Space-use scaling and home range overlap in primates

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Space use is an important aspect of animal ecology, yet our understanding is limited by a lack of synthesis between interspecific and intraspecific studies. We present analyses of a dataset of 286 estimates of home range overlap from 100 primate species, with comparable samples for other space-use traits. To the best of our knowledge, this represents the first multispecies study using overlap data estimated directly from field observations. We find that space-use traits in primates are only weakly related to body mass, reflecting their largely arboreal habits. Our results confirm a theory that home range overlap explains the differences in allometric scaling between population density and home range size. We then test a suite of hypotheses to explain home range overlap, both among and within species. We find that overlap is highest for larger-bodied species living in large home ranges at high population densities, where annual rainfall is low, and is higher for arboreal than terrestrial species. Most of these results are consistent with the economics of resource defence, although the predictions of one specific theory of home range overlap are not supported. We conclude that home range overlap is somewhat predictable, but the theoretical basis of animal space use remains patchy.

1. Introduction

The way animals use space is an important aspect of their ecology, and has implications for human–wildlife conflict [1–2], mate searching [3] and species interactions [4]. Three key measures of space use that have been studied for mammals are population density [5], home range [6] and day range [7]. All three measures of space use increase with species’ body size (i.e. they display allometric scaling), as larger-bodied mammals require more space to meet their metabolic requirements [8]. Much research has been carried out into the relationships between body mass, metabolic rate and space use, but the scaling relationships of these space-use measures are not always straightforward or easy to understand [9]. Although their interactions have been described using simple models [10], the influence of other aspects of ecology, such as diet, terrain and group size remains poorly understood.

A home range is defined as the area an animal uses over the course of a year in its normal activities [11]. McNab [6] estimated allometric scaling exponents close to 0.75 for both basal mammalian metabolic rate and home range, leading to the assertion that home range sizes are directly proportional to energetic requirements (see Isaac et al. [12]). However, subsequent analyses have obtained exponents substantially higher than the theoretical 0.75 [9,13,14]. One explanation for this discrepancy is that home ranges include areas shared with conspecifics, and that the extent of home range overlap increases with body size [15]. In an attempt to explain this, Jetz et al. [10] developed a simple theoretical model based on the assumption that home ranges are defended and that the cost of defence increases with body mass and home range size. They reported a home range scaling exponent that was 0.26–0.39 units steeper than population density, suggesting that home ranges overlap more in larger species, confirming the predictions of their
‘gas model’. However, few comparative data on home range overlap exist, and in Jetz et al. [10], overlap was not directly measured but inferred from differences in scaling relationships. Thus, our understanding of space use in general, and of overlap in particular, remains limited.

The study of animal space use is complicated because factors other than body mass (or metabolic requirements) might be important drivers of variation in home range overlap. In particular, group living is likely to confound the simple relationships between body size, home range size and overlap, especially if species’ mean group size scales with body size [16]. A species’ diet type [10] and the dimensionality of its foraging environment (e.g. terrestrial versus arboreal, benthic versus pelagic; [7,17]) have both been suggested as important determinants of space-use scaling. Moreover, most space-use traits vary markedly within species [18,19], perhaps covarying with habitat quality: highly productive environments are expected to produce small exclusive home ranges, whereas low productivity should be associated with large overlapping ones [19,20]. Modelling both inter- and intraspecific variation together, rather than separately, is therefore important to gain a deeper understanding of the factors influencing space use (cf. [21]).

Primates are an excellent model system for exploring space-use variation. They span three orders of magnitude in body size and display a diversity of life-history and ecological strategies (including terrestrial and arboreal, solitary and social, territorial and non-territorial species). They are extremely well studied, such that a wealth of knowledge exists about space-use patterns [22,23], including a large amount of comparative data [24–26]. Moreover, primates are highly threatened, so understanding their space requirements is important for applied conservation [1,21].

In this study, we address three key questions on space use in primates using an extensive database on the ecological traits of wild primate populations (including home range overlap), gathered from the primary literature. First, we estimate the allometric scaling relationships of key space-use variables and test whether these relationships covary in the manner predicted by theory. Second, we estimate the relative amount of variation in home range overlap among and within species. Third, we explore the factors that explain this variation, including the general hypothesis of the gas model [10]. Specifically, we predict that a high degree of home range overlap is associated with large home range, short day range, low population density, large body size and low annual rainfall, and is higher for arboreal than terrestrial species.

### Table 1. Sample sizes for traits used in the statistical modelling. Sample size refers to the full sample, including interpolated data. Interpolated refers to the number of records for which external data sources were used to fill gaps in the dataset: see text for further details.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Species</th>
<th>Sample Size</th>
<th>Interpolated</th>
</tr>
</thead>
<tbody>
<tr>
<td>overlap</td>
<td>100</td>
<td>286</td>
<td>n.a.</td>
</tr>
<tr>
<td>home range</td>
<td>100</td>
<td>286</td>
<td>4</td>
</tr>
<tr>
<td>day range</td>
<td>82</td>
<td>247</td>
<td>69</td>
</tr>
<tr>
<td>group size</td>
<td>100</td>
<td>285</td>
<td>32</td>
</tr>
<tr>
<td>population</td>
<td>96</td>
<td>278</td>
<td>66</td>
</tr>
<tr>
<td>density</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>annual rainfall</td>
<td>n.a.</td>
<td>280</td>
<td>62</td>
</tr>
<tr>
<td>body mass</td>
<td>100</td>
<td>286</td>
<td>40</td>
</tr>
<tr>
<td>terrestrial</td>
<td>100</td>
<td>286</td>
<td>0</td>
</tr>
</tbody>
</table>

(categorical)

#### (b) Statistical modelling

We explored the allometric scaling of space-use traits, following Jetz et al. [10]. To do this, we aggregated all traits to species mean values. For four species where only exclusive home ranges have been reported, we set the overlap values to 0.2 per cent. We then calculated per capita home range as home range divided by group size [10]. We tested for simple power–law relationships between each trait and body mass. We then tested whether these relationships differed between arboreal and terrestrial species by refitting each model with the addition of a main effect for terrestriality and its interaction with the trait of interest. We fitted both ordinary least squares (OLS) regression and phylogenetic generalized least squares (PGLS) models. PGLS models were implemented by the caper package [31] in R with the phylogeny of Fritz et al. [32], and with the maximum-likelihood value of λ (the strength of the phylogenetic signal; [33]) for that model.

Next, we used mixed effects models to explore both the intraspecific and interspecific variation in home range overlap. We modelled the logit transformation of proportional recent taxonomy [27]: the resultant dataset contains overlap estimates for 100 species (median of two estimates per species, maximum of 12) across 112 study sites, which we georeferenced using information in the primary literature and from online gazetteers (e.g. Google Earth). We classified 81 species as arboreal and 19 as terrestrial (including semi-terrestrial vervets, chimpanzees and macaques).

Many field studies yielded matching data for home range size, group size, day range and population density. We filled gaps in these variables from other studies encountered in our literature search. Where possible, we matched data from the same study site; otherwise, we used species average values (table 1). Our search also yielded annual rainfall data for 86 study sites: rainfall is an important determinant of habitat productivity [28]. We extracted rainfall data for a further 21 sites (representing 62 overlap estimates), using the SAGE Atlas of the Biosphere [29].

We extracted species’ body masses from the Pantheria dataset [30]. For 15 species whose taxonomy has recently changed, we used the mean mass of its congeners. Our dataset spans the full range of primate body sizes, from 69 g (Microcebus murinus) to 149 kg (Gorilla beringei). The full database is available in the electronic supplementary material.

#### (a) Primate ecological data

Data on primate ecology were collected from the primary literature, through comprehensive searches of the four main primate journals (American Journal of Primatology, Folia Primatologica, International Journal of Primatology, Primates) and keyword searches of other ecology journals. We collated 286 estimates of home range overlap spanning the years 1965–2010; each estimate refers to the area lying within multiple home ranges, expressed as a percentage of the total area covered by those home ranges. Overlap ranges from 0 per cent to 100 per cent, with a median of 31.5 per cent. Species names were converted to the most recent taxonomy [27]: the resultant dataset contains overlap estimates for 100 species (median of two estimates per species, maximum of 12) across 112 study sites, which we georeferenced using information in the primary literature and from online gazetteers (e.g. Google Earth). We classified 81 species as arboreal and 19 as terrestrial (including semi-terrestrial vervets, chimpanzees and macaques).

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#### 2. Methods

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Table 2. Allometric scaling of space-use parameters in primates. Each line describes a separate set of linear regression models fitted to log-transformed species’ average values. $n$ is the number of species, $b$, s.e. and $p$ denote the parameter estimate, standard error and $p$-value for the simple allometric relationship; $p_2$ is the $p$-value of an interaction term testing for differences between terrestrial and arboreal species (in a separate model); parameter $\lambda$ estimates the strength of the phylogenetic signal.

<table>
<thead>
<tr>
<th></th>
<th>ordinary least squares</th>
<th></th>
<th>phylogenetic model</th>
<th></th>
</tr>
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<tbody>
<tr>
<td></td>
<td>$n$</td>
<td>$b$</td>
<td>s.e.</td>
<td>$p_1$</td>
</tr>
<tr>
<td>home range</td>
<td>100</td>
<td>0.777</td>
<td>0.0936</td>
<td>***</td>
</tr>
<tr>
<td>per capita home range</td>
<td>100</td>
<td>0.468</td>
<td>0.0882</td>
<td>***</td>
</tr>
<tr>
<td>population density</td>
<td>96</td>
<td>-0.330</td>
<td>0.0843</td>
<td>***</td>
</tr>
<tr>
<td>overlap</td>
<td>100</td>
<td>0.114</td>
<td>0.0914</td>
<td>n.s.</td>
</tr>
<tr>
<td>group size</td>
<td>100</td>
<td>0.309</td>
<td>0.0629</td>
<td>***</td>
</tr>
<tr>
<td>day range</td>
<td>82</td>
<td>-0.009</td>
<td>0.0564</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, —$p \sim 0.06$. 

overlap, after setting extreme values (zero and complete overlap) to 0.01 and 0.99, respectively. We included species and site identity as crossed random effects. All models were fitted using the `lme4` package [34] in R, with parameters estimated using maximum likelihood. Body mass, population density, day range and per capita home range were all log-transformed. We also fitted a model containing only random effects, in order to explore the components of variance in overlap.

We used multimodel inference [35] to test six predictions about the factors determining home range overlap in primates, namely that overlap should be positively correlated with per capita home range size and body size, negatively correlated with day range, population density and annual rainfall, and is higher for arboreal than terrestrial species. Most of these traits vary within species, as well as among them. Day range has a much smaller sample size than other variables (table 1), so we used a separate test for this trait. We fitted the model with five fixed effects (body mass, home range, day range, population density and group size) using the 272 observations with no missing values for these traits. We then fitted all 31 simpler models using the dredge function in the `MuMIn` package [36]. Our fullest model has nine parameters (including random effects), so we used the Akaiki information criterion with small sample size (AIC$_c$) to estimate model weights. We calculated variable importance scores and model average parameters based on the 95 per cent confidence set of models [35]. Importance scores range between 0 and 1; an importance score of 0.5 implies equal AIC$_c$ for model pairs that differ only in whether the focal variable is included. We estimated the importance of day range by taking the best model from our multimodel inference, refitting it using the 238 observations with day range data and measuring the change in AIC$_c$ by adding a term for day range.

3. Results

As expected, home range, group size and population density all show strong allometric scaling (table 2), but overlap and day range were both uncorrelated with mass. The relationships were generally steeper using PGLS than OLS, but the relative effect sizes, and significance levels, are broadly similar in both.

The scaling relationships of per capita home range and population density were found to differ between terrestrial and arboreal species using OLS (table 2): the latter is also significant using PGLS. As predicted, relationships were steeper among terrestrial than arboreal species. For per capita home range, we estimate scaling exponents of 0.353 for arboreal species compared with 1.28 for terrestrial species. For population density, the equivalent values were $-0.144$ and $-1.27$ using OLS and $-0.229$ and $-1.08$ using PGLS.

The scaling exponent for home range overlap is 0.114 (figure 1), although this is not significantly different from zero (table 2). The relationship does become significant after removing four species in which only exclusive territories (i.e. zero overlap) have been reported ($b = 0.166$, s.e. = 0.695, $t_{b} = 2.39$, $p = 0.019$). These two estimates for overlap scaling straddle the value of 0.138 predicted by the gas model (the difference in the absolute values of the scaling exponents for per capita home range and population density). The gas model prediction based on PGLS is much larger (0.375), although it is difficult to compare this value with the observed scaling exponent because overlap itself has no detectable phylogenetic signal ($\lambda = 0$), indicating that closely related species show no tendency to have similar levels of overlap.

Figure 1. Allometric scaling of home range overlap among 100 primate species. Arboreal species are denoted by open circles, terrestrial species by filled circles. The line is the fit of an ordinary least squares regression.
Table 3. Model average parameter estimates of overlap in home range. \( b \) denotes the raw parameter estimate; \( b' \) is the standardized estimate.

<table>
<thead>
<tr>
<th></th>
<th>importance</th>
<th>raw estimates</th>
<th></th>
<th>standardized</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>( b )</td>
<td>s.e.</td>
<td>( b' )</td>
</tr>
<tr>
<td>( \log(\text{body mass}) )</td>
<td>0.385</td>
<td>0.205</td>
<td>0.181</td>
<td>0.116</td>
</tr>
<tr>
<td>( \log(\text{home range}) )</td>
<td>1</td>
<td>0.505</td>
<td>0.150</td>
<td>0.401</td>
</tr>
<tr>
<td>( \log(\text{population density}) )</td>
<td>1</td>
<td>0.576</td>
<td>0.166</td>
<td>0.348</td>
</tr>
<tr>
<td>terrestriality</td>
<td>0.717</td>
<td>-1.29</td>
<td>0.619</td>
<td>-0.231</td>
</tr>
<tr>
<td>annual rainfall</td>
<td>0.831</td>
<td>-0.00057</td>
<td>0.00026</td>
<td>-0.199</td>
</tr>
</tbody>
</table>

Our variance components analysis returned an estimate for the interspecific variance in overlap of 0.425, compared with an intersite component of 0.518. Thus, most variation in overlap is found among populations of the same species with a slightly smaller portion among species.

Our multimodel inference revealed that seven of the 32 candidate models constitute the 95 per cent ‘confidence set’, and the best model contains all terms except body mass. All fixed effect terms appear in at least three candidate models, with importance scores ranging from 0.39 to 1.0 (table 3). The addition of a term for day range led to a marginally worse model (\( \Delta \text{AIC}_c = 1.4 \)). While importance scores provide a measure of the statistical significance, the absolute values of the standardized effect sizes, \( |b'| \), estimate the ecological significance of each term. In fact, there is good agreement between these measures, with the highest ‘significance’ attributable to home range and population density, intermediate levels for rainfall and terrestriality, and lowest for body size. The direction of the model average parameters reveal that overlap is high for larger-bodied species, when home range and population density are large, where annual rainfall is low and is higher for arboreal species than terrestrial ones (table 3). Of these, four trends are in the predicted direction but the relationship with population density is contrary to expectation.

4. Discussion

We have provided the most extensive analysis of space-use traits in wild mammals to date. Our results demonstrate that overlap among adjacent home ranges is predictable from ecological parameters at the species, site and population level.

The scaling exponents for space-use traits in primates are broadly consistent with theory, being somewhat shallower than other mammals [5,6,9,10,37]. Likewise, the scaling of group size, for which there is less theory [38], is much shallower than the value of 0.66 reported among artiodactyls [16]. These results are consistent with the fact that most primates are arboreal: organisms foraging in three dimensions are predicted to display much shallower scaling than exclusively terrestrial species [7,17]. This interpretation is strengthened by the finding that some relationships were steeper among the subset of terrestrial primates (table 2).

We then tested the predictions of the ‘gas model’ [10]. We found extremely good agreement between the observed scaling exponent for overlap and the difference in scaling of per capita home range and (inverse) population density. Paradoxically, we cannot reject the null hypothesis that overlap is independent of body size, yet our results are entirely consistent with the conclusion that overlap explains the discrepancy between the scaling of home range and population density [10,15]. Overlap in the gas model is an inverse function of the neighbour interaction frequency, which itself is given by the product of population density, day range and detection distance (the distance at which neighbours can detect one another). All three traits are assumed to show simple allometric relationships, thus leading to the prediction that overlap itself increases with body size [10]. From this, population density and day range are expected to show strong relationships with overlap, yet our data reveal no correlation with day range and that the population density relationship is positive, not negative. These complications emphasize that simple allometric arguments have limited explanatory power at the population scale [8].

Our results examine the degree to which home range overlap varies between and within species. While territoriality tends to be a fixed species trait, these data suggest that overlap, in contrast, is very plastic. Modelling both inter- and intraspecific variation together allowed us to compare the role of conserved species traits (body size), plastic traits (home range and population density) and spatial covariates (rainfall). Many of these patterns are consistent with the economics of defendability [26,39]. The key finding is that overlap increases with home range size: large home ranges are more difficult to patrol (all other things being equal) owing to the lower likelihood of detecting an intruder. Overlap is also higher when annual rainfall (i.e. habitat productivity) is low: home ranges in unproductive habitats have lower energetic value, making them less worth defending than if productivity was high [19,20]. Moreover, primates living in habitats of low productivity must spend more time foraging, leaving less time to spend patrolling the home range. These arguments are based on the average level of resources in a given habitat, but are equally applicable to the patchiness of resources in space and time [15,19,22,23].

High population density was predicted to be associated with low overlap, through its impact on the neighbour interaction frequency [10], but we found the opposite relationship. However, the predicted mechanism operates only if home ranges are actively defended against intruders. While many primates are territorial, others make no attempt to exclude either conspecifics or heterospecifics (e.g. proboscis monkeys [40]). In the absence of active defence, and after controlling for other variables (especially home range size), high density populations will be have a higher frequency of incursions into neighbouring home ranges (i.e. high overlap). Thus, the economics of defendability is likely to determine whether
the relationship between population density and overlap is positive or negative.

While the diversity of primate life history and ecology make them a useful group for testing comparative hypotheses, some aspects of this variation confound our ability to draw general conclusions. For example, many species use behavioural strategies such as scent marking (e.g. lemurs) and loud calls (e.g. mangabeys, gibbons, howler monkeys) to minimize overlap between adjacent groups [41, 42], such that detection distance is far from a simple power law function of body size [10]. Simple arguments about defendability are further complicated by species that patrol in fission–fusion subgroups (spider monkeys, chimpanzees), or where territory existence to defend females rather than ecological resources [43, 44]. Despite these complexities, our analyses demonstrate the potential to recognize fundamental interspecific relationships between space-use traits. Moreover, our models incorporating intraspecific variation reveal the relationships with site-level factors (i.e. productivity) that are independent of species’ mode of territoriality.

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