 2012) as well as greater overall fruit biomass (Sorensen & Fedigan, 2000), because of the greater resource-holding potential of larger groups and their greater overall success in between-group competition (Childers, 2008; Crofoot & Gilby, 2012; Crofoot, Gilby, Wikelski, & Kays, 2008).

Second, weather and other climatic factors are key drivers of home range size in many animals (Morellet et al., 2013; Rivrud et al., 2010). Capuchins at our study site reduce activity levels and increase their use of areas that contain permanent water sources as the hot dry season intensifies (Campos & Fedigan, 2009). The effects of this behavioural adjustment on home range size are unclear: the animals could maintain smaller home ranges to conserve water or energy, or they could compensate for lost foraging time by moving more quickly over similarly sized areas during cooler times of day. If white-faced capuchins follow the former strategy, we predicted that hotter, dryer conditions would be associated with smaller home range size, and that this effect would be manifested more clearly for high-use zones because of long resting periods. Alternatively, if capuchins follow the latter strategy, with rapid compensatory foraging excursions, then we predicted that total home range size would not be affected by climatic conditions. In either case, we predicted that hotter, dryer conditions would lead to increased use of mature evergreen forest, which provides shade and cooler microhabitats (Chapman, 1988).

Third, many animals adjust their ranging behaviour based on temporal variation in available food resources (reviewed by Hemingway & Bynum, 2005, for the order Primates; Asensio, Korstjens, & Aureli, 2009). During seasonal food scarcity, animals may pursue different coping strategies, some of which manifest effects on home range size (Brockman & van Schaik, 2005; van Schaik, Terborgh, & Wright, 1993). Previous studies have found that capuchin monkeys (*Cebus* and *Sapajus* spp.) use a habitat-shifting strategy to cope with seasonal food scarcity (Di Bitetti, 2001; Peres, 1994; Terborgh, 1983), with concomitant increases in home range size (Peres, 1994). This occurs when the animals increase foraging effort to maintain a high level of food intake, which usually requires moving farther and over a larger area. Thus, we predicted that decreasing food abundance would be associated with larger home range size, and that these effects would be most evident for relatively low-use (noncore) home range zones.

METHODS

Study Site

We carried out this study in the Área de Conservación Guanacaste (ACG), a UNESCO World Heritage Site in northwestern Costa Rica. Our study was confined to the ACG's Sector Santa Rosa (SSR), which comprises 10 600 ha of tropical dry forest. Although the SSR once consisted of continuous semievergreen forest, a complex history of anthropogenic disturbance has produced a patchwork of regenerating and pristine habitats including mixed deciduous forest, oak forest, mangroves, lightly wooded savannas and open grasslands (Fedigan & Jack, 2012). The SSR experiences a severe, 6-month dry season during which most plants shed their leaves and few sources of surface water remain. The median total yearly rainfall at the site during our study period (2006–2013) was 2129 mm (range during study period 1436–3639 mm).

Study Species and Subjects

White-faced capuchins live in cohesive social groups that are typically composed of one or more adult males, several adult females and numerous immature animals. All members of the group travel in a roughly coordinated fashion, in that each animal usually remains in visual and/or vocal contact with at least some other group members, and it is usually possible to discern the overall direction of group movement. Thus, all animals of a given social group share a home range, and accordingly, we treat the social group as the unit of analysis in our study. The home ranges of neighbouring white-faced capuchin groups overlap extensively (Crofoot, 2007; Rose & Fedigan, 1995), with up to 60% dyadic overlap among our study groups (Campos & Fedigan, 2011). Intergroup relationships may be best characterized as 'xenophobic' rather than territorial, in that groups do not defend well-defined spaces, but their interactions are usually highly agonistic (Crofoot et al., 2008). Their diet is dominated by fruits and insects, which are consumed in roughly similar proportions (McCabe & Fedigan, 2007), although fruits are generally preferred and are consumed in proportion to their relative abundance (Melin, Young, Mosdossy, & Fedigan, 2014). We observed seven neighbouring groups of wild white-faced capuchins (AD, BH, CP, EX, GN, LV and RM) in SSR. Two of these groups, AD and RM, formed in late 2012 as fission products of group CP. There is some contiguous forest that extends over the total area traversed by the seven study groups, but the age and structure of the forest varies markedly within each group's range (Fig. A1). Total group sizes ranged from a minimum of 8 in EX group to a maximum of 37 in GN group (Table 1).

Data Collection

Location data

We collected location data at irregular intervals between May 2006 and August 2013. Each observer's observation schedule and study groups differed to accommodate other data collection requirements, but we used a common methodology to collect location points while observing each group. Observers typically followed a given group from sleep tree to sleep tree (~12 h), but shorter data collection days occurred occasionally if observers lost the group or were unable to locate the group quickly in the morning. The group's location was recorded every 30 min on the hour and half-hour using a hand-held GPS receiver (Garmin GPSMAP 62s and 76cx). Whenever possible, we recorded the location point at the group's approximate geometric centre. However, other data collection requirements, large group spread and/or poor visibility occasionally prevented observers from confidently identifying the group's geometric centre. In these cases, we nevertheless recorded the point as long as some animals were visible directly overhead. If no animals were visible at the half-hour, observers recorded the location point as soon as they re-established visual contact with the focal group, as long as this occurred within 15 min. After settling into a sleep tree shortly after sunset, capuchins remain stationary throughout the night. Thus, roughly half of their time is spent immobile at a sleep tree. As we were concerned only with diurnal use of space, we did not include nocturnal location data. Our final set of location data included 40 745 points, which represented over 20 000 observation hours on the seven study groups (Table 1). All data collection protocols were approved by the University of Calgary's Life and Environmental Sciences Animal Care Committee (BIO8R-03 to L.M.F.) and Tulane University's Institutional Animal Care and Use Committee (A4499, 2006-2014 to K.M.J.), and the study adhered to the national laws of Costa Rica (research permit issued by MINAET ACG-PI-046-2009 to F.A.C.).

Environmental and ecological data

We used a Kestrel weather meter to record ambient temperature every 30 min on the half-hour. The weather meter was located in a deeply shaded location near the geographic centre of the five groups' ranges. Daily total rainfall was recorded using a standard cylindrical rain gauge. To monitor the availability of food, we used both phenological data and tree abundance data on 53 commonly eaten fruit species. The methods involved in collecting these data sets are described in detail elsewhere (Melin, 2011; Melin, Hiramatsu, et al., 2014). The phenology record spans 81 months from February 2007 to October 2013. The data consist of monthly measurements of fruit coverage and maturity on a median of eight individual trees of each species in each month. The tree abundance data were obtained from 151 botanical transects distributed throughout the study site and covering a total area of 3.02 ha (Melin, 2011).

We created maps of land cover (Fig. A1) and normalized difference vegetation index (NDVI) from a Landsat Surface Reflectance Climate Data Record (LSR-CDR) product (Masek et al., 2006) derived from a Landsat 5 TM image (scene ID: LT5016053 2011065CHM00). LSR-CDR data products have been processed to remove artefacts produced by atmospheric conditions, illumination, elevation and viewing geometry. The image was acquired on 6 March 2011, which corresponds to the peak dry season in SSR. Research on the relationship between forest maturity stage and NDVI in the SSR has shown that dry season NDVI values can be used to discriminate maturity stages of forest in this ecosystem (Arroyo-Mora et al., 2005; Kalacska et al., 2004). This is due to the approximately linear relationship between forest stand age and the degree of evergreenness (Sorensen, 1998). To obtain land cover, we classified the image into four habitat categories, as defined in Kalacska et al. (2004), including open grassland and bare soil, early successional stage forest, intermediate successional stage forest and mature/late successional stage forest. The classification process involved selecting threshold values for NDVI that minimized the number of classification errors in 409 ground control points. We recorded habitat type for each ground control point within about 1 month of the image acquisition date during the peak dry season of 2011 (date range 3 March–15 May). Based on the ground control points, the overall accuracy of this classification method was 76%.

Data Analysis

Spatiotemporal scales and home range estimation

Burt's (1943, p. 351) commonly cited definition of the home range as the 'area traversed by the individual in its normal activities' has no inherent temporal or spatial specification. Indeed, home ranges may be continuously dynamic, and their characteristics may therefore vary depending on how they are defined both temporally and spatially. We estimated home ranges for each study group at four nested temporal scales (monthly, quarterly, half-yearly and yearly) and three spatial scales (core zone, primary ranging zone and total home range zone; Fig. 1). Table 2 provides definitions and biological interpretations of the temporal scales, whereas the spatial scales are defined below. Because sampling effort varied considerably over the study period, we excluded time intervals with very few location points (Fig. A2), and we accounted for sampling effort in our statistical models (see below). After excluding time periods with insufficient data, we were left with 175 monthly ranges, 73 quarterly ranges, 41 half-yearly ranges and 22 yearly ranges (Fig. A2). To estimate home ranges, we used a recently developed movement-based kernel method that is based on biased random bridges (BRB) (Benhamou, 2011; Benhamou & Cornélis, 2010). Like other movement-based home range methods, the BRB method's primary advantage over more commonly used location-based methods is that it estimates the utilization distribution from a time-ordered movement path rather than from unlinked points, thereby accounting for autocorrelation and increasing

Table 1
Data summary and group sizes of white-faced capuchins

Focal group	Total size	Observation days	Location points
AD	20–22	44	915
BH	17–24	115	2077
CP	17–37	510	9822
EX	8–13	236	4292
GN	20–37	618	12 051
LV	12–23	582	10 645
RM	17–18	45	943
Total		**2150**	**40 745**

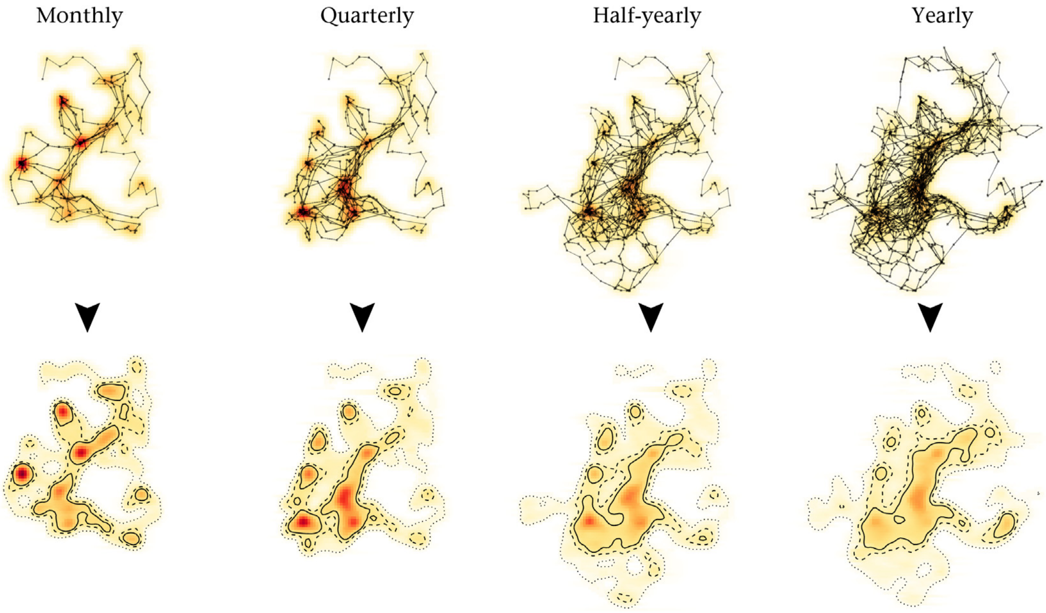

Figure 1. Illustration of the movement-based kernel method used for estimating home ranges of white-faced capuchins in this study. Home ranges shown are for group BH at each of four nested temporal scales. The upper panels show the recorded location points (small dots) and the inferred movement paths (black line segments) of BH group during the relevant period. The coloured shading represents the utilization distribution. The lower panels show the three home range zones delineated for each home range: core zone (50% isopleth, solid line); primary ranging zone (70% isopleth, dashed line); and total home range zone (95% isopleth; dotted line).

biological realism (Benhamou, 2011; Horne et al., 2007; Kranstauber et al., 2012). We implemented the BRB method using the adehabitat family of packages (Calenge, 2006) for R version 3.0.1 (R Development Core Team, 2013). The parameters that we used for the BRB home range method are detailed and justified in the Appendix.

Calculation of predictor and response variables

To account for possible group size and body size effects, we multiplied the number of sexually mature animals by the mean body mass reported for different age/sex classes of this species: 2.54 kg for adult females and 3.68 kg for adult males (Smith & Jungers, 1997). We also used 2.54 kg for subadult males, which have slight build similar to that of adult females. As group compositions fluctuated continuously throughout the study, we calculated a mean group body mass for the time interval that defined each home range based on a continuous daily record of demographic changes such as dispersal events, deaths and disappearances. We excluded immature animals in this calculation because their weights were likely to vary considerably over the time intervals of interest, and because the expected allometric scaling relationship between home range area and body mass probably differs for nursing or recently weaned animals. The number of immature animals was strongly correlated with the number of sexually mature animals (Pearson correlation: $r = 0.70$), which suggests that our conclusions are unlikely to be affected strongly by the exclusion of immature animals from the group mass calculation.

To represent climatic effects in our analyses, we used mean daily maximum temperature, calculated as the mean of each daily maximum temperature for all days contained within the time interval that defined the home range. Because season, temperature and precipitation were strongly correlated at this site, including more than one of these variables in our models would introduce multicollinearity issues, and attempting to disentangle their individual effects on home range size would be problematic. We used maximum temperature because at our study site, temperatures are generally warm throughout the year (Campos & Fedigan, 2013), seasonal variation in maximum daily temperature is much greater

Table 2
Temporal scale definitions and biological interpretations

Temporal scale	Start	End	Environmental conditions and biological significance
Monthly	First of month	Last of month	Calendar months: no biological significance
Quarterly	16 Feb	15 May	Late dry season: temperatures warm steadily and deciduous trees lose their leaves; green vegetation remains only in mature forest; natural sources of drinking water exhausted
	16 May	15 Aug	Early wet season: arrival of regular rains, high relative humidity and rapid leaf onset in most deciduous plants; temperatures fall immediately after heavy rains begin
	16 Aug	15 Nov	Late wet season: frequent rain and maximum fruit abundance; October typically characterized by prolonged torrential rain
	16 Nov	15 Feb	Early dry season: green vegetation, moderate temperatures and clear skies; dry conditions and frequent high wind in January and February hasten leaf shedding; natural sources of drinking water are abundant
Half-yearly	16 May	15 Nov	Wet season: comprising early and late wet seasons
	16 Nov	15 May	Dry season: comprising early and late dry seasons
Yearly	1 Jan	31 Dec	Complete annual cycle: comprising both wet and dry seasons

than variation in minimum or mean daily temperature (Campos & Fedigan, 2013; Melin, Young, et al., 2014) and previous research has shown that high temperature strongly affects our study animals' activity patterns (Campos & Fedigan, 2009). Thus, of all the climatic variables that we considered, the possible effects of maximum temperature on space use patterns were the most biologically straightforward to interpret.

To represent dietary factors in our analyses, we calculated monthly estimates of available fruit biomass by combining the phenology and tree abundance data sets. We converted each phenology record to an availability index that integrates information about fruit maturity and coverage and is scaled between zero (no mature fruit) and one (full coverage of mature fruit) (see Appendix for additional detail). For each species separately, we used a generalized additive model to smooth the availability indices over a yearly cycle using a cyclic cubic regression spline smoother, which forces the ends (1 January/31 December) to match. Following Melin (2011), for each appropriately sized tree in the botanical transects, we used a formula to estimate fruit biomass from the tree's diameter at breast height (DBH) (Peters et al., 1988). We summed these estimates for all individual trees of a given species and divided them by the total transect area to obtain a maximum fruit biomass value per hectare per species. We multiplied these values by the smoothed monthly availability indices for each species, then summed across species to obtain the total available fruit biomass for each month. Finally, because our home range timescales did not correspond to calendar months, we interpolated daily fruit biomass values using a cubic smoothing spline (Fig. A3b). We used these daily values to calculate the mean available fruit biomass for the time interval that defined the home range. Insects also contribute substantially to the capuchin diet, but we currently lack the data necessary to make objective, realistic estimates of available insect-food biomass.

We were interested in determining how these predictor variables affected home range size and habitat composition within the home range. For home range size, we calculated area at three spatial scales: the core zone, defined as the 50% isopleth; the primary ranging zone, defined as the 70% isopleth; and total home range zone, defined as the 95% isopleth. For home range habitat composition, we calculated an index of forest maturity as the mean NDVI of all pixels contained within the core zone (high use), outside the core zone but within the primary ranging zone (medium use), and outside the primary ranging zone but within the total home range zone (low use). It is important to note that these pixel values are valid measurements of NDVI per se only for the date of image acquisition and not for the time intervals corresponding to each home range. Because peak dry season NDVI is an indicator of forest maturity stage in SSR, we refer to this measurement hereafter as 'forest maturity' to avoid confusion.

Model formulation and statistical analysis

We used the R package lme4 (Bates & Maechler, 2009) to fit linear mixed effects models (LMM) for each response variable with sets of candidate predictor variables selected a priori based on our predictions. The models described below were applied only at the two smaller temporal scales, monthly ($N = 175$) and quarterly ($N = 73$), because there were relatively few home ranges available for analysis at the larger temporal scales (41 half-yearly ranges and 22 yearly ranges). We carried out model selection and model averaging based on Akaike's Information Criterion values corrected for small sample size, AICc, a procedure advocated by Burnham & Anderson (2002) to reduce the risk of overfitting and to account for model selection uncertainty when sample sizes are relatively small.

We evaluated a set of eight candidate models (Tables A1, A2) for home range area and habitat composition, with focal group as a random factor to control for repeated observations on the same groups (Börger et al., 2006). We applied a log transformation to the response variables representing area (following van Beest et al., 2011; Börger et al., 2006; Morellet et al., 2013; Rivrud et al., 2010) because the variance of the model residuals increased in proportion to the untransformed response. Following the log transformation, we confirmed that the residuals were well behaved by visual examination of the residuals plotted against fitted values. The basic model for home range area (Table A1) included the square root of the number of locations as a fixed effect to account for the theoretical scaling relationship between sampling effort and home range area expansion (Gautestad & Mysterud, 1993). Additional predictor variables included mean daily maximum temperature, mean available fruit biomass and group mass (Tables A1, A2). Prior to running the models, we converted these three predictor variables to unitless Z scores to facilitate direct visual comparison of their relative effects in a coefficient plot (i.e. to remove the influence the different units in which they were measured). We were also interested in determining whether there were systematic differences among the three measures of forest maturity for the different usage zones of each home range. We therefore restructured the data by aggregating the measured forest maturity values in each usage zone (high use, medium use, low use) into a new variable called maturity value, which we grouped by focal group, usage zone and a numerical home range identifier shared by each of the three maturity value measurements obtained from the same home range. We then applied an LMM using maturity value as a response variable, usage zone (high, medium or low) as a fixed effect, and focal group and home range identifier as random effects. For this analysis only, we carried out separate models for each temporal scale. We tested for significant pairwise differences among all linear combinations of levels for that variable (i.e. all combinations of home range zones) using adjusted P values (single-step method) with the R package multcomp (Hothorn, Bretz, & Westfall, 2008).

RESULTS

Home Range Size

Descriptive statistics for home ranges and predictor variables at each spatiotemporal scale are presented in Tables A3 and A4 of the Appendix, respectively. As expected for an animal that shows seasonal home range shifts, home range size tended to increase with the duration of the temporal scale (Fig. 2). However, there was extensive overlap across scales both within and between groups. Data exploration revealed that group mass alone explained 13–38% of the variance in home range size, depending on the spatiotemporal scale of analysis (Fig. A4), with the caveat that the exploratory regressions did not account for repeated measures on the same groups or differences in sampling effort. After accounting for these and other possible influences in the LMM framework (Table A1), group mass remained the most important and influential determinant of home range size at all scales analysed (Fig. 3). For example, at the quarterly timescale, group mass and sampling effort, together with the random effect focal group, explained about 66.4% of the variance in total home range area ($R_{\mathrm{GLMM}}(c)^2$: Nakagawa & Schielzeth, 2013). The other two predictor variables that we analysed, available fruit biomass and mean daily maximum temperature, showed more subtle, scale-dependent effects on home range area. Available fruit biomass had a consistently negative influence on home range area at the smaller monthly timescale but no influence at the larger quarterly timescale (Fig. 3). The effects of mean daily maximum temperature followed a similar pattern, with higher temperatures predicting smaller areas at the monthly timescale but not the quarterly timescale. Moreover, the

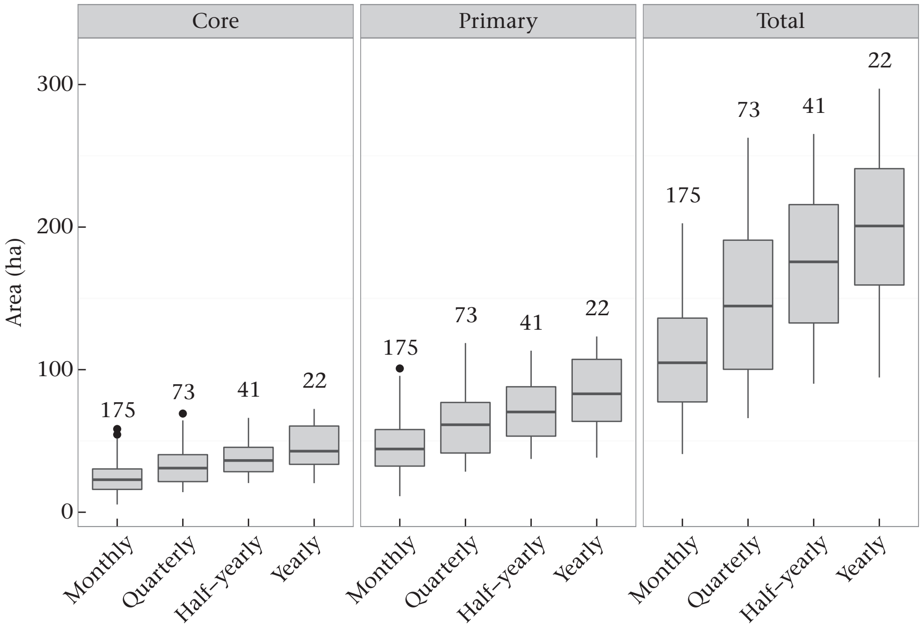

Figure 2. Home range area for the seven study groups at three spatial scales and four temporal scales. The box plots show medians (thick horizontal lines), first and third quartiles (box hinges), and the data range (whiskers). Sample sizes above each box plot indicate the number of distinct home ranges used to construct the box plot (e.g. we calculated a total of 22 yearly ranges, as shown in Fig. A2).

effects of maximum temperature on home range area were clearly dependent on spatial scale: temperature had a relatively strong influence on the core zone but essentially no influence on the total home range zone (Fig. 3).

Home Range Composition

The LMMs for forest maturity that considered the effects of maximum temperature, fruit availability and group body mass showed relatively high consistency across spatial and temporal scales (Table A2). Model averaging revealed that mean daily maximum temperature was the most important determinant of home range composition at both the monthly and quarterly timescales, with higher temperatures predicting increased use of older, more evergreen forest (Fig. 4). The home ranges of larger groups (as measured by group mass) did not contain consistently more mature forest than those of smaller groups (Fig. 4). The LMMs that modelled forest maturity as a function of usage intensity (high, medium, low) were also highly consistent at the monthly, quarterly, half-yearly and yearly timescales. Zones of higher use were significantly older, on average, than zones of lesser use (Fig. A5, Table A5). However, the preference for mature forest was not unvarying: for a relatively small number of home ranges, space use was concentrated on younger forests (negatively sloped line segments in Fig. 5).

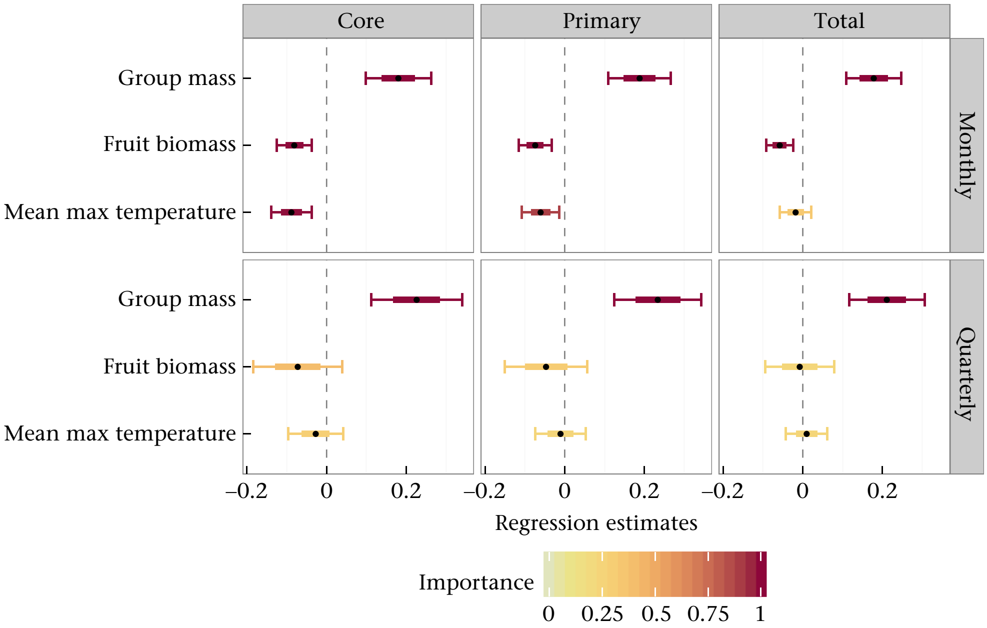

Figure 3. Model-averaged regression coefficients and relative variable importance for linear mixed models of home range size. Thin error bars show 95% confidence intervals, and thick bars show ±1 SD. The predictor variables were scaled to facilitate direct comparison of their relative effects. All models included the random effect focal group. The relative importance of each predictor variable was calculated as the sum of the Akaike weights for each model in which the variable appeared.

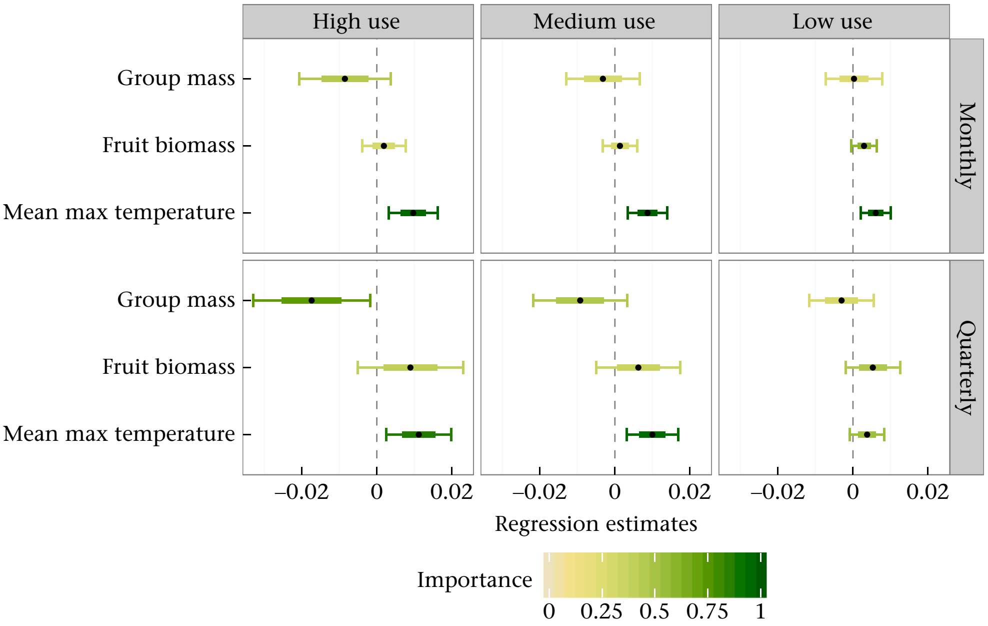

Figure 4. Model-averaged regression coefficients and relative variable importance for linear mixed models of mean forest maturity index contained within the home range. Thin error bars show 95% confidence intervals, and thick bars show ±1 SD. The predictor variables were scaled to facilitate direct comparison of their relative effects. All models included the random effect focal group. The relative importance of each predictor variable was calculated as the sum of the Akaike weights for each model in which the variable appeared.

DISCUSSION

Determinants of Home Range Size

Group mass was consistently the most important predictor of home range size in our models, and its effects were relatively insensitive to spatial or temporal scale. This finding is consistent with the allometric scaling relationship between body mass and space requirements that explains a significant amount of cross-species variation in home range size among primates (Clutton-Brock & Harvey, 1977; Harvey & Clutton-Brock, 1981; Milton & May, 1976). This scaling relationship has also been proposed to

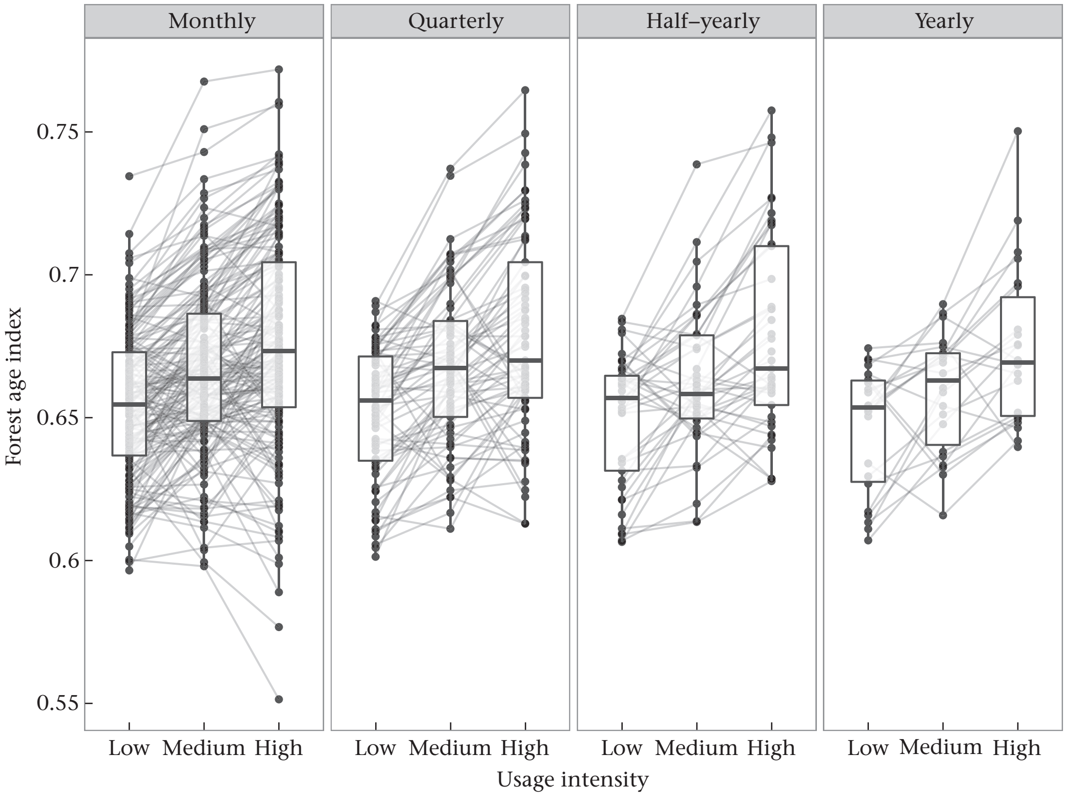

Figure 5. Comparison of NDVI-based forest maturity indices at three spatial scales and four temporal scales. Each home range contributes three mean forest maturity measurements, one for each home range use zone (low use, medium use, high use). This trio of points is linked by grey line segments. Most of the line segments were positively sloped, indicating an increase in mean forest maturity from a less intensively used home range zone to a more intensively used zone. The components of the box plots are as described in the caption for Fig. 2.

explain within-species and within-population variation in home range size (e.g. Isbell, 1991; Janson & Goldsmith, 1995). However, given that primate group sizes change relatively slowly, there are few studies on wild primates with a sufficiently large sample of longitudinal home range measurements and/or separate groups to demonstrate this relationship convincingly. Our 8-year longitudinal ranging data set therefore provides valuable and robust evidence that grouping patterns drive within-species and even within-group variation in home range size as group compositions vary over time. This finding also has important implications for theoretical models that examine the costs of group living, because as group size increases, so too does home range size. Further study is needed to determine whether *C. capucinus* individuals in groups with larger home ranges incur metabolic costs by ranging over larger areas, as seems to be the case for most frugivorous primates (Janson & Goldsmith, 1995). Alternatively, larger groups may be able to maintain larger home ranges without increased individual foraging effort if their relative dominance over neighbouring groups gives them greater freedom to shift their geographical focus to the most productive areas (Majolo et al., 2008).

At the monthly timescale, our results demonstrate that seasonal climatic and phenological fluctuations also play important roles in determining home range size. The effect of climate, represented in our models by mean daily maximum temperature, was an important explanatory variable in the monthly home range models. Hotter conditions were associated with smaller monthly ranges, a finding consistent with previous research that found reduced activity levels with increasing temperature (Campos & Fedigan, 2009). As predicted, the temperature-driven reduction of home range size was greatest on high-use core zones. This pattern is consistent with extended resting periods (a behavioural response to hot, dry weather), which produce more uneven utilization distributions and small, dense core zones. The spatial-scale-dependent effects of temperature on different usage zones may suggest some behavioural compensation for lost foraging time during cooler hours of the day, for example, by travelling more quickly and/or travelling longer distances (van Schaik & Brockman, 2005), resulting in only marginal reduction of the total home range area, as was the case in the present study.

Food resource effects on home range size, represented in our models by available fruit biomass, were also consistent with previous research on other capuchin species (Di Bitetti, 2001; Peres, 1994; Terborgh, 1983) in that greater food abundance was associated with smaller home range size at the monthly timescale. A possible explanation for this pattern is movement-related compensation for nutritional shortfalls during seasonal fruit scarcity, which may include area shifting or increased foraging effort (Hemingway & Bynum, 2005; van Schaik & Brockman, 2005; van Schaik et al., 1993). Future studies will attempt to quantify such behavioural adjustments by examining movement parameters in relation to energy intake rates. There was only minimal evidence of spatial scale dependence for food resource effects on home range size, as the parameter estimates and model-averaged importance attributed to fruit biomass were all strikingly similar for the core, primary and total home range areas.

Intensity of Use and Forest Maturity

The forest maturity models that considered the effects of temperature, group mass and food revealed that only temperature had a consistently strong influence on the habitat composition of home ranges. Consistent with our predictions, hotter conditions were associated with more mature evergreen forest contained within the home range. As in the case of home range area, temperature-driven effects on home range forest composition were manifested most clearly on the core zone. Surprisingly, and contrary to our prediction, group mass did not show a consistent positive relationship with home range forest maturity, which suggests that large groups were either not able or not motivated to secure the most mature forest patches, despite their dominance over smaller groups (Childers, 2008). The reasons for this finding are unclear, but we offer three possible explanations. First, our use of forest maturity as a proxy for habitat quality may be a flawed approach because it only considers the greater abundance of fruit in mature forest. Other important food resources, such as seeds, insects and small vertebrates may be more abundant in secondary forest, but their distributions have not been adequately quantified in our study system. Second, the most critically limiting resource in our study is probably access to water during the dry season (Fedigan, Rose, & Avila, 1996). Large groups may gain little from relocating to a slightly more productive (i.e. mature) area if they can meet their basic food requirements while maintaining control over one of the scarce waterholes, none of which are located in mature forest. Third, reliance on long-term spatial memory of specific food resources (Janson, 1998) probably discourages radical shifts to new and unfamiliar areas. This inertia may keep formerly small groups that established themselves in marginal habitat from relocating even if they later grow large enough to displace a smaller group from a more productive area.

We predicted that more intensively used home range zones would consist of older forest, on average, than low-use zones. The prediction was borne out robustly at all temporal scales analysed (Fig. 4). Together, these findings suggest a movement strategy in which the capuchins generally avoid using young forest intensively, but they do not exclude such areas entirely from their total home ranges. It is likely that the heterogeneous landscape at SSR forces capuchins to pass through young, regenerating habitats regularly as they move between more highly preferred areas with mature forest. Despite the overall support for our prediction, it is clear from the numerous negatively sloped line segments in Fig. 5 that more intensively used home range zones were not always older than less intensively used home range zones. This observation provides an interesting basis for comparison with sympatric howler monkeys (*Alouatta palliata*) and spider monkeys (*A. geoffroyi*), which also prefer mature forest but appear to be more reliant on access to a mature, high-quality core zone (Asensio, Lusseau, et al., 2012; Sorensen & Fedigan, 2000). Differences in diet provide a possible explanation for the species differences. Our results suggest that the capuchins heavily utilize different types of forest at different times or for different purposes, even if older forests are used more heavily on average. Some fruit-bearing tree species that contribute substantially to the capuchin diet (e.g. *Vachellia collinsii*, *Randia monantha* and *Byrsonima crassifolia*) are relatively abundant in young forest (Kalacska et al., 2004), and during their fruiting seasons, young forest may become more attractive. Moreover capuchins feed more heavily on insects than do howler or spider monkeys, and previous primate-focused studies at other sites have found that insect-food abundance may be greater in regenerating forest habitats (Parry, Barlow, & Peres, 2007; Vulinec, Lambert, & Mellow, 2006). The scenario we describe is consistent with capuchins' well-known ability to exploit varied forest types and their willingness to forage in very young regenerating forest (Sorensen & Fedigan, 2000). For example, the yearly home range of group BH was geographically centred on the only large patch of primary forest in the study area, but they made frequent forays into very young regenerating areas, especially during the cooler wet season. In the relatively open conditions of young forest, data indicate that our study animals perceive reduced predation risk from predatory raptors, which are most frequently encountered in mature forest (Campos & Fedigan, 2014). Thus, capuchins may benefit from maintaining home ranges that include a mix of habitat types.

Implications for Capuchin Behavioural Ecology and Conservation

Our study illustrates the complex ecological processes that affect movement behaviour in a Neotropical primate across a range of spatial and temporal scales. We found clear evidence that group mass is a fundamental driver of home range size in this species, and that climatic seasonality, food resources and landscape heterogeneity also play important roles in shaping home ranges at relatively short temporal scales. These findings help to contextualize the ecological role of capuchins in Neotropical dry forest ecosystems, which are gravely threatened by climate change and human disturbance (Portillo-Quintero & Sánchez-Azofeifa, 2010). Our findings also have important implications for conservation planning in tropical dry forests. Although mature tropical dry forest is undeniably of high conservation value, our findings suggest that some potential flagship species may benefit from the conservation of a variety of contiguous habitat types, including degraded forest habitats, which may form effective buffer zones or corridors that promote connectivity among remaining mature forest patches.

The Importance of Scale

Inferences about sociality and competitive regime are often made based on the relationship between space use variables and environmental factors such as food availability. Our study demonstrates that such inferences are likely to change depending on the scale of analysis. For example, the effects of both temperature and fruit availability on home range size were strong at the monthly timescale but essentially disappeared at the quarterly timescale. One possible explanation for this result is that at relatively long timescales (e.g. several months), important variability in these quickly changing environmental drivers is averaged out as the climate changes and different fruit species come into season. Indeed, when plotted at the monthly timescale, climatic and dietary influences on home range area were clearly evident: home range area exhibited a strong bimodal pattern with peaks in November–January and June–July, and troughs in April and August–September (Fig. A3a). This pattern showed a near-perfect inverse relationship with fruit abundance (Fig. A3b); the trough in April also coincided with the annual peak in maximum temperature (Fig. A3c). However, as temporal scale increased, these important ecological patterns became increasingly unclear because the longer time intervals spanned both peaks and troughs. The relevance of this finding extends beyond animal home ranges, as it demonstrates that important ecological drivers of animal behaviour may go undetected if the scale of analysis is not well matched to the underlying ecological processes.

Given the increasing popularity of phylogenetic meta-analyses that require the use of species mean values (e.g. the home ranges analysed by Pearce et al., 2013), our study provides an important cautionary demonstration that such values may depend critically on somewhat arbitrary decisions regarding temporal scale. The home range sizes reported here at various temporal scales, all of which have been used commonly in the primate literature, almost completely span the range of sizes reported elsewhere for capuchin monkeys in a wide variety of ecosystems (Chapman, 1988; Crofoot, 2007; Defler, 1979, 1982; Di Bitetti, 2001; Izawa, 1980; Matthews, 2009; Terborgh, 1983; Zhang, 1995). We found extensive overlap in home range sizes across temporal scales, an observation that would appear puzzling if important factors such as group mass were not considered. For example, the total area traversed in a typical month by the large group GN was comparable to (and often greater than) the total area traversed by the much smaller groups EX and RM over an entire year. Nevertheless, for a given group, mean home range size increased monotonically with temporal scale up to a full annual cycle. This pattern is consistent with observations that capuchin home ranges shift throughout the year, possibly in response to spatiotemporal variation in food and water availability. As temporal scale increases, more home range shifts, and thus more new areas, are likely to be included in the home range. The tendency for home range size to increase with temporal scale was less pronounced for primary ranging zones and especially core zones. This suggests a lesser degree of shifting among heavily used zones and may indicate frequent reuse of high-value locations throughout the year despite ephemeral shifts in the total home range. Such inferences highlight the power of our longitudinal, multiscale mixed modelling approach to analysing capuchin movement ecology.

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Appendix

Justification for Using the Biased Random Bridge (BRB) Home Range Method

A major theoretical weakness with common location-based kernel methods is the assumption that each recorded location point is independent. However, sequential location points are typically highly autocorrelated in both time and space, especially with high-frequency, GPS-based data sets (Boyce et al., 2010; Fieberg, Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010). This problem is commonly addressed by data filtering (which results in data loss), rationalizing about the value of autocorrelation itself (which violates the assumptions of the statistical model), or ignoring the problem altogether. By treating the location data as a movement process (i.e. an ordered series of track segments) rather than a point process, movement-based kernel methods explicitly account for autocorrelated data to produce a more biologically relevant home range estimate (Benhamou & Cornélis, 2010). In brief, the movement-based kernel method is as follows: (1) each movement step linking pairs of successive location points is divided into subsegments based on a specified time interval; (2) locations are interpolated for the end points of each subsegment; (3) kernel density estimation is applied to each interpolated location, with a smoothing parameter that varies with the uncertainty of the animal's location; that is, the smoothing parameter is minimal at the movement step's end points (because this is where the animal's location was recorded) and maximal at the step's midpoint (Benhamou & Cornélis, 2010). Crucially, the BRB method implements this framework by including both a 'biased' component (the animal's tendency to drift in the direction on the next location point) and a 'random' component (the animal's tendency to deviate from a straight path to the next location point) that form a bridge between each pair of successive location points (Benhamou, 2011).

Parameterization of the BRB Home Range Method

The BRB method requires several parameters that should be based on biological knowledge. First, habitat-specific movement parameters can be used to control the random component of the movement process. Using the habitat map described in the main text, we calculated habitat-specific diffusion coefficients for each group using the BRB.D function in adehabitatHR on the full set of location points for that focal group (Calenge, 2006). These coefficients govern the speed of random drift through each habitat type. Second, it is necessary to specify a maximum time threshold ($T_{\max}$) beyond which pairs of successive location points are not considered linked. Given the discontinuous nature of the location data, with long gaps each night and between different observation blocks, this threshold is necessary to remove these long gaps from the home range calculations. In our data set, time gaps associated with night-time and interblock intervals were all greater than 8 h.

Ignoring these gaps, 99.9% of the recording intervals were less than 65 min, with 94.7% falling within 5 min of the scheduled 30 min recording interval. We decided that 90 min would be a reasonable $T_{\max}$, as recording interval gaps of longer duration are likely to represent cases in which the focal group was lost or not observed for a significant amount of time, but shorter intervals are likely to represent location points with a high degree of autocorrelation. Third, we specified a minimum kernel smoothing parameter ($h_{\min}$) of

50 m, a value which accounts for various sources of error in the location data: the group's centre of mass was not always identifiable, the GPS is not perfectly accurate, and the habitat map is subject to georeferrencing errors, classification errors and geometric distortions due to terrain. Given these sources of error, 50 m seems a reasonable value for $h_{\min}$, as it does not assume unrealistic accuracy for the group's centre, and it corresponds approximately to a typical group spread in this species. Finally, the parameter $L_{\min}$ corresponds to a minimum step length, below which the animal is considered to be stationary. However, even if the group's centre is stationary, there are usually at least some animals who continue to move around while other group members are resting. We therefore included even very short steps in our home range estimates by setting $L_{\min}$ to a small value of 5 m. Steps with a recorded distance less than 5 m occurred rarely (2.26% of all steps), and in these cases, we set the smoothing parameter to $h_{\min}$ for the entire step (i.e. the uncertainty of the group's location did not vary during the step).

Calculation of the Fruit Availability Index

The tree crown coverage and fruit ripeness scores are described by Melin, Young, et al. (in press), but here we provide additional detail and an explanation of the availability index used for this study. The coverage score represents the percentage of fruit (both ripe and unripe) present in the tree crown relative to the estimated total that could be produced by the tree if all branches were bearing fruit. The ripeness score represents the percentage of fruit present in the tree crown that is fully ripe. Both of these scores were converted to ranks of 0, 1, 2, 3 or 4, which correspond to the percentage ranges 0%, 1–25%, 26–50%, 51–75% or 76–100%. To calculate the availability index, we took the reciprocal of each rank score, then multiplied the two together. Thus, an index value of 1 implies coverage/maturity ranks of 4/4, whereas an index value of 0 could be generated by a zero in either or both of the coverage/maturity ranks.

Table A1
Candidate model set and model selection results for home range area

Zone	Model	Fixed effects	Monthly				Quarterly			
			AICc	ΔAICc	w_i	Rank	AICc	ΔAICc	w_i	Rank
Core	1	Basic model	195.285	40.823	1.35E-09	8	60.027	11.913	0.001	6
	2	Basic model+$T_{\max}$	178.295	23.833	6.58E-06	5	60.722	12.608	7.45E-04	7
	3	Basic model+Fruit	180.444	25.982	2.25E-06	7	59.540	11.426	0.001	5
	4	Basic model+Mass	180.406	25.944	2.29E-06	6	48.114	0.000	0.407	1
	5	Basic model+$T_{\max}$+Fruit	169.385	14.923	5.66E-04	4	61.239	13.125	5.75E-04	8
	6	Basic model+$T_{\max}$+Mass	165.173	10.711	0.005	3	49.657	1.543	0.188	3
	7	Basic model+Fruit+Mass	163.720	9.258	0.010	2	48.738	0.624	0.298	2
	8	Basic model+$T_{\max}$+Fruit+Mass	154.462	0.000	0.985	1	50.872	2.758	0.103	4
Primary	1	Basic model	164.925	36.681	9.56E-09	8	52.273	13.672	5.58E-04	5
	2	Basic model+$T_{\max}$	154.408	26.164	1.84E-06	7	53.903	15.302	2.47E-04	7
	3	Basic model+Fruit	152.264	24.020	5.37E-06	6	52.937	14.336	4.00E-04	6
	4	Basic model+Mass	146.989	18.746	7.50E-05	5	38.600	0.000	0.520	1
	5	Basic model+$T_{\max}$+Fruit	146.457	18.213	9.79E-05	4	55.094	16.494	1.36E-04	8
	6	Basic model+$T_{\max}$+Mass	138.173	9.929	0.006	3	40.818	2.217	0.171	3
	7	Basic model+Fruit+Mass	132.388	4.144	0.111	2	40.169	1.568	0.237	2
	8	Basic model+$T_{\max}$+Fruit+Mass	128.244	0.000	0.883	1	42.597	3.997	0.070	4
Total	1	Basic model	100.620	29.615	2.45E-07	8	27.937	14.641	3.82E-04	5
	2	Basic model+$T_{\max}$	98.831	27.826	5.99E-07	7	30.220	16.924	1.22E-04	7
	3	Basic model+Fruit	92.464	21.459	1.45E-05	5	29.906	16.610	1.43E-04	6
	4	Basic model+Mass	80.683	9.678	0.005	4	13.296	0.000	0.578	1
	5	Basic model+$T_{\max}$+Fruit	92.949	21.944	1.13E-05	6	32.283	18.987	4.35E-05	8
	6	Basic model+$T_{\max}$+Mass	80.144	9.139	0.007	3	15.550	2.254	0.187	2
	7	Basic model+Fruit+Mass	71.005	0.000	0.661	1	15.652	2.356	0.178	3
	8	Basic model+$T_{\max}$+Fruit+Mass	72.409	1.404	0.327	2	17.933	4.637	0.057	4

AICc: Akaike's Information Criterion; ΔAICc: difference in AICc compared to the best model; w_i: Akaike weight. The basic model included the intercept, the square root of the number of location points and the random effect focal group. The model-averaged coefficients are plotted in Fig. 3.

Table A2
Candidate model set and model selection for mean forest maturity index within each home range zone

Zone	Model	Fixed effects	Monthly				Quarterly			
			AICc	ΔAICc	w_i	Rank	AICc	ΔAICc	w_i	Rank
High use	1	Basic model	−541.909	6.868	0.012	6	−242.832	7.195	0.011	8
	2	Basic model+$T_{\max}$	−548.777	0.000	0.369	1	−248.120	1.907	0.151	3
	3	Basic model+Fruit	−541.242	7.535	0.009	8	−243.771	6.257	0.017	7
	4	Basic model+Mass	−542.364	6.413	0.015	5	−245.524	4.503	0.041	6
	5	Basic model+$T_{\max}$+Fruit	−546.976	1.801	0.150	3	−247.107	2.920	0.091	4
	6	Basic model+$T_{\max}$+Mass	−548.399	0.378	0.305	2	−250.027	0.000	0.392	1
	7	Basic model+Fruit+Mass	−541.841	6.936	0.012	7	−246.343	3.685	0.062	5
	8	Basic model+$T_{\max}$+Fruit+Mass	−546.677	2.100	0.129	4	−249.004	1.024	0.235	2
Medium use	1	Basic model	−618.816	8.737	0.006	5	−276.290	6.564	0.012	8
	2	Basic model+$T_{\max}$	−627.553	0.000	0.493	1	−282.853	0.000	0.327	1
	3	Basic model+Fruit	−618.269	9.284	0.005	6	−277.072	5.781	0.018	6
	4	Basic model+Mass	−617.600	9.953	0.003	7	−276.776	6.077	0.016	7
	5	Basic model+$T_{\max}$+Fruit	−625.737	1.816	0.199	3	−281.623	1.230	0.177	3

Table A2 (*continued*)

Zone	Model	Fixed effects	Monthly				Quarterly			
			AICc	ΔAICc	w_i	Rank	AICc	ΔAICc	w_i	Rank
	6	Basic model+T_{max}+Mass	−625.811	1.742	0.206	2	−282.552	0.302	0.281	2
	7	Basic model+Fruit+Mass	−617.125	10.429	0.003	8	−277.372	5.482	0.021	5
	8	Basic model+T_{max}+Fruit+Mass	−624.015	3.539	0.084	4	−281.258	1.595	0.147	4
Low use	1	Basic model	−715.331	8.810	0.005	7	−338.399	0.959	0.145	4
	2	Basic model+T_{max}	−723.527	0.614	0.303	2	−339.358	0.000	0.234	1
	3	Basic model+Fruit	−718.425	5.716	0.024	5	−338.832	0.526	0.180	2
	4	Basic model+Mass	−713.278	10.863	0.002	8	−336.800	2.559	0.065	7
	5	Basic model+T_{max}+Fruit	−724.141	0.000	0.411	1	−338.531	0.827	0.155	3
	6	Basic model+T_{max}+Mass	−721.428	2.713	0.106	4	−337.421	1.937	0.089	5
	7	Basic model+Fruit+Mass	−716.391	7.750	0.009	6	−337.096	2.263	0.076	6
	8	Basic model+T_{max}+Fruit+Mass	−721.998	2.143	0.141	3	−336.525	2.833	0.057	8

AICc: Akaike's Information Criterion; ΔAICc: difference in AICc compared to the best model; w_i: Akaike weight. The basic model included the intercept and the random effect focal group. The model-averaged coefficients are plotted in Fig. 4.

Table A3
Summary of home range characteristics at four temporal scales

Variable	Temporal scale	Zone	Min	Max	Mean	SD
Home range size (ha)	Monthly	Core	5.437	58.375	24.423	10.593
		Primary	11.251	100.836	46.668	18.644
		Total	40.805	202.657	108.762	38.434
	Quarterly	Core	14.085	69.194	33.275	13.001
		Primary	28.448	118.667	62.551	22.807
		Total	65.998	262.666	148.172	48.293
	Half-yearly	Core	20.476	66.185	38.603	11.972
		Primary	37.365	113.305	72.648	21.514
		Total	90.146	265.303	175.286	48.438
	Yearly	Core	20.375	72.446	45.484	15.919
		Primary	38.283	123.283	83.828	26.915
		Total	94.529	297.072	197.768	58.718
Mean age index	Monthly	High use	0.551	0.772	0.676	0.038
		Medium use	0.598	0.768	0.667	0.030
		Low use	0.597	0.734	0.654	0.025
	Quarterly	High use	0.613	0.765	0.679	0.035
		Medium use	0.611	0.737	0.668	0.027
		Low use	0.601	0.691	0.652	0.024
	Half-yearly	High use	0.628	0.758	0.679	0.035
		Medium use	0.614	0.739	0.663	0.025
		Low use	0.607	0.685	0.650	0.023
	Yearly	High use	0.640	0.750	0.675	0.028
		Medium use	0.616	0.690	0.659	0.021
		Low use	0.607	0.674	0.646	0.022

Table A4
Descriptive statistics of the predictor variables used for modelling home range size and composition

Variable	Temporal scale	Min	Max	Mean	SD
T_{max}	Monthly	25.36	36.07	30.22	2.53
	Quarterly	26.16	33.60	29.99	2.35
	Half-yearly	26.41	31.56	29.60	1.64
	Yearly	27.57	31.26	29.39	1.16
Fruit biomass	Monthly	95.57	202.39	140.87	29.05
	Quarterly	109.58	159.17	140.47	15.01
	Half-yearly	128.00	149.82	137.57	10.90
	Yearly	138.93	139.00	138.99	0.03
Group mass	Monthly	11.05	52.82	31.01	12.12
	Quarterly	11.30	52.82	29.85	11.98
	Half-yearly	11.20	52.57	30.87	11.69
	Yearly	11.30	50.02	31.27	11.40
Number of locations	Monthly	96	470	196.73	81.75
	Quarterly	193	1088	494.70	241.80
	Half-yearly	385	1985	869.37	473.35
	Yearly	773	3636	1615.09	844.12

Table A5
Pairwise comparisons among factor levels for the linear mixed effects models for forest age as a function of usage intensity

Temporal scale	Linear hypothesis	*Z*	P_{adj}
Monthly	Low use−Medium use=0	−7.461	<0.001
	High use−Medium use=0	4.818	<0.001
	High use−Low use=0	12.279	<0.001
Quarterly	Low use−Medium use=0	−5.362	<0.001
	High use−Medium use=0	3.620	<0.001
	High use−Low use=0	8.982	<0.001
Half-yearly	Low use−Medium use=0	−3.180	0.004
	High use−Medium use=0	3.810	<0.001
	High use−Low use=0	6.991	<0.001
Yearly	Low use−Medium use=0	−2.446	0.038
	High use−Medium use=0	3.094	0.006
	High use−Low use=0	5.540	<0.001

P values were adjusted using the single-step method.

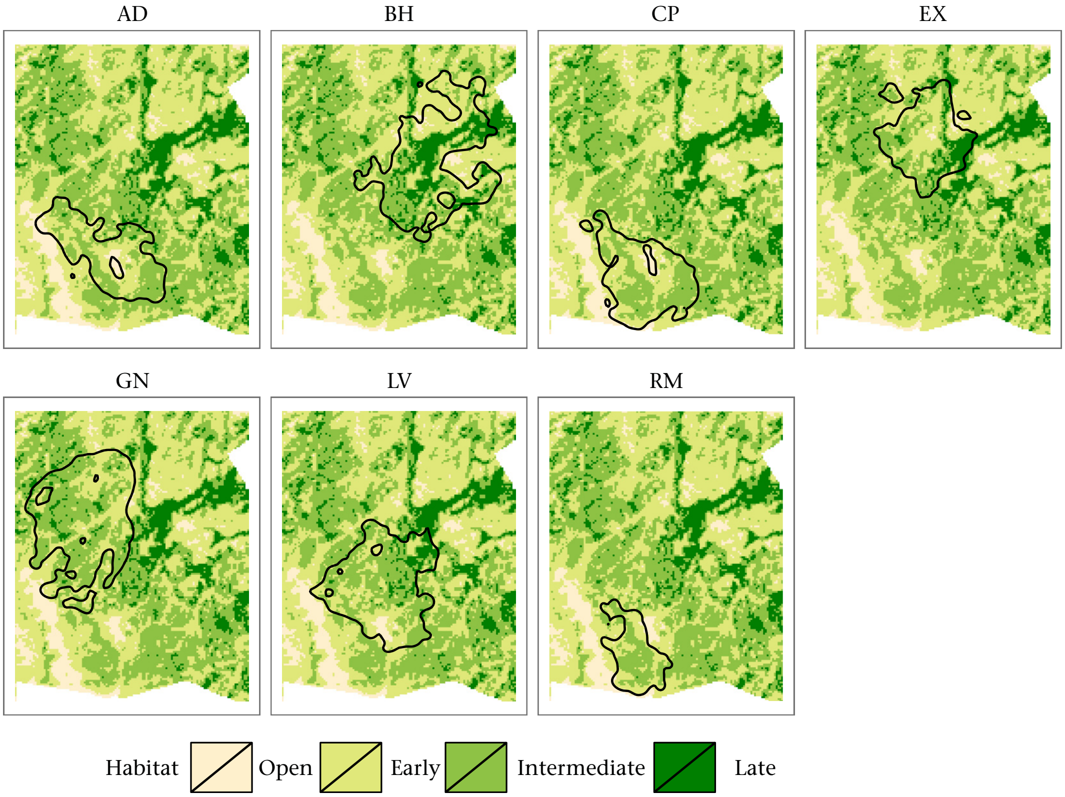

Figure A1. Habitat maps of the study area, with a single, multiyear home range for each study group. The multiyear ranges depicted here show the 95% isopleth based on every available location point for each study group. These ranges were not used for analysis and are presented for illustrative purposes only. Their relative sizes should be treated with caution because they have not been adjusted for sampling effort, which differed greatly among the study groups.

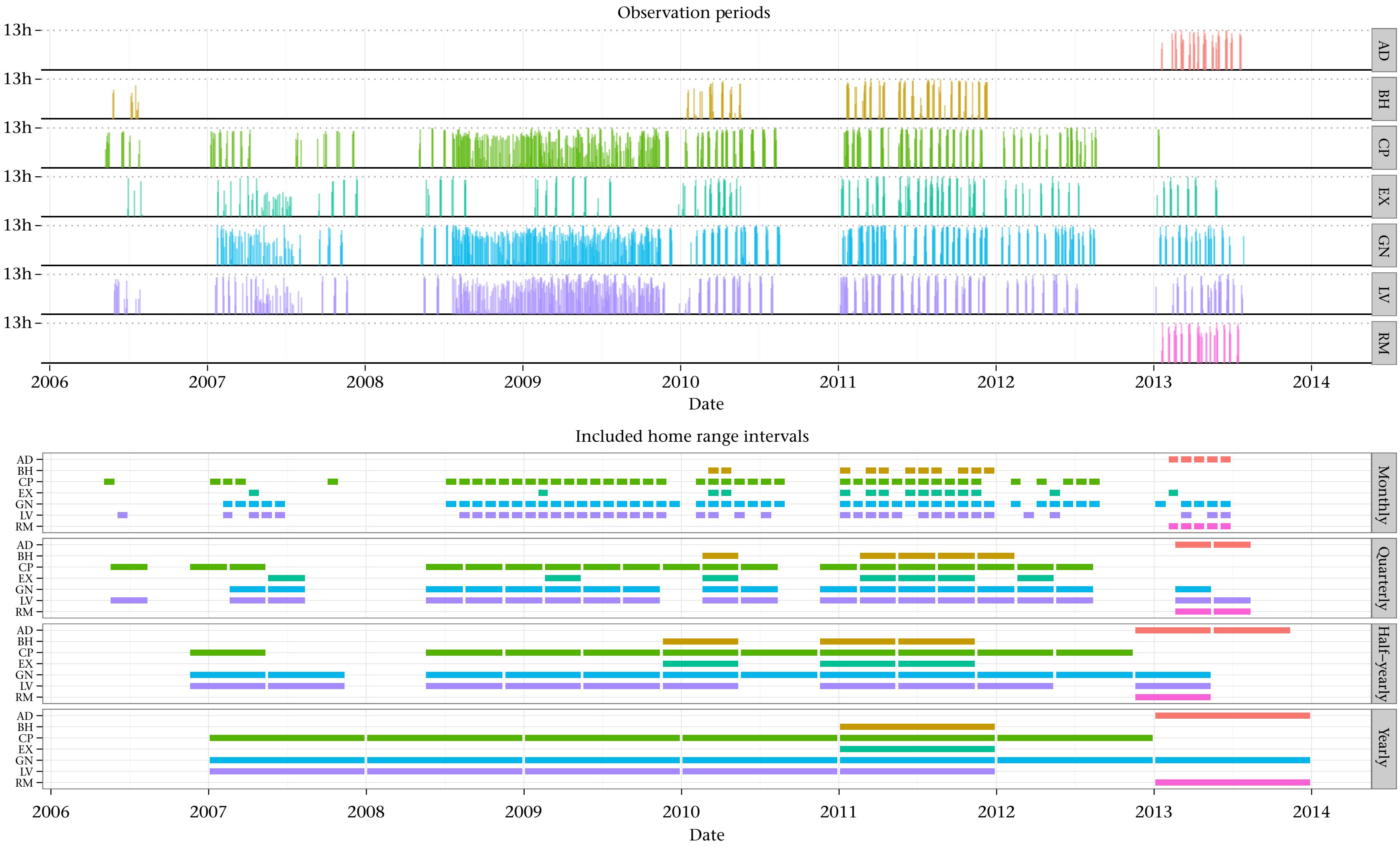

Figure A2. Top panel: data coverage, with each day of data collection represented by a thin vertical segment. Contact hours relative to a full 13 h day are represented by the segment's height ($N_{\text{days}} = 2150$; $N_{\text{points}} = 40\,745$). Bottom panel: home range time intervals with sufficient data to be included in the study. Horizontal separation between intervals exaggerated for clarity, but actual intervals were contiguous.

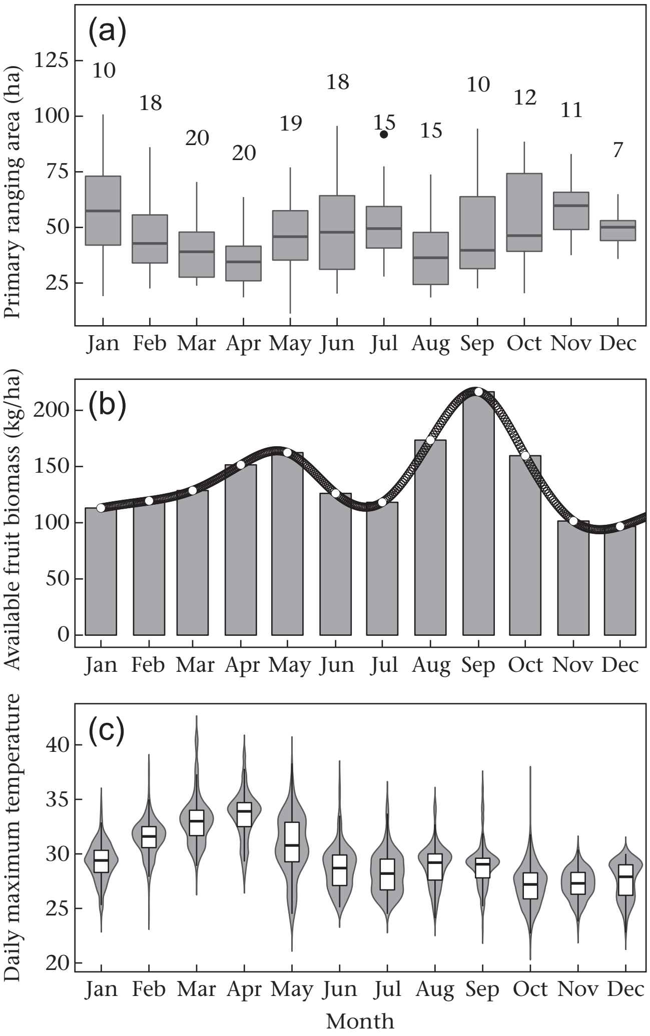

Figure A3. (a) Primary ranging area for each month of the year for all study groups. The components of the box plot are as described in the caption for Fig. 2. Numbers above the box plots indicate sample size. Plots were similar for other home range zones at the monthly scale (not shown). (b) Estimated total fruit biomass (kg/ha) in the study area for each month of the year (bars). We interpolated between measured values (white dots) for each day of the year (unfilled black dots) using spline smoothing. (c) Box plots and violin plots of daily maximum temperatures for each month of the year during the study period. The box plots are as described above, whereas the violin plots reveal higher-order moments of the temperature distributions, such as skewness and kurtosis.

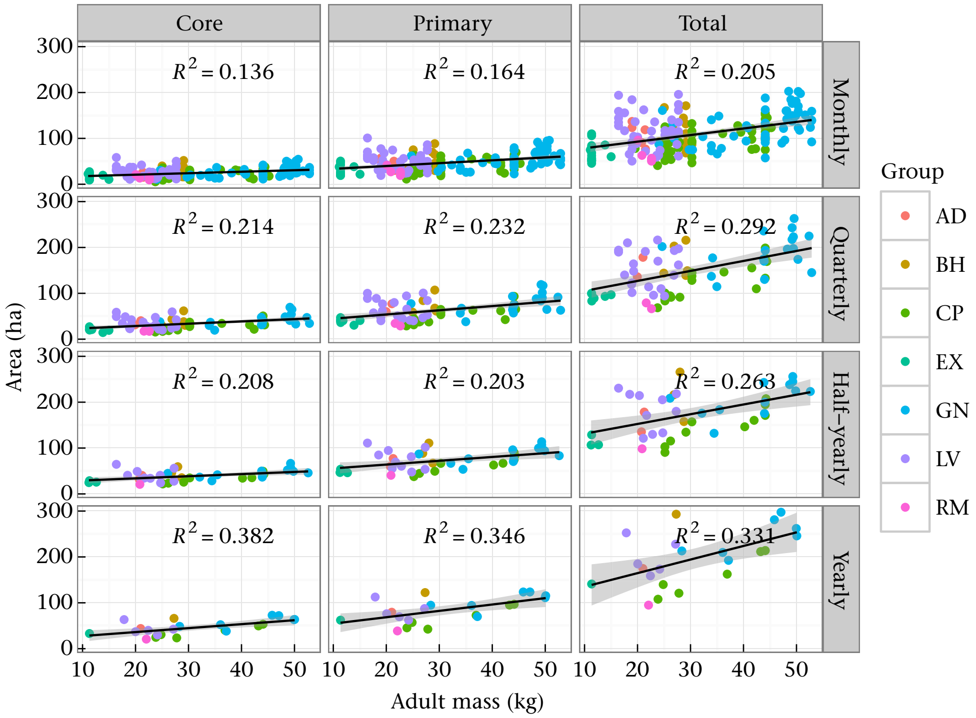

Figure A4. Relationship between total body mass of adult animals and home range area measured at three spatial scales (horizontal facets) and four temporal scales (vertical facets). See the main text for definitions of these scales. Linear regression lines with 95% confidence intervals are shown.

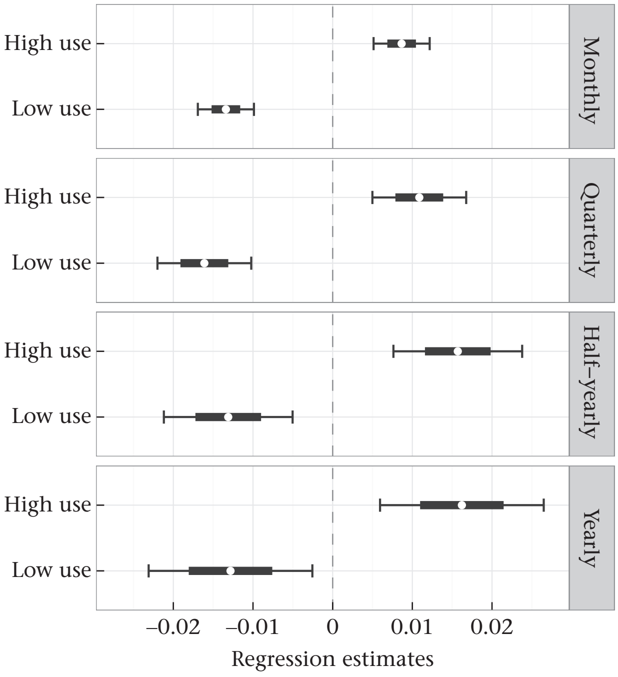

Figure A5. Estimated coefficients for linear mixed models of mean forest maturity index as a function of usage zone (see main text for definitions of these zones). All models included the focal group and home range ID number as random effects. The forest maturity index is scaled between 0 and 1, and is based on peak dry season NDVI values (see Methods). Parameter estimates are relative to the baseline category ‘medium use’, which is defined as zero. Thin error bars show 95% confidence intervals, and thick bars show 1 SD.