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1 **Immigrant males' knowledge influences baboon troop movements to**  
2 **reduce home range overlap and mating competition**

3

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19

## 20 **Abstract**

21 Mechanistic models suggest that individuals' memories could shape home range patterns and  
22 dynamics, and how neighbours share space. In social species, such dynamics of home range overlap  
23 may be affected by the pre-dispersal memories of immigrants. We tested this "immigrant knowledge  
24 hypothesis" in a wild population of chacma baboons (*Papio ursinus*). We predicted that overlap  
25 dynamics with a given neighbouring troop's home range should reflect males' adaptive interests in  
26 overlap when the alpha male had immigrated from this neighbouring troop but less so when the  
27 alpha male originated from elsewhere. We used data collected between 2005 and 2013 on two  
28 neighbouring troops in Namibia, comprising GPS records of daily ranges, male natal origins, daily  
29 females' reproductive status, and a satellite index of vegetation growth. We found support for our  
30 prediction in line with male reproductive strategies but not in line with foraging conditions. In  
31 periods with a higher relative number of fertile females over adult males in the focal troop, male  
32 baboons would benefit from reducing overlap with their neighbours to mitigate the costs of  
33 between-troop mating competition. This was indeed observed but only when the alpha male of the  
34 focal troop was an immigrant from that neighbouring troop, and not with alpha males of other  
35 origins, presumably due to their different knowledge of the neighbouring troop. Our findings  
36 highlight the role of reproductive competition in the range dynamics of social groups, and suggest  
37 that spatial segregation between groups could increase through the combination of dispersal and  
38 memory.

39

40

## 41 **Keywords**

42 Home range overlap – Dispersal – Collective decision-making – Spatial memory – Mating competition  
43 strategies – Chacma baboons

## 44 Introduction

45 How animals use space deeply affects ecological processes (Burt, 1943; Clutton-Brock, 1989; Riotte-  
46 Lambert et al., 2017). Home ranging patterns, when individuals or social units range within restricted  
47 areas across their daily lives, are ubiquitous (Börger et al., 2008; Burt, 1943). The size and overlap of  
48 adjacent home ranges is variable, and can change through time (Duncan et al., 2015; Kranstauber et  
49 al., 2019; Pearce et al., 2013). Classical ecological theory posits that these home range properties are  
50 largely determined by the interplay between resource distribution and abundance in the landscape  
51 (Duncan et al., 2015; Kelt & Van Vuren, 2001), and/or the nature of interactions between neighbours:  
52 potential mates might be attractive, but rivals and territorially-enforced borders can be repulsive  
53 (Börger et al., 2008; Burt, 1943; Clutton-Brock, 1989; Markham et al., 2013). Recent mechanistic  
54 movement models suggest that memories acquired by individuals during their life could also be key  
55 to understand home range properties (Börger et al., 2008; Riotte-Lambert et al., 2015; Wakefield et  
56 al., 2013). According to this latter view, changes in the information possessed by animals  
57 (“knowledge”), for instance through learning, could alter subsequent home range shapes and  
58 dynamics as well as their consequences on ecological processes (Riotte-Lambert et al., 2017;  
59 Spencer, 2012).

60 In group-living species, the information possessed by social units may also change through  
61 demographic processes. While groups may lose information through the loss of keystone individuals  
62 due to death or emigration (Brent et al., 2015; Foley et al., 2008), immigrants may bring new and  
63 potentially non-local information into the group (Cote & Clobert, 2007; Jacob et al., 2015; Whiten et  
64 al., 2007). In the case of home ranges, the effective transfer of spatial information between groups  
65 through individual dispersal, i.e., whether the information carried by an immigrant is shared with its  
66 new group, may be dependent on the influence of immigrants on the collective decision-making  
67 processes involved in group movements (Couzin et al., 2005), (van de Waal et al., 2013).  
68 Nevertheless, where the necessary conditions are met, the exchange of group members between  
69 neighbouring social groups could affect how these groups subsequently share space, amplifying or

70 buffering the effects of more classical determinants of overlap such as territoriality (Burt, 1943) or  
71 competition for resources (Duncan et al., 2015; Kelt & Van Vuren, 2001). Thus, the origin of  
72 immigrants in a troop (as a proxy for their expected knowledge of neighbouring troop's ranges) may  
73 help to predict the range overlap dynamics of this troop with the home ranges of its neighbours: the  
74 "immigrant knowledge hypothesis".

75         The immigrant knowledge hypothesis generates several alternative predictions. First,  
76 immigrants using their knowledge to visit resources located in the area "traditionally" used by their  
77 old (pre-dispersal) group could influence their new (post-dispersal) group to overlap more with their  
78 old group than other neighbouring groups. We would then observe higher overlap of a focal troop  
79 with a neighbouring home range when immigrants in the focal troop originate from this neighbouring  
80 group than from elsewhere, an effect akin to the homogenizing effect of dispersal classically  
81 described in population genetics or cultural transmission theories (Cavalli-Sforza & Feldman, 1981;  
82 Henrich & Boyd, 1998; Mesoudi, 2018). Alternatively if immigrants do not use memory acquired pre-  
83 dispersal and/or if immigrants are not influential on collective decisions (Luncz & Boesch, 2014; van  
84 de Waal et al., 2013; Whiten et al., 2007), dispersal should have no effect on the ranging behaviour  
85 of the new host group, and home range dynamics should be poorly predicted by the origin of  
86 immigrants. As yet another possibility, immigrants could use their spatial memory to avoid rather  
87 than return to the ranging areas traditionally used by their pre-dispersal group (Ellison et al., 2020;  
88 Wolf et al., 2009), which could help them to reduce between-group competition (Ellison et al., 2020;  
89 Markham et al., 2013; Riotte-Lambert et al., 2017) and/or avoid inbreeding (Alberts & Altmann,  
90 1995). Overall, immigrant pre-dispersal memory may be expected to have various effects on ranging  
91 overlap between neighbours. To our knowledge, however, these ideas have never been tested.

92         In this study, we investigated the links between immigrant knowledge and home range  
93 overlap in chacma baboons (*Papio ursinus*), by testing whether the origin (and hence expected  
94 knowledge) of dominant (alpha) males could help to predict patterns of home range overlap

95 between neighbouring troops. Baboons (*Papio spp*) are well-suited to explore these questions.  
96 Baboon troops are not territorial (they do not actively defend or patrol borders) and their home  
97 ranges partly overlap with those of their neighbours (e.g. Markham et al., 2013). In this taxon,  
98 females are philopatric while males typically disperse to surrounding troops when they reach  
99 maturity (Alberts & Altmann, 1995; Packer, 1979). Male baboons in captivity show long-term  
100 memory spanning years (Fagot & Cook, 2006), suggesting that immigrant males may be able to  
101 remember the spatiotemporal distribution of food and other resources used by their pre-dispersal  
102 troop. Finally, the collective decision-making processes in baboon groups have been intensively  
103 studied (e.g. see review in Montanari, 2019), which helped guide our analyses and interpretations.

104 In baboon troops, dominant males, and especially alpha males, can have a disproportionate  
105 influence on the collective movement decisions (e.g. in three distinct populations of chacma  
106 baboons: Kaplan et al., 2011; King et al., 2008; Stueckle & Zinner, 2008). Such males are likely to have  
107 a detectable impact on large-scale troop ranging patterns. Our initial focus was therefore to test the  
108 prediction that a focal troop's pattern of overlap with a neighbouring troop would depend on  
109 whether or not the focal troop's alpha male was an immigrant originating from that particular  
110 neighbouring troop. However, dominant males are not the only individuals that influence collective  
111 movement decisions in baboons (Strandburg-Peshkin et al., 2015; Stueckle & Zinner, 2008), and their  
112 influence may be limited to specific contexts and too ephemeral to affect large-scale ranging  
113 patterns. We thus also considered whether the observed overlap fitted with the expected adaptive  
114 interests of alpha males versus those of other troop members (Conradt et al., 2009; King et al., 2008;  
115 Strandburg-Peshkin et al., 2018). In order to do this, we reviewed and synthesized for different group  
116 members (males of different origins and dominance rank; females at different stages of their  
117 reproductive cycle) their likely preferences for home range overlap with neighbours according to  
118 their adaptive interests (food resources, mating strategies). To keep the main text relatively simple  
119 and concise, this review is presented in the supplementary information (Appendix S1, synthesized in  
120 Tables S1 and S2). In the main paper, we go on to consider the two main predictions for alpha males

121 arising from this review, while in the supplementary information we also consider alternative  
122 explanations (as well as alternative analytical approaches), such as the potential role of inbreeding  
123 avoidance by alpha males (see Appendices S1-S4).

124         The two predictions we test for the immigrant knowledge hypothesis relate to variation in  
125 foraging conditions and mating competition respectively, two key determinants of fitness known to  
126 affect range overlap in baboons (Markham et al., 2013). First (Prediction 1), during periods when  
127 food is scarce, a focal troop will show greater range overlap with a neighbouring troop's home range  
128 when the focal troop contains a knowledgeable alpha male (i.e. an immigrant from this neighbouring  
129 troop) compared to when the focal troop has an alpha male that is not knowledgeable (i.e. a natal  
130 alpha male, or an immigrant from another troop). This pattern is predicted on the basis that the  
131 alpha male will respond to poor foraging conditions by returning to areas where he remembers  
132 finding food previously. Second (Prediction 2), when the focal troop contains a relatively higher  
133 number of fertile females per adult males (i.e. has a female-biased operational sex ratio), the focal  
134 troop will overlap less with the neighbouring troop's home range when the focal troop has a  
135 knowledgeable alpha male than when it does not. This pattern is predicted on the basis that males  
136 use inter-troop encounters to assess reproductive opportunities, and when a female-biased  
137 operational sex ratio in the focal troop increases the likelihood of male immigration from the  
138 neighbouring troop (with its associated challenges for the alpha male position and infanticidal attacks  
139 on the alpha male's offspring), the alpha male will avoid those areas where he knows encounters  
140 with that neighbouring troop are more likely. We tested our two predictions using observational data  
141 from a long-term field study of two neighbouring chacma baboon troops.

## 142 **Materials and Methods**

### 143 **Study system**

144 We used data collected episodically over a nine-year period (2005-2013) from two neighbouring  
145 troops of chacma baboons *Papio ursinus* (named L and J) living at Tsaobis Nature Park (22.38°S,

146 15.75°E), Namibia. The study area consists of arid hills and plains crossed by the ephemeral Swakop  
147 riverbed. The baboons forage on sparse vegetation across this landscape as well as in patches of  
148 riparian woodland (Cowlshaw, 1997). Individuals in both troops are habituated to human observers  
149 and individually identifiable. Troop sizes (including juveniles) during this period ranged from 29-55 in  
150 troop L and 37-59 in troop J, including between 1-10 (median: 3) and 1-11 (median: 4) adult males,  
151 respectively.

152 Each year, a field season of variable length (2-7 months) took place, centered on the dry austral  
153 winter (details on study periods in Appendix S2). The two troops were followed daily on foot from  
154 dawn to dusk, and data on demography, behaviour, and ranging patterns were recorded. We  
155 restricted our analyses to those periods where demographic data were simultaneously available for  
156 both troops, leading to the exclusion of two field seasons (2007, 2011: Table S3). In addition, due to  
157 the routine capture of the baboon troops and three large-scale feeding experiments between 2005-  
158 2013, there were several periods of provisioning at fixed locations during the study (e.g. King et al.,  
159 2008). Due to the potential disruption of natural ranging patterns at these times, data from these  
160 periods were discarded (Table S3). All observation protocols were approved by the ZSL Ethics  
161 Committee and by the Ministry of Environment and Tourism in Namibia, and adhered to the  
162 ASAB/ABS Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

## 163 **Data collection protocols**

### 164 ***Ranging data***

165 The daily travel route of each troop was recorded by observers with handheld GPS. GPS fixes were  
166 taken every 30 mins from the moment the troop left the morning sleeping cliff until it reached the  
167 evening sleeping cliff. Additional GPS fixes were recorded *ad libitum* at each waterhole visited, when  
168 an encounter with another troop occurred, and when the troop produced alarm calls from a  
169 perceived source of danger.



## 170 *Group demography*

171 Troop censuses were carried out at the beginning and end of each field season, and migration, birth  
172 and death events were recorded throughout. In addition, the reproductive states of females were  
173 recorded daily. In our population, oestrous cycles last  $24.1 \pm 6.8$  days (range 10-45 days) and are not  
174 synchronised (Clarke et al., 2012). We categorized females as sexually receptive or not by the  
175 presence/absence of a sexual swelling (lasting on average  $49.8 \pm 13.4$  % of the female's full oestrous  
176 cycle, median 50%). The Operational Sex Ratio (OSR) of each troop was then calculated daily as the  
177 number of sexually receptive females divided by the number of adult males.

178 For each adult male, we determined whether he was born in one of the two study troops or  
179 in another troop. In 2005-2006, this was inferred by genetic relatedness and the capture history of  
180 the local baboon troops since 2000 (Huchard et al., 2010). Since 2006, males dispersing between the  
181 two troops were identified from direct observations, meaning all new unidentified males were born  
182 in an unstudied troop. From these records, we categorized males in each troop as either born in the  
183 neighbouring troop (i.e. if a male observed in troop J was born in troop L, and vice versa) or  
184 elsewhere (i.e. either born in an unstudied troop, or natal to the focal troop). For the purpose of  
185 testing our hypothesis we did not differentiate between natal males and males born in unstudied  
186 troops, since neither would be considered as knowledgeable of the neighbouring troop's range as  
187 males born in the neighbouring troop (see Appendix S1).

## 188 *Male dominance hierarchy*

189 Agonistic interactions, comprising displacements, supplants, threats, chases, and attacks, were  
190 recorded daily using *ad libitum* and focal observations with a standard protocol (described in  
191 Huchard & Cowlshaw, 2011). Dominance hierarchies have been calculated each year as part of  
192 previous studies, using the I&SI method (De Vries, 1998) implemented in Matman 1.1.4. software  
193 (Noldus Information Technology 2003) and were found to be consistently linear across all troop  
194 members (e.g., King et al. 2008, Marshall et al. 2013). During all but one field season, a single alpha

195 male could be reliably identified in each troop, but the ranks of subordinate males were not always  
196 clearly resolved. In total, 10 different alpha males (out of a total of 41 adult males) were identified  
197 across both troops over the study period. There was unusually high instability in the male dominance  
198 hierarchy in 2013 in L troop (Baniel et al., 2018) but all males contesting for the alpha position at that  
199 time were born in J troop, and thus could be considered together as born in the neighbouring troop  
200 for our purposes.

201 We also explored the use of a dominance-weighted mean of the number of males within  
202 each troop that were born in the neighbouring troop (or not), rather than focusing only on the alpha-  
203 male's origin (Appendix S3). This tested the possibility that other high-ranking males collectively  
204 influenced group movements according to their potential pre-dispersal memory. However, this  
205 variable was negatively correlated with alpha male origin (Appendix S3), introducing issues of  
206 multicollinearity (Graham, 2003). Because of this complication, and two further drawbacks of the  
207 dominance-weighted mean (the subordinate male hierarchies were not always clearly resolved, and  
208 the choice of weighting system was arbitrary), in this paper we report only those results obtained  
209 using the alpha male origin. Nevertheless, using the weighted mean did not affect our conclusions  
210 (Appendix S4).

### 211 *Environmental Data*

212 In our study area, baboons mainly forage on the leaves, flowers, berries and/or pods of either small,  
213 homogeneously scattered, herbs and dwarf shrubs in the desert hills, or larger, more localized, trees  
214 and shrubs along the dry Swakop riverbed. In the late winter months, five plant species alone make-  
215 up 92-97% of male and female feeding time, respectively (Cowlshaw, 1997). The availability of these  
216 different plant foods varies across seasons and between years: drier climatic conditions during the  
217 winter months and in drought years are characterized by a much lower availability of food, especially  
218 in the hills. At these times, the baboons focus on finding scarcer and more heterogeneously  
219 distributed food patches, mainly along the riverbed. To estimate these seasonal and inter-annual

220 variations in foraging conditions, we used the Normalized Difference Vegetation Index (NDVI;  
221 Pettorelli, 2013). NDVI is a satellite-based proxy of primary productivity ('greenness'). This index  
222 varies between -1 and +1, with higher positive values representing more productive areas. We used  
223 NDVI data at a 16-day and 250mx250m resolution (MODIS 13Q1), downloaded from the NASA Land  
224 Processes Distributed Active Archive Center (Reverb|ECHO service, <http://reverb.echo.nasa.gov/>,  
225 2013), across a rectangle defined by the extreme latitude and longitude reached by either troop  
226 between 2005 and 2013 plus an external margin of 0.01°. For the NDVI measures reported in the  
227 main text, we averaged for each 16-day period the values across all pixels of the study area. This  
228 resolution provides a coarse but informative proxy for conditions of access to food resources by  
229 baboons in our study area and period, capturing especially the within- and between-year seasonal  
230 trends (see Results). In the Tsaobis population, similar NDVI measures have been found to predict  
231 the rate of infant development during the winter period when we study them (Dezeure et al., 2020)  
232 as well as individual body condition across all age-sex classes (Cowlshaw et al., *unpublished*).

### 233 **Data processing and statistical analyses**

#### 234 *Traditional core areas ("MASK") as proxies of male pre-dispersal memory*

235 To test our hypothesis, we first needed to estimate what information immigrant males could have  
236 previously acquired about their pre-dispersal ranging area. Given our annual data gaps on ranging  
237 and on the exact timing of dispersal, uncertainty about what every male could remember about pre-  
238 dispersal ranges, and further variation arising from their different dispersal dates, it was not possible  
239 to develop individual-level memory estimates. Nevertheless, since both troops were consistently  
240 found within the same areas over our winter study periods (see below), with L troop tending to range  
241 north-eastward of J troop, it was possible to use these areas to develop a troop-level estimate of  
242 spatial memory that captured the different experiences of males born in different troops. These  
243 "traditional" core ranging areas were thus used to define a Minimum Area of Shared Knowledge  
244 ("MASK") for each troop. According to our immigrant knowledge hypothesis, if information about  
245 natal areas possessed by immigrant males from a neighbouring troop influences the ranging

246 behaviour of their new resident (focal) troop, then it should affect the extent of overlap of the focal  
247 troop with that neighbour's MASK, irrespective of minor variations in memory that may occur across  
248 different males born in that neighbouring troop.

249         To define the MASK of each troop, we first estimated their (winter) home range for each field  
250 season. Then, for each troop, we intersected these annual range estimates to identify the MASK as  
251 the area consistently used by the troop every season we studied them (so that any male born in this  
252 troop would have experience of this area). We explored three alternative methods to estimate  
253 annual ranges (Appendix S3): Minimum Convex Polygons (MCPs) accounting for either 100% or 95%  
254 of recorded locations, and isopleth (95% contours) of Utilisation Distributions (UDs) based on spatial  
255 kernels (using default parameterisation, see Appendix S5 for the statistical packages used). Although  
256 the MASKs show some variation in shape and size between these different methods, our conclusions  
257 remained the same irrespective of the approach adopted (Appendix S4). Unless stated otherwise we  
258 report our 95% kernel UD results here, although occasionally we also compare these results with  
259 those obtained using the 100% MCP approach. Note that irrespective of the method used, the  
260 MASKs should not be interpreted as accurate home range estimators but rather as semi-quantitative  
261 estimates of potential differences in the spatial memory of males from different natal troops during  
262 the winter months.

263         The data used in the calculation of the MASKS included all years in the sample except 2008.  
264 Because the 2008 field season was short (<2 months, cf. 4.5-6.0 months in other years), the annual  
265 ranges appeared smaller than in other years (60% and 65% of the mean other annual areas for  
266 troops J and L, respectively), and they were almost entirely contained within the intersecting area of  
267 all other annual ranges, we discarded this year from the MASK calculations (but not from the  
268 remainder of the analyses). For the remaining six years, for each troop, the size of the annual winter  
269 ranges did not correlate with the number of days of observations (Pearson's correlations, J troop:

270  $t=1.28$ ,  $df=4$ ,  $p=0.27$ ; L troop:  $t=1.14$ ,  $df=4$ ,  $p=0.32$ ), suggesting that our annual estimates were good  
271 indicators of stationary winter troop ranges.

### 272 *Temporal scale of analyses*

273 Once the two MASKs had been calculated to estimate males' memories of the ranging area  
274 traditionally used by their natal troop, we then analysed on a much finer temporal scale the extent to  
275 which a troop ranged in areas overlapping with the MASK of the neighbouring troop. For these  
276 analyses we chose to work on a temporal scale of 5-day periods, as a compromise between statistical  
277 power (finer temporal scales provide more data points) on the one hand and potential issues of both  
278 auto-correlation (at finer temporal scales, consecutive ranging and demographic records cannot be  
279 considered independent data points) and robustness to errors in GPS and/or demographic records  
280 (finer temporal scales are more sensitive to occasional mistakes by observers that can be smoothed  
281 out by averaging records over longer periods) on the other. Inspection of model residuals plotted  
282 against dates indicated there was no spatial autocorrelation. Furthermore, our conclusions were  
283 unchanged when running the same analyses with either 2- or 16-day periods (Appendix S4).

### 284 *Statistical models*

285 To test our hypothesis, we assessed how the extent of overlap of a troop's 5-day range with its  
286 neighbour's MASK (our response variable) varied in relation to the knowledge of the alpha male, the  
287 quality of the environment, and the relative number of fertile females in the focal troop (our  
288 explanatory variables). To calculate our response variable, "*Overlap*", we calculated the 95% kernel  
289 UD contour of each troop over each successive 5-day period, and then measured the overlap of this  
290 5-day range with the neighbouring troop's MASK (in  $\text{km}^2$ ). Periods where more than two days out of  
291 five had  $\geq 3$  hours missing GPS data were discarded. Our three explanatory variables were then  
292 calculated as 5-day means from the available daily values: alpha male knowledge, "*Alpha Origin*",  
293 was a binomial predictor which was scored as 1 if the alpha male was an immigrant from the  
294 neighbouring troop and 0 if he was not; environmental quality "*NDVI*" was a continuous predictor

295 where daily values were drawn from 16-day resolution data; and the relative number of fertile  
296 females “*OSRfocal*” was also a continuous predictor which scored more highly when there were  
297 relatively more sexually receptive females than adult males in the focal troop. In addition, because  
298 the value of *Overlap* is limited by the size of the total ranging area covered by the troop during these  
299 five days, which is likely to vary, we included an additional control variable, “*Area*”. This was  
300 calculated as the total 5-day range size, with the expectation that periods of smaller overall ranging  
301 would show lower *Overlap* values. Using *Area* as an explanatory variable (rather than as an offset)  
302 allowed us to more easily compare models with and without it (Appendix S4).

303 To check the robustness of our results, we also explored how our conclusions would be  
304 affected if we used alternative response variables or included additional, potentially confounding,  
305 explanatory variables. As these analyses did not change our conclusions, we only report them in  
306 Appendix S3 and Appendix S4 (which describe the definitions of these variables and overall multi-  
307 collinearity structure, and the alternative model outcomes, respectively). First, with respect to  
308 alternative response variables, we explored the effects of using different methods to calculate the  
309 MASK and 5-day range, on which the *Overlap* variable is based, comparing between MCPs and 95%  
310 kernel UDs. We also re-ran our models replacing *Overlap* with a response variable quantifying the  
311 time spent in the neighbouring MASK rather than the extent of spatial overlap, assessed as the  
312 proportion of all GPS locations of each 5-day period falling into the neighbouring MASK. Second, with  
313 respect to additional explanatory variables, we explored the influence of the relative number of  
314 fertile females over adult males in the neighbouring (rather than focal) troop (“*OSRneighbour*”), the  
315 dominance-weighted mean of all males’ origins in the focal troop (“*MalesOri*”), and the difference in  
316 NDVI values between the two neighbouring MASKs (“*DiffNDVI*”) on patterns of *Overlap*.

317 In total, 171 5-day periods from seven seasons between 2005 and 2013 were analyzed (for  
318 further details on data structure, see Appendix S2). We used linear mixed models (LMMs) with the  
319 response and explanatory variables described above, further including interactions between *Alpha*

320 *origin* and both *NDVI* and *OSRfocal* to test Predictions 1 and 2 respectively, i.e., that a troop  
321 containing a knowledgeable alpha male will show greater range overlap with their neighbour's MASK  
322 when food is scarce, but lower overlap when his troop contains relatively more fertile females,  
323 respectively. Our random effects comprised year, troop and alpha male identity, to control for the  
324 potential non-independence of data from particular males in a troop within and across years. We  
325 checked and corrected for co-linearity between our explanatory variables (Appendix S3), following  
326 the residual (or sequential) regression approach (following Graham 2003). We therefore replaced  
327 *NDVI* with the residuals of *NDVI* (*resNDVI*) regressed against *Area* to avoid co-linearity effects  
328 between these variables (see Appendix S3). However, including *NDVI* (instead of *resNDVI*) without  
329 *Area* in the models led to the same conclusions (Appendix S4).

330 We computed (with maximum-likelihood estimation) all nested models from the full model  
331 and ranked them by Akaike's Information Criterion corrected for small sample size (AICc). We then  
332 discarded "uninformative" models that were nested within better ranked models, without  
333 decreasing AICc values of more than 2 units per parameter added (Arnold, 2010). We present a  
334 model-averaging outcome of this ranking and the support for retaining each variable. We checked  
335 the first-ranking model's validity (variance homogeneity and balanced residual values) by visual  
336 inspection of residuals versus fitted values and versus date.

337 All analyses were carried in the R environment version 3.1.3 (2015-03-09). Packages used for  
338 analyses and their associated references are listed in Appendix S5. Data and code will be deposited in  
339 Dryad following acceptance for publication.

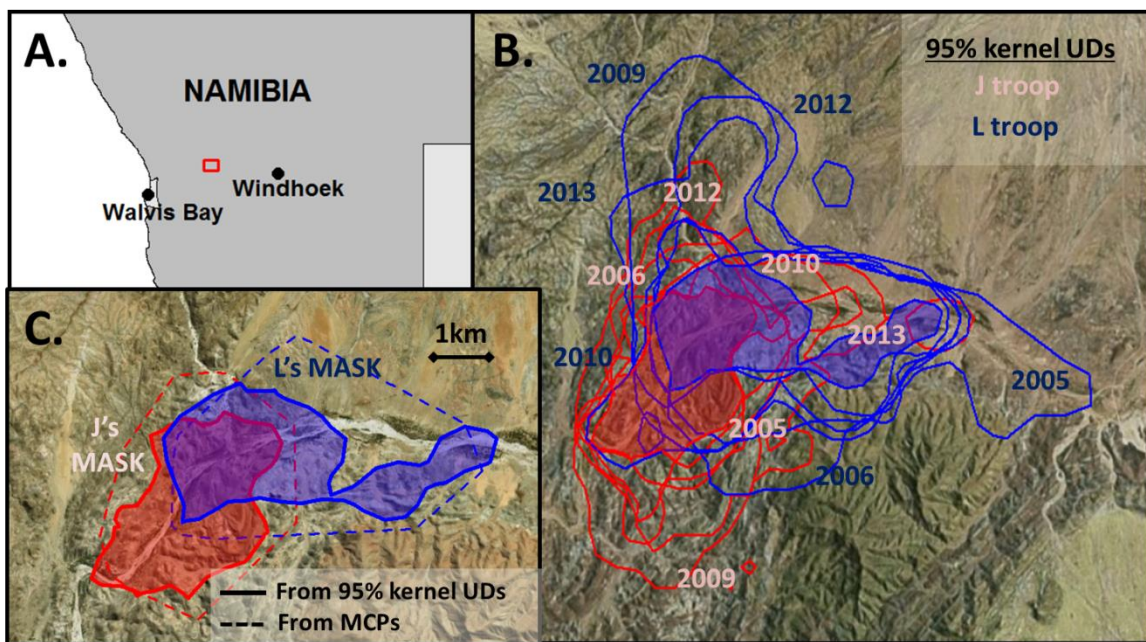
340

341

342 **Results**

343 **Large-scale home ranges: stability and variability through time**

344 The baboon troop “winter” ranges at Tsaobis (Fig.1A), estimated by the 95% kernel Utilization  
345 Distribution (UD) during each field season, extended from 13.3 km<sup>2</sup> to 33.0 km<sup>2</sup> in J troop (mean =  
346 24.0km<sup>2</sup>, median = 26.8km<sup>2</sup>), and from 24.6 km<sup>2</sup> to 44.9 km<sup>2</sup> in L troop (mean = 33.7km<sup>2</sup>, median =  
347 33.2km<sup>2</sup>) (Fig.1B). Calculation of the Minimum Area of Shared Knowledge (MASK) for each of the two  
348 troops (as the intersecting area of these annual winter range estimates) revealed that J troop’s MASK  
349 was 10.6 km<sup>2</sup> and extended to the west of L troop’s MASK, which was of similar area (11.5 km<sup>2</sup>,  
350 Fig.1C). The two MASKs overlapped onto a ‘shared’ area of 4.2 km<sup>2</sup>. These MASKs comprised 32-79%  
351 of each annual winter ranging area in J troop (median: 39.6%) and 14-42% in L troop (median:  
352 18.8%). Despite the variance in each year’s ranges not captured by the MASKs, the consistency in  
353 both the absolute size of the MASKs and their location relative to one another, regardless of the  
354 method used to calculate them (see Fig.1C and Appendix 3), shows that a significant part of each  
355 troop’s range, i.e., the MASK, remained stable across field seasons.



356

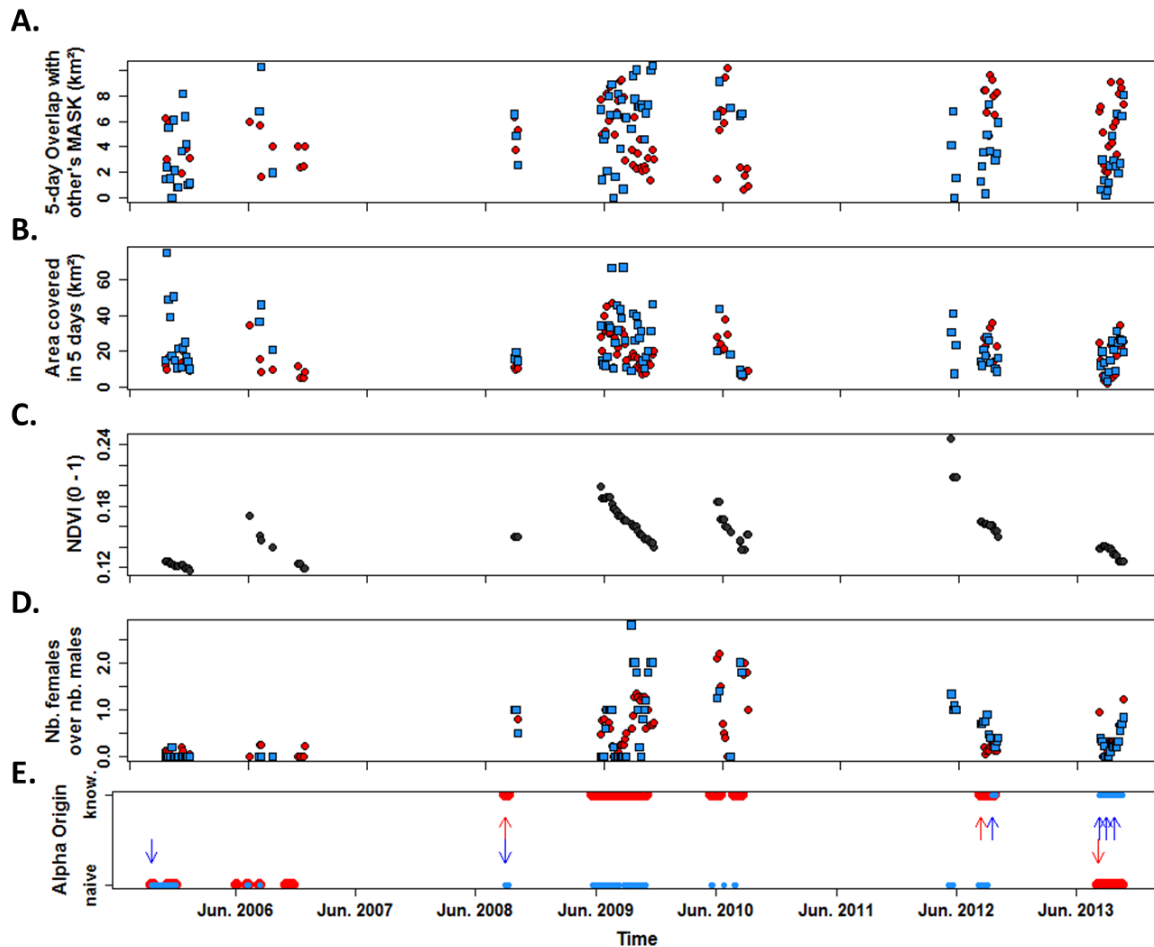
357 **Figure 1: (A) The study site location in central Namibia (red rectangle); (B) Annual winter ranging areas (95% kernel UD**  
358 **contours) for J troop (red) and L troop (blue) in 2005-2013; (C) The MASKs of each troop, defined as the intersection of**



359 each annual winter range, used to approximate the pre-dispersal memories of males born into that troop. In (C), the  
360 MASKs obtained using 95% kernel UDs, shaded with solid lines, are compared to those obtained using 100% MCPs,  
361 unshaded with dashed lines; the 95% kernel UD MASKs comprised a median and range of 39.6% (32-79%) of each J troop  
362 winter range and 18.8% (14-42%) of each L troop winter range, while the 100% MCP MASKs comprised 45% (35-73%) and  
363 44% (36-49%) respectively; the shared area of overlap between the two MASKs is 4.2 km<sup>2</sup> for the 95% kernel UD and and  
364 7.8km<sup>2</sup> for the 100% MCP (see also Appendix 3). Satellite images from Bing Map data © 2017 Microsoft.

### 365 **General overlap with the neighbour's MASK every 5 days**

366 Troops showed extensive variation in their overlap with the neighbouring troop's MASK (Fig.2A) and  
367 more generally in the total area they covered during each 5-day period (*Area*: J troop, mean and s.d.  
368 = 18.3 ± 10.5 km<sup>2</sup>, range: 2.0-47.1 km<sup>2</sup>, median = 16.7km<sup>2</sup>; L troop, 24.2 ± 14.4 km<sup>2</sup>, range: 2.2-30.9  
369 km<sup>2</sup>, median = 20.3km<sup>2</sup>; Fig.2B). As expected, *Overlap* tended to be higher in periods when troops  
370 covered larger areas (mean model weight for *Area* = 1.00; Table 1). When troops overlapped with the  
371 neighbouring MASK (*Overlap* value > 0), most of the overlap surface was within the shared part  
372 common to both MASKs (mean ± s.d.: 71.3 ± 22.5%, median: 65.9%, the shared area between MASKs  
373 represented at least 40% of the Overlap in 95% of 5-day Overlap values, these proportions were even  
374 greater when considering MCP-based MASKs) and therefore largely remained within the focal troop's  
375 MASK rather than venturing into the "exclusive part" of the neighbour's MASK.



376

377 Figure 2: Time series used for our analyses (red: J troop; blue: L troop; black: common to both troops) in top-to-bottom  
 378 order (panels A-E, respectively): *Overlap*; *Area*; *NDVI* (before correction for collinearity with *Area*); *OSR<sub>focal</sub>*; and *Alpha*  
 379 *Origin* ("know.": alpha male born in the neighbouring troop; "naïve": alpha male NOT born in the neighbouring troop;  
 380 arrows indicate change of alpha male identity).

381

### 382 Testing the Immigrant Knowledge hypothesis

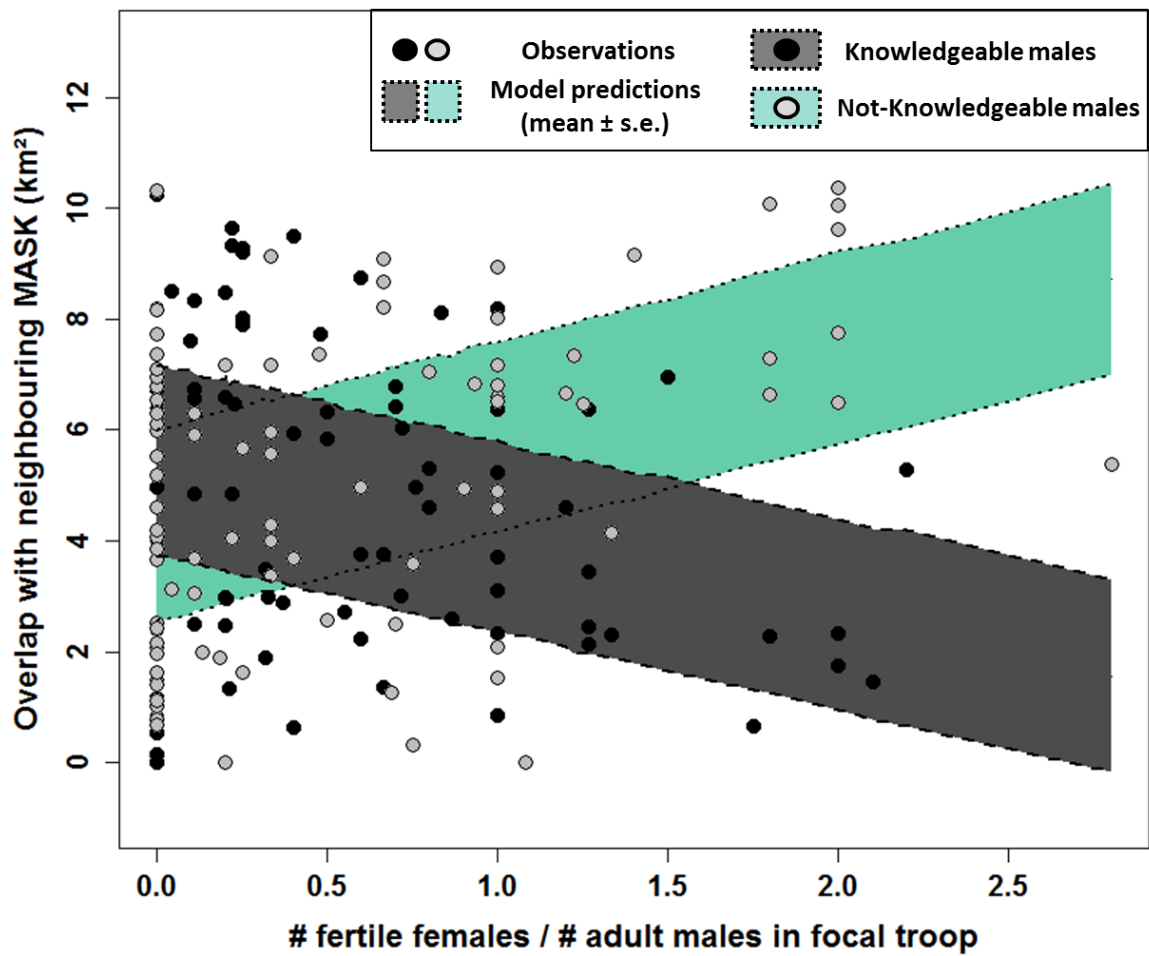
383 Our test of the immigrant Knowledge hypothesis utilised marked variation in NDVI, the focal troop's  
 384 operational sex ratio, and the origin of the focal troop's alpha male, across the study period (Fig.2C-E,  
 385 respectively). Assessment of the interaction terms in the full, averaged, model (Table 1) found little  
 386 support for Prediction 1 (*Alpha Origin\*resNDVI*), according to both the low AICc weight and  
 387 sensitivity of both the AICc weight and sign of the estimator sensitive to alternative modelling  
 388 decisions (see Appendix S4). Thus, there was no clear tendency for troops containing a  
 389 knowledgeable alpha male to show greater home range range overlap with that male's natal troop  
 390 range when primary productivity declined. However, there was strong support for Prediction 2

391 (*Alpha Origin\*OSRfocal*), with respect to both a high AICc weight and the consistent sign of the  
 392 estimator regardless of alternative modelling decisions (Appendix S4). Thus, when troops contained a  
 393 knowledgeable alpha male they showed lower range overlap with that male's natal troop range than  
 394 when they contained relatively more fertile females (Fig.3). Unexpectedly, this interaction also  
 395 indicated the reverse pattern was observed when the alpha male was not knowledgeable, i.e., that  
 396 troops showed greater range overlap with their neighbour when they contained relatively more  
 397 fertile females (Fig.3).

	Estimate	Adjusted Std. Error	z	AICc weight
<b>(Intercept)</b>	2.11	0.94	2.248	
<b>Alpha origin</b> (born in neighbouring troop)	1.22	0.78	1.565	1
<b>Area</b>	0.10	0.01	7.739	1
<b>OSRfocal</b>	1.56	0.39	4.061	1
<b>Alpha origin</b> (born in neighbouring troop) * <b>OSRfocal</b>	-2.95	0.64	4.604	1
<b>NDVI</b> (res)	-5.46e-4	1.08e-03	0.502	0.28
<b>Alpha origin</b> (born in neighbouring troop) * <b>NDVI</b> (res)	8.82e-04	1.91e-03	0.460	0.28

398 **Table 1: Average model of *Overlap* (extent of focal troop's overlap with neighbouring troop's MASK), based on AICc**  
 399 **weighting (with shrinkage, i.e. parameters not included in a model were set to 0 for model averaging). The *Alpha origin***  
 400 **of the focal troop was a categorical variable with alpha male not born in the neighbouring troop as the reference state.**  
 401 **The OSR of the focal troop indicates the Operational Sex Ratio in this troop (# fertile females/ # adult males). The *NDVI* of**  
 402 **the local environment was included as residuals (res) from the regression against the *Area* of the focal troop's home**  
 403 **range (see Methods).**

404



406

407 Figure 3: Observed (dots) and modelled (shaded) values of *Overlap* of a troop over the neighbouring MASK, per 5-day  
 408 period, for troops containing an alpha male either born in the neighbouring troop (“Knowledgeable”: black circles, dark  
 409 grey shading) or not (“not knowledgeable”: light grey circles, green shading) as a function of the relative number of  
 410 fertile females per adult male in the focal troop. The shaded model predictions were obtained by measuring the average  
 411 and s.d. of values predicted by the best-fitting model after randomly reshuffling combinations of observed predictor  
 412 values: the shaded areas thus illustrate that part of the variance our modelled predictors explained, rather than the  
 413 model uncertainty.

## 414 Discussion

415 We found that alpha males' natal origins helped to predict range overlap dynamics between  
416 neighbouring baboon groups, consistent with the immigrant knowledge hypothesis. Specifically, in  
417 support of our Prediction 2, when a focal troop contained a greater number of fertile females relative  
418 to males it was more likely to avoid overlap with a neighbouring troop (consistent with males'  
419 adaptive interests; Appendix S1), but only when its alpha male was an immigrant from that troop and  
420 not when the alpha male had another origin. However, contrary to Prediction 1, we found no  
421 evidence for an effect of alpha male knowledge on range overlap that was dependent upon our NDVI  
422 measure of foraging conditions. Overall, these results suggest that, in baboons, when alpha males  
423 exert an influence on troop movements, this influence is more likely to be in response to mating  
424 competition than to foraging conditions. Furthermore, our results suggest that the dispersal of male  
425 baboons may act to increase rather than decrease spatial segregation between the pre- and post-  
426 dispersal troops.

427 Our approach is indirect in its estimation of group members' respective knowledge and their  
428 influence on collective movement decisions, and relies on our review of the potential costs and  
429 benefits of overlapping with the neighbouring MASK for different troop members (Appendix S1). The  
430 observation that the focal troop increased overlap with the neighbour's home range when the alpha  
431 male was not originating from this neighbouring troop and it was against his adaptive interests (i.e.,  
432 when there was an excess of fertile females relative to males in his troop) suggests that these alpha  
433 males were not influencing collective movements at these times. The fact that this increase in  
434 overlap would be beneficial to the fertile females in the focal troop but detrimental to all other adult  
435 troop members (Appendix S1) suggests that it was these females who drove these movements. Yet  
436 the reverse patterns of overlap were observed when alpha males were immigrants from that  
437 neighbouring troop. This interaction effect of alpha male origin and mating competition is difficult to  
438 explain without assuming a difference in the knowledge (or use of knowledge) of alpha males of  
439 different origins exerting an influence on collective movements.

440 A difference in knowledge, or use of knowledge, between group members – and especially  
441 between males of different pre-dispersal origins – seems the most parsimonious explanation. Indeed,  
442 even though our two troops showed extensive range overlap over our study period, each had distinct  
443 home ranges consistently used over the years. If we split each troop’s MASK into two sections,  
444 according to whether or not it overlaps with it’s neighbour’s MASK, and call the exclusive, non-  
445 overlapping section the ‘core area’, it is clear that visits to the core area of one troop by the other  
446 troop were rare and limited (i.e. overlap between neighbouring MASKs was mainly restricted to the  
447 same small area over the years, common to both MASKs, Fig.1). This supports the view that  
448 individuals should not possess or make use of similar spatial memories if they belong to different  
449 troops, since there is no other identified mechanism of spatial segregation in the absence of  
450 territoriality (Börger et al., 2008; Riotte-Lambert et al., 2015). Nevertheless, it does seem likely that  
451 males would eventually learn to identify the whereabouts of the neighbouring troops, e.g., by  
452 monitoring where they encounter them (Ellison et al., 2020; Markham et al., 2013), leading to the  
453 fading away of the male origins effect as time since immigration passes. Unfortunately, our sample  
454 size and uncertainty on some immigration dates did not permit a direct test of this prediction. Male  
455 baboons in captivity can demonstrate remarkable learning capacities (Fagot & Cook, 2006), yet in  
456 contrast to these controlled experimental situations, there are several sources of noise that may  
457 affect learning rates in the wild, including the fact that neighbours will not always be present in the  
458 area of overlap between neighbouring home ranges. Despite extensive exploration of potential  
459 confounding factors (Appendix S3), we could not find a better explanation of our results. In Appendix  
460 S6, we discuss further the implications of our findings on the potential collective-decision  
461 mechanisms involved.

462 Apart from pre-dispersal memory, males of different origins also differ in their kin  
463 relationships with neighbouring troops. Consequently, the differential avoidance patterns we report  
464 (Fig.3) may be linked to strategies of inbreeding avoidance and/or lowering competition with kin  
465 (Alberts & Altmann, 1995; Packer, 1979). However, this alternative hypothesis alone does not easily

466 explain why the avoidance effect is not observed permanently rather than when there is a relative  
467 excess of fertile females in the focal troop (Table 1, Fig.3). We explore and discuss some additional  
468 explanations trying to reconcile inbreeding avoidance and kin competition with our results in the  
469 supplementary information (see Appendices S1, S3 and S4). In a nutshell, these additional analyses  
470 (Appendix S3) suggest that there may be effects of inbreeding and/or kin competition, but if so they  
471 are additive rather than competing with the effects of mating competition reported in the main  
472 paper (Appendix S4). However, these analyses also received less statistical support and were less  
473 robust to alternative modelling decisions (Appendix S4). This is unsurprising, given the relatively  
474 lower costs of inbreeding in comparison to the costs associated with male-male competition for  
475 dominance and access to mates, and the risks of infanticide by neighbouring males (as captured by  
476 our *OSR<sub>focal</sub>* index, Appendix S1).

477         Notwithstanding these discussions on the exact behavioural mechanisms involved, our  
478 results suggest that mating competition may have a strong influence on home range overlap  
479 dynamics, consistent with a previous study in another baboon species (Markham et al., 2013). This  
480 finding is in line with the fact that male dispersal decisions are generally related to reproductive  
481 opportunities and constraints, such as the operational sex ratios of the natal and target troops and  
482 inbreeding avoidance (Alberts & Altmann, 1995; Packer, 1979). Substantial work has described how  
483 range size and overlap vary with sex and reproductive season in solitary species (e.g. Attuquayefio et  
484 al., 1986; Edelman & Koprowski, 2006), while in social species research has tended to focus on the  
485 wider relationships found between home range and mating systems (Clutton-Brock, 1989; Emlen &  
486 Oring, 1977). Yet (Markham et al., 2013) noted that mating strategies are rarely considered in finer-  
487 scale studies looking at how neighbouring social groups dynamically use and share space, and we  
488 have been unable to find any further research in this area since Markham et al.'s study. The  
489 mechanistic framework we have developed here suggests a possible general explanation for this  
490 deficiency. Analyses that do not account for temporal fluctuations in both the divergent adaptive  
491 interests between group members (e.g. arising from fluctuations in members' reproductive status)

492 and fluctuations in members' influences on collective movements (e.g. arising from changes in group  
493 composition and dominance hierarchies) may result in the averaging-out of the fluctuating effects of  
494 mating competition on group ranges, making the detection of such effects extremely difficult (e.g.  
495 see sensitivity analyses in Markham et al., 2013). For instance, we would not have detected our  
496 observed effect of mating competition on overlap had we not accounted for a mechanistic  
497 interaction term with alpha males' origin (Fig.3). The development of more mechanistic approaches  
498 to collective home range behaviour (Börger et al., 2008; Conradt et al., 2009; Couzin et al., 2005) may  
499 thus help to better reveal such cryptic forces at play on group ranging dynamics.

500 In contrast with previous studies, where a disproportionate influence of the alpha male on  
501 baboon troop movements was revealed by experimentally manipulating food distribution (Kaplan et  
502 al., 2011; King et al., 2008), we did not find support for Prediction 1: i.e., natural variation in foraging  
503 conditions did not reveal an influence of alpha males on group ranging behaviour. One explanation is  
504 that our NDVI index poorly reflects fine temporal scale variation in local food availability, especially  
505 since baboons can be opportunistic, generalist foragers. Yet our index strongly correlated with the 5-  
506 day range sizes (Area) of troops, capturing well this aspect of variation in baboon foraging behaviour.  
507 In our study population, as NDVI declines with the die-back of vegetation during the dry winter  
508 season (Fig.2), food resources for the baboons become more concentrated in spatially restricted  
509 riparian areas, leading to a reduction in the baboons' 5-day ranges and indirectly to a reduction in  
510 overlap with the neighbouring troop. We also observed that overlap was rare with the exclusive part  
511 of the neighbouring troop's MASK (see above), suggesting that even if our measure of food  
512 availability is imperfect, males rarely use their memory to range into these 'core areas' of their pre-  
513 dispersal troop. An alternative explanation for the lack of support for Prediction 1 may be that males  
514 have little adaptive interest in influencing collective movements for foraging. Specifically, because  
515 food is patchy and monopolisable, alpha males have priority of access and are therefore rarely  
516 motivated to incur the costs of leadership to guide their troop to alternative foraging grounds, in  
517 contrast to previous studies where the distribution of food was artificially manipulated to exceptional



518 levels (Kaplan et al., 2011; King et al., 2008). The observed lack of alpha male response to low food  
519 availability may also reflect a minimal difference in range quality between the two troops (Appendix  
520 S3). Overall, our support for Prediction 2 (male influence dependent on mating competition) and not  
521 for Prediction 1 (male influence dependent on food availability) is consistent with a general trend  
522 across mammals for male reproductive success to be more strongly limited by mating competition  
523 than access to food (e.g. Clutton-Brock, 2016).

524         Our study has clear limits: it was conducted on only two troops for a relatively limited  
525 number of years, our model of males' memory is rudimentary, and further work is needed to validate  
526 our mechanistic interpretations. Yet our results are very robust to alternative modelling decisions  
527 (Appendix S4), and seem to fit very well with what we know about the socio-ecology of baboons  
528 (Appendix S1) and other social mammals (Clutton-Brock, 2016). We hope that our study will help to  
529 promote promising new approaches and research questions to understanding the processes  
530 underlying home range dynamics in social species. Our results may help to resolve the apparent  
531 contradictions in the literature on collective movement mechanisms in baboon groups (King et al.,  
532 2008; Strandburg-Peshkin et al., 2015), by suggesting that the influence each individual exerts may  
533 be highly context-dependent within troops. More generally, our results suggest that dispersal and  
534 memory could act to increase spatial segregation between pre- and post-dispersal groups, rather  
535 than act as a form of cultural transmission of space use between groups. Finally, our results also  
536 emphasize that mating strategies may play a key but overlooked role in how groups dynamically  
537 share space. Altogether, we suggest that accounting for the underlying processes of collective  
538 decision-making and/or individual knowledge may help to better reveal the determinants of ranging  
539 behaviour in social species. Home range behaviour and space use mediate a variety of ecological  
540 encounters, with resources, pathogens, and conspecifics. To better understand and predict such  
541 encounters in a rapidly changing world, we thus hope our study will inspire further research on the  
542 social- and information-related processes underlying home range dynamics across species.

## 543 **Authors' contributions**

544 GC directed the long-term field study; JC, NP & GC conceived the ideas and designed methodology;  
545 AB, AC, AK, AL, HM, EH & GC managed and carried data collection and storage and provided  
546 dominance hierarchies established in previous studies ; JC analyzed the data ; JC & GC led the writing  
547 of the manuscript, all authors enthusiastically and critically contributed to the drafts and approved  
548 submission.

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565 **Data availability statement**

566 Analyses reported in this article can be reproduced using the data provided by Collet et al (2021):

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