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

Julien Collet[1,*], Nathalie Pettorelli[2], Alice Baniel[3], Alecia J. Carter[4], Elise Huchard[5], Andrew J. King[6,7], Alexander E.G. Lee[2], Harry H. Marshall[8], Guy Cowlishaw[2]

1 Zoology Department, University of Oxford, OX1 3QT Oxford, UK

2 Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

3 Department of Anthropology, Stony Brook University, Stony Brook, NY, USA

4 Department of Anthropology, University College London, UK

5 ISEM, Université de Montpellier, CNRS, IRD, EPHE, Montpellier, France

6 Department of Biosciences, College of Science, Swansea University, Singleton Park, Swansea, SA2 8PP, UK

7 Institute for Communities and Wildlife in Africa, Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

8 Centre for Research in Ecology, Evolution and Behaviour, University of Roehampton, London, SW15 4JD, UK

*Author for correspondence, pro@colletj.fr

Abstract

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

Keywords

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

Introduction

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

In group-living species, the information possessed by social units may also change through demographic processes. While groups may lose information through the loss of keystone individuals due to death or emigration (Brent et al., 2015; Foley et al., 2008), immigrants may bring new and potentially non-local information into the group (Cote & Clobert, 2007; Jacob et al., 2015; Whiten et al., 2007). In the case of home ranges, the effective transfer of spatial information between groups through individual dispersal, i.e., whether the information carried by an immigrant is shared with its new group, may be dependent on the influence of immigrants on the collective decision-making processes involved in group movements (Couzin et al., 2005), (van de Waal et al., 2013). Nevertheless, where the necessary conditions are met, the exchange of group members between neighbouring social groups could affect how these groups subsequently share space, amplifying or buffering the effects of more classical determinants of overlap such as territoriality (Burt, 1943) or competition for resources (Duncan et al., 2015; Kelt & Van Vuren, 2001). Thus, the origin of immigrants in a troop (as a proxy for their expected knowledge of neighbouring troop's ranges) may help to predict the range overlap dynamics of this troop with the home ranges of its neighbours: the "immigrant knowledge hypothesis".

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

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

In baboon troops, dominant males, and especially alpha males, can have a disproportionate influence on the collective movement decisions (e.g. in three distinct populations of chacma baboons: Kaplan et al., 2011; King et al., 2008; Stueckle & Zinner, 2008). Such males are likely to have a detectable impact on large-scale troop ranging patterns. Our initial focus was therefore to test the prediction that a focal troop's pattern of overlap with a neighbouring troop would depend on whether or not the focal troop's alpha male was an immigrant originating from that particular neighbouring troop. However, dominant males are not the only individuals that influence collective movement decisions in baboons (Strandburg-Peshkin et al., 2015; Stueckle & Zinner, 2008), and their influence may be limited to specific contexts and too ephemeral to affect large-scale ranging patterns. We thus also considered whether the observed overlap fitted with the expected adaptive interests of alpha males versus those of other troop members (Conradt et al., 2009; King et al., 2008; Strandburg-Peshkin et al., 2018). In order to do this, we reviewed and synthesized for different group members (males of different origins and dominance rank; females at different stages of their reproductive cycle) their likely preferences for home range overlap with neighbours according to their adaptive interests (food resources, mating strategies). To keep the main text relatively simple and concise, this review is presented in the supplementary information (Appendix S1, synthesized in Tables S1 and S2). In the main paper, we go on to consider the two main predictions for alpha males arising from this review, while in the supplementary information we also consider alternative explanations (as well as alternative analytical approaches), such as the potential role of inbreeding avoidance by alpha males (see Appendices S1-S4).

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

Materials and Methods

Study system

We used data collected episodically over a nine-year period (2005-2013) from two neighbouring troops of chacma baboons *Papio ursinus* (named L and J) living at Tsaobis Nature Park (22.38°S, 15.75°E), Namibia. The study area consists of arid hills and plains crossed by the ephemeral Swakop riverbed. The baboons forage on sparse vegetation across this landscape as well as in patches of riparian woodland (Cowlishaw, 1997). Individuals in both troops are habituated to human observers and individually identifiable. Troop sizes (including juveniles) during this period ranged from 29-55 in troop L and 37-59 in troop J, including between 1-10 (median: 3) and 1-11 (median: 4) adult males, respectively.

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

Data collection protocols

Ranging data

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

Group demography

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

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

Male dominance hierarchy

Agonistic interactions, comprising displacements, supplants, threats, chases, and attacks, were recorded daily using *ad libitum* and focal observations with a standard protocol (described in Huchard & Cowlishaw, 2011). Dominance hierarchies have been calculated each year as part of previous studies, using the I&SI method (De Vries, 1998) implemented in Matman 1.1.4. software (Noldus Information Technology 2003) and were found to be consistently linear across all troop members (e.g., King et al. 2008, Marshall et al. 2013). During all but one field season, a single alpha male could be reliably identified in each troop, but the ranks of subordinate males were not always clearly resolved. In total, 10 different alpha males (out of a total of 41 adult males) were identified across both troops over the study period. There was unusually high instability in the male dominance hierarchy in 2013 in L troop (Baniel et al., 2018) but all males contesting for the alpha position at that time were born in J troop, and thus could be considered together as born in the neighbouring troop for our purposes.

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

Environmental Data

In our study area, baboons mainly forage on the leaves, flowers, berries and/or pods of either small, homogeneously scattered, herbs and dwarf shrubs in the desert hills, or larger, more localized, trees and shrubs along the dry Swakop riverbed. In the late winter months, five plant species alone make-up 92-97% of male and female feeding time, respectively (Cowlishaw, 1997). The availability of these different plant foods varies across seasons and between years: drier climatic conditions during the winter months and in drought years are characterized by a much lower availability of food, especially in the hills. At these times, the baboons focus on finding scarcer and more heterogeneously distributed food patches, mainly along the riverbed. To estimate these seasonal and inter-annual variations in foraging conditions, we used the Normalized Difference Vegetation Index (NDVI; Pettorelli, 2013). NDVI is a satellite-based proxy of primary productivity (‘greenness’). This index varies between -1 and +1, with higher positive values representing more productive areas. We used NDVI data at a 16-day and 250mx250m resolution (MODIS 13Q1), downloaded from the NASA Land Processes Distributed Active Archive Center (Reverb|ECHO service, http://reverb.echo.nasa.gov/, 2013), across a rectangle defined by the extreme latitude and longitude reached by either troop between 2005 and 2013 plus an external margin of 0.01°. For the NDVI measures reported in the main text, we averaged for each 16-day period the values across all pixels of the study area. This resolution provides a coarse but informative proxy for conditions of access to food resources by baboons in our study area and period, capturing especially the within- and between-year seasonal trends (see Results). In the Tsaobis population, similar NDVI measures have been found to predict the rate of infant development during the winter period when we study them (Dezeure et al., 2020) as well as individual body condition across all age-sex classes (Cowlishaw et al., *unpublished*).

Data processing and statistical analyses

Traditional core areas (“MASK”) as proxies of male pre-dispersal memory

To test our hypothesis, we first needed to estimate what information immigrant males could have previously acquired about their pre-dispersal ranging area. Given our annual data gaps on ranging and on the exact timing of dispersal, uncertainty about what every male could remember about pre-dispersal ranges, and further variation arising from their different dispersal dates, it was not possible to develop individual-level memory estimates. Nevertheless, since both troops were consistently found within the same areas over our winter study periods (see below), with L troop tending to range north-eastward of J troop, it was possible to use these areas to develop a troop-level estimate of spatial memory that captured the different experiences of males born in different troops. These “traditional” core ranging areas were thus used to define a Minimum Area of Shared Knowledge (“MASK”) for each troop. According to our immigrant knowledge hypothesis, if information about natal areas possessed by immigrant males from a neighbouring troop influences the ranging behaviour of their new resident (focal) troop, then it should affect the extent of overlap of the focal troop with that neighbour's MASK, irrespective of minor variations in memory that may occur across different males born in that neighbouring troop.

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

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

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 indicators of stationary winter troop ranges.

Temporal scale of analyses

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

Statistical models

To test our hypothesis, we assessed how the extent of overlap of a troop's 5-day range with its neighbour's MASK (our response variable) varied in relation to the knowledge of the alpha male, the quality of the environment, and the relative number of fertile females in the focal troop (our explanatory variables). To calculate our response variable, "*Overlap*", we calculated the 95% kernel UD contour of each troop over each successive 5-day period, and then measured the overlap of this 5-day range with the neighbouring troop's MASK (in km^2). Periods where more than two days out of five had ≥3 hours missing GPS data were discarded. Our three explanatory variables were then calculated as 5-day means from the available daily values: alpha male knowledge, "*Alpha Origin*", was a binomial predictor which was scored as 1 if the alpha male was an immigrant from the neighbouring troop and 0 if he was not; environmental quality "*NDVI*" was a continuous predictor where daily values were drawn from 16-day resolution data; and the relative number of fertile females "*OSRfocal*" was also a continuous predictor which scored more highly when there were relatively more sexually receptive females than adult males in the focal troop. In addition, because the value of *Overlap* is limited by the size of the total ranging area covered by the troop during these five days, which is likely to vary, we included an additional control variable, "*Area*". This was calculated as the total 5-day range size, with the expectation that periods of smaller overall ranging would show lower *Overlap* values. Using *Area* as an explanatory variable (rather than as an offset) allowed us to more easily compare models with and without it (Appendix S4).

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

In total, 171 5-day periods from seven seasons between 2005 and 2013 were analyzed (for further details on data structure, see Appendix S2). We used linear mixed models (LMMs) with the response and explanatory variables described above, further including interactions between *Alpha* *origin* and both *NDVI* and *OSRfocal* to test Predictions 1 and 2 respectively, i.e., that a troop containing a knowledgeable alpha male will show greater range overlap with their neighbour's MASK when food is scarce, but lower overlap when his troop contains relatively more fertile females, respectively. Our random effects comprised year, troop and alpha male identity, to control for the potential non-independence of data from particular males in a troop within and across years. We checked and corrected for co-linearity between our explanatory variables (Appendix S3), following the residual (or sequential) regression approach (following Graham 2003). We therefore replaced *NDVI* with the residuals of *NDVI (resNDVI)* regressed against *Area* to avoid co-linearity effects between these variables (see Appendix S3). However, including *NDVI* (instead of *resNDVI*) without *Area* in the models led to the same conclusions (Appendix S4).

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

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

Results

Large-scale home ranges: stability and variability through time

The baboon troop “winter” ranges at Tsaobis (Fig.1A), estimated by the 95% kernel Utilization Distribution (UD) during each field season, extended from 13.3 km² to 33.0 km² in J troop (mean = 24.0km², median = 26.8km²), and from 24.6 km² to 44.9 km² in L troop (mean = 33.7km², median = 33.2km²) (Fig.1B). Calculation of the Minimum Area of Shared Knowledge (MASK) for each of the two troops (as the intersecting area of these annual winter range estimates) revealed that J troop’s MASK was 10.6 km² and extended to the west of L troop’s MASK, which was of similar area (11.5 km², Fig.1C). The two MASKs overlapped onto a ‘shared’ area of 4.2 km². These MASKs comprised 32-79% of each annual winter ranging area in J troop (median: 39.6%) and 14-42% in L troop (median: 18.8%). Despite the variance in each year’s ranges not captured by the MASKs, the consistency in both the absolute size of the MASKs and their location relative to one another, regardless of the method used to calculate them (see Fig.1C and Appendix 3), shows that a significant part of each troop’s range, i.e., the MASK, remained stable across field seasons.

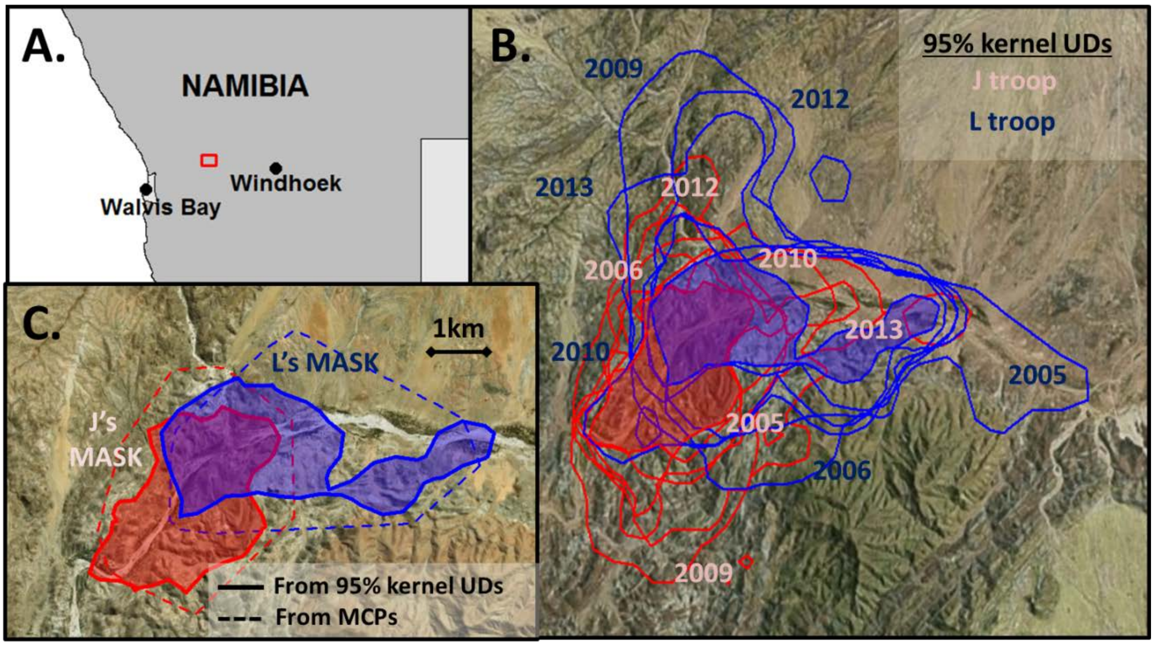

Figure 1: (A) The study site location in central Namibia (red rectangle); (B) Annual winter ranging areas (95% kernel UD contours) for J troop (red) and L troop (blue) in 2005-2013; (C) The MASKs of each troop, defined as the intersection of

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

General overlap with the neighbour's MASK every 5 days

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

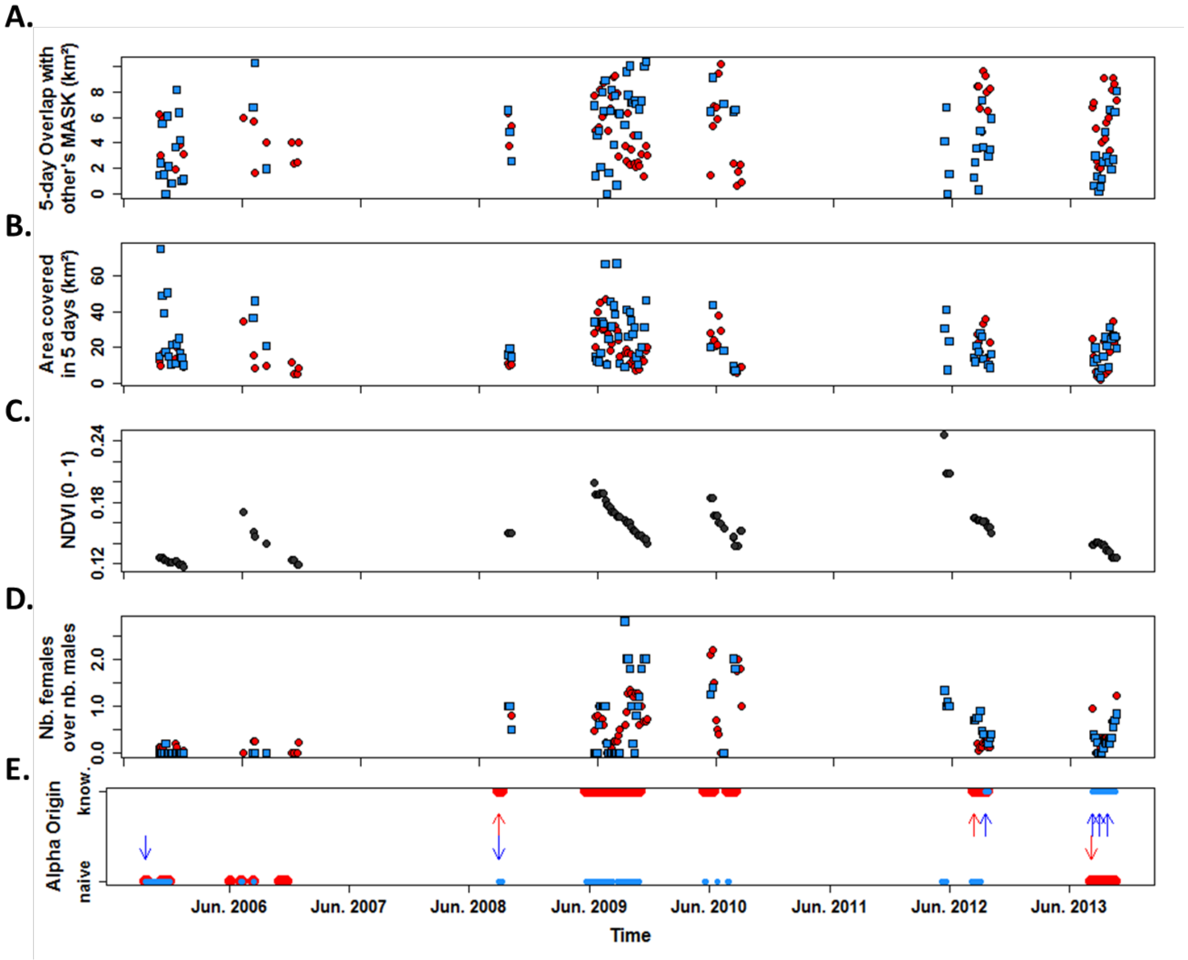

Figure 2: Time series used for our analyses (red: J troop; blue: L troop; black: common to both troops) in top-to-bottom order (panels A-E, respectively): *Overlap*; *Area*; *NDVI* (before correction for collinearity with *Area*); *OSRfocal*; and *Alpha Origin* ("know.": alpha male born in the neighbouring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

Testing the Immigrant Knowledge hypothesis

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

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

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

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

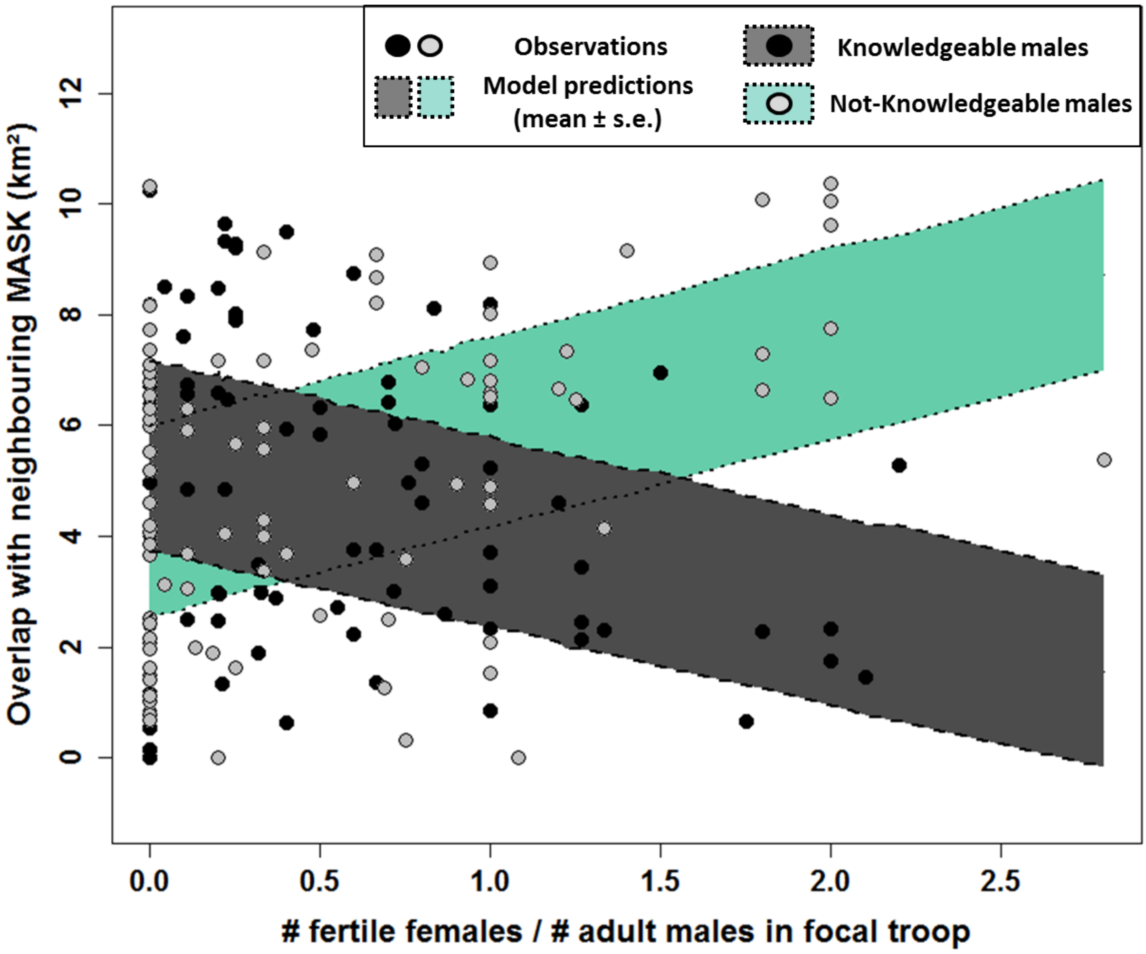

Figure 3: Observed (dots) and modelled (shaded) values of *Overlap* of a troop over the neighbouring MASK, per 5-day period, for troops containing an alpha male either born in the neighbouring troop ("Knowledgeable": black circles, dark grey shading) or not ("not knowledgeable": light grey circles, green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

Discussion

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

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

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

Apart from pre-dispersal memory, males of different origins also differ in their kin relationships with neighbouring troops. Consequently, the differential avoidance patterns we report (Fig.3) may be linked to strategies of inbreeding avoidance and/or lowering competition with kin (Alberts & Altmann, 1995; Packer, 1979). However, this alternative hypothesis alone does not easily explain why the avoidance effect is not observed permanently rather than when there is a relative excess of fertile females in the focal troop (Table 1, Fig.3). We explore and discuss some additional explanations trying to reconcile inbreeding avoidance and kin competition with our results in the supplementary information (see Appendices S1, S3 and S4). In a nutshell, these additional analyses (Appendix S3) suggest that there may be effects of inbreeding and/or kin competition, but if so they are additive rather than competing with the effects of mating competition reported in the main paper (Appendix S4). However, these analyses also received less statistical support and were less robust to alternative modelling decisions (Appendix S4). This is unsurprising, given the relatively lower costs of inbreeding in comparison to the costs associated with male-male competition for dominance and access to mates, and the risks of infanticide by neighbouring males (as captured by our *OSRfocal* index, Appendix S1).

Notwithstanding these discussions on the exact behavioural mechanisms involved, our results suggest that mating competition may have a strong influence on home range overlap dynamics, consistent with a previous study in another baboon species (Markham et al., 2013). This finding is in line with the fact that male dispersal decisions are generally related to reproductive opportunities and constraints, such as the operational sex ratios of the natal and target troops and inbreeding avoidance (Alberts & Altmann, 1995; Packer, 1979). Substantial work has described how range size and overlap vary with sex and reproductive season in solitary species (e.g. Attuquayefio et al., 1986; Edelman & Koprowski, 2006), while in social species research has tended to focus on the wider relationships found between home range and mating systems (Clutton-Brock, 1989; Emlen & Oring, 1977). Yet (Markham et al., 2013) noted that mating strategies are rarely considered in finer-scale studies looking at how neighbouring social groups dynamically use and share space, and we have been unable to find any further research in this area since Markham et al.'s study. The mechanistic framework we have developed here suggests a possible general explanation for this deficiency. Analyses that do not account for temporal fluctuations in both the divergent adaptive interests between group members (e.g. arising from fluctuations in members' reproductive status) and fluctuations in members' influences on collective movements (e.g. arising from changes in group composition and dominance hierarchies) may result in the averaging-out of the fluctuating effects of mating competition on group ranges, making the detection of such effects extremely difficult (e.g. see sensitivity analyses in Markham et al., 2013). For instance, we would not have detected our observed effect of mating competition on overlap had we not accounted for a mechanistic interaction term with alpha males' origin (Fig.3). The development of more mechanistic approaches to collective home range behaviour (Börger et al., 2008; Conradt et al., 2009; Couzin et al., 2005) may thus help to better reveal such cryptic forces at play on group ranging dynamics.

In contrast with previous studies, where a disproportionate influence of the alpha male on baboon troop movements was revealed by experimentally manipulating food distribution (Kaplan et al., 2011; King et al., 2008), we did not find support for Prediction 1: i.e., natural variation in foraging conditions did not reveal an influence of alpha males on group ranging behaviour. One explanation is that our NDVI index poorly reflects fine temporal scale variation in local food availability, especially since baboons can be opportunistic, generalist foragers. Yet our index strongly correlated with the 5-day range sizes (Area) of troops, capturing well this aspect of variation in baboon foraging behaviour. In our study population, as NDVI declines with the die-back of vegetation during the dry winter season (Fig.2), food resources for the baboons become more concentrated in spatially restricted riparian areas, leading to a reduction in the baboons' 5-day ranges and indirectly to a reduction in overlap with the neighbouring troop. We also observed that overlap was rare with the exclusive part of the neighbouring troop's MASK (see above), suggesting that even if our measure of food availability is imperfect, males rarely use their memory to range into these 'core areas' of their pre-dispersal troop. An alternative explanation for the lack of support for Prediction 1 may be that males have little adaptive interest in influencing collective movements for foraging. Specifically, because food is patchy and monopolisable, alpha males have priority of access and are therefore rarely motivated to incur the costs of leadership to guide their troop to alternative foraging grounds, in contrast to previous studies where the distribution of food was artificially manipulated to exceptional levels (Kaplan et al., 2011; King et al., 2008). The observed lack of alpha male response to low food availability may also reflect a minimal difference in range quality between the two troops (Appendix S3). Overall, our support for Prediction 2 (male influence dependent on mating competition) and not for Prediction 1 (male influence dependent on food availability) is consistent with a general trend across mammals for male reproductive success to be more strongly limited by mating competition than access to food (e.g. Clutton-Brock, 2016).

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

Authors' contributions

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

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Data availability statement

Analyses reported in this article can be reproduced using the data provided by Collet et al (2021): doi:10.5061/dryad.j3tx95xfw

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Supplementary Information for
"Immigrant males' knowledge influences baboon troop movements to reduce home range overlap and mating competition"

Appendix S1: Overlap with neighbours: Review and synthesis of different adaptive interests and knowledge between baboon group members

Appendix S2: Data collection periods and attributes

Appendix S3: Potential confounding factors and collinearity between explanatory variables

Appendix S4: Model selection outcomes

Appendix S5: R packages and associated references

Appendix S6: Discussion of collective decision-making mechanisms in chacma baboons

Appendix S1. Overlap with neighbours: Review and synthesis of different adaptive interests and knowledge between baboon group members

In this Appendix, we provide a detailed assessment of which group members should experience adaptive benefits or costs when their troop ventures into the home range of a neighbouring troop. We focus on the costs and benefits associated with access to food resources and reproductive opportunities. We also consider the potential states of individual knowledge about a neighbouring troop's range independently of any adaptive interests. We then use this combination of adaptive interests and potential knowledge to predict home range overlap preferences across a range of different individual classes, including immigrant males, natal males, fertile females, and pregnant and lactating females. Although our study focuses on the overlap preferences of immigrant versus natal males, in order to test the immigrant knowledge hypothesis it is necessary to understand the likely preferences of all group members who may influence group ranging patterns.

The costs and benefits of home range overlap related to food resources and reproductive opportunities are likely to be mediated by two consequences of such spatial coincidence, namely gaining access to a wider range of options for food resources in the neighbouring range, and increasing the probability of physical encounter with the neighbouring troop. We consider both effects in turn below (Sections A and B, respectively), together with an assessment of the potential role of 'familiarity effects' in mediating these benefits (Section C). Finally, a synthesis of this review is presented in Section D. Note that because the alpha male is likely to have a disproportionate influence on collective movements compared to other males, and because there were more uncertainties associated with using a variable integrating all adult males' origins (see main text, Appendix S3 for collinearity issues and Appendix S4 for supplementary analyses), the analyses we present in the main paper focuses on the origin of the alpha male to test predictions pertaining to the origin, likely knowledge and collective movement influence of males.

A. Effects of range overlap on foraging options

When food resources become scarcer, the costs and benefits of foraging decisions can become more limiting on fitness (Stephens et al., 2007). We then expect individuals to influence collective movements so as to increase their own foraging success (Conradt et al., 2009; Couzin et al., 2005; Giraldeau & Caraco, 2000). In this population, male baboons are almost twice as large as females (Cowlishaw, 2013), and thus have higher food requirements; they may therefore be more rapidly affected by dwindling food resources, and be more rapidly incentivised to influence collective movements to improve their foraging success. Experimental manipulations of food resources were indeed instrumental to reveal the disproportionate influence alpha males can have on collective movements in chacma baboon troops (Kaplan et al., 2011; King et al., 2008). Assuming that males will be familiar with the areas used by the troop they have grown-up in, perhaps more than the areas used by the troop they have immigrated into (especially shortly after their immigration), we may expect an increased overlap of their new focal troop with the areas of their past neighbouring troop of origin when food becomes scarcer. We would thus predict an increase in overlap of the focal troop with the "traditional" ranging area of the neighbouring troop when there is a decline in food availability, but only when influential males in the focal troop were born in that neighbouring troop and not when these males originated from another troop (this corresponds to our Prediction 1 in the main text).

On the other hand, male baboons – and particularly the alpha male – are at the top of the dominance hierarchy and as such have a privileged access to monopolisable resources in any patch exploited by the troop (King et al., 2008; Lee & Cowlishaw, 2017; Lee et al., 2016). It is therefore possible that, depending on the abundance and monopolisability of resources in the environment, males may be less rapidly affected by declining food resources than other group members. In this case, they may have less interest in influencing their focal troop's movement towards the area used by their neighbouring troop of origin, even when resources get scarcer. We would then expect that overlap patterns would reflect the adaptive interests of other members in the focal group (Conradt et al., 2009).

When non-male members of the focal group are influencing collective movements (King et al., 2011; Strandburg-Peshkin et al., 2015; Stueckle & Zinner, 2008), food-related predictions on the overlap with neighbouring troop's ranges are more complex. The adaptive costs and benefits of foraging within the neighbours' home ranges can vary with the respective quality of adjacent home ranges in terms of food resources (Kaplan et al., 2011; Mcloughlin et al., 2000), a factor that in our case was difficult to measure (see further below for our approach). In particular, it has previously been shown in several baboon populations that the daily path length and/or the overlap rate with neighbouring areas can vary with food availability (Dunbar, 1992; Johnson et al., 2015; Markham et al., 2013). If troops move more every day to reach dispersed food patches, these troops may increase their overlap with the neighbours' home ranges simply because they are travelling over larger areas and therefore more likely to overlap by chance with the areas traditionally used by their neighbours. However, if we assume that non-male group members in a focal troop are less familiar with food distribution within neighbouring home ranges than within their own focal troop's home range; and/or if we assume that the risks of competition or local depletion of food is significantly increased in areas used by another troop (Riotte-Lambert et al., 2015, 2017); we would not expect that collective movements influenced by non-male members of the focal group would be particularly oriented towards the home range of the alpha male's troop of origin more than towards any other neighbouring home ranges. Under these conditions we would expect that a focal troop's overlap with a specific neighbouring home range would vary with the daily movement rate of the focal troop, but not directly with the food availability in the environment, and we would not predict any effects of the alpha male origin on overlap patterns of the focal troop over a specific neighbouring troop's home range. This corresponds to our observations (main text, Table 1; Appendix S3).

Finally, to assess the hypothesis that the overlap patterns of a focal troop with the home range of a neighbouring troop could be driven by a difference in quality between these two adjacent home ranges, we tested the prediction that overlap would increase when the neighbouring home range is more productive than the focal home range. For this prediction, we indexed food availability in both home ranges, and calculated the difference between them, using the remotely sensed Normalised Difference Vegetation Index, NDVI, extracted every 16 days (see Methods in the main text). These analyses were complicated by collinearity between the NDVI difference and the alpha male origin (Appendix S3). However, we found that the differences in NDVI between home ranges were marginal (Appendix S3) and, after controlling for collinearity with Alpha Origin, if there was an effect of NDVI difference, it was in the opposite direction to our prediction (Appendix S4): overlap with the neighbouring area was observed to increase when the neighbouring home range was *less* productive than the focal home range. This suggests that patterns of overlap were mediated by another covarying factor than by a difference of quality between adjacent home ranges.

B. Effects of range overlap on inter-troop encounters and reproductive opportunities

To assess the possibility that individual troop members might influence group movements to increase the probability of encountering neighbouring troops, it is necessary to consider not only the costs and benefits of encounter for different group members relating to reproductive opportunities, but also their ability to predict where such encounters are most likely to occur. We consider both of these elements below (Sections B1 and B2, respectively). Up to this point, we have considered troop encounters with respect to the operational sex ratio of the focal troop, but it is also possible that the operational sex ratio of the neighbouring troop might play a role. We consider this possibility, and the potential role of inbreeding avoidance, in Section B3.

B1. Costs and benefits of encounters for various group members

The second consequence of a focal troop overlapping with the traditional ranging area of a neighbouring troop is the increasing probability of encountering those neighbours. Empirical studies indicate that different group members can experience a variety of different costs and benefits from these encounters. During group encounters, oestrous females from one troop can mate with males from the other troop (Alberts & Altmann, 1995; Henzi et al., 1998; Packer, 1979; Rasmussen, 1979), introducing to the focal troop a cost for males (a lower chance of paternity) but a clear benefit for oestrous, fertile females through access to a broader mating pool for mate selection (Huchard et al., 2010; Isvaran & Clutton-Brock, 2007; Nichols et al., 2015) and/or a dilution effect on paternity certainty preventing later infanticides from males of either group (Cowlishaw & O'Connell, 1996; Lukas & Huchard, 2014; O'Connell & Cowlishaw, 1994). Infanticidal attacks by males can also occur during these encounters, or after them when they result in male transfer between troops (Lukas & Huchard, 2014; Palombit, 2003; Shopland, 1982), introducing high costs for lactating (and perhaps pregnant) females and for the fathers of killed infants. Consistent with these high fitness costs for males, encounters can elicit costly responses in males (in terms of time, energy and/or mate-guarding efficiency) such as displays and/or herding behaviour (Cheney & Seyfarth, 1977; Henzi et al., 1998; Kitchen et al., 2004). However, these are not always successful in mitigating extra-troop mating or infanticidal raids (Alberts & Altmann, 1995; Henzi et al., 1998; Packer, 1979; Rasmussen, 1979). On these occasions, fertile females can get injured from herding and aggressive attacks by males in their own troop (Baniel et al., 2017) which may temper their adaptive interests in encountering neighbours, although occasions when this leads to a net adaptive cost to fertile females are likely to be rare. Finally, group encounters are also an opportunity for males in the focal troop to gauge reproductive opportunities in the neighbouring group (Alberts & Altmann, 1995; Henzi et al., 1998; Packer, 1979; Rasmussen, 1979), potentially engaging in cross-group copulations if oestrous females are present and accessible in the neighbouring group, and guiding their future dispersal decisions (both of which are benefits to males). In contrast, such male immigration from the neighbouring troop can be costly for resident males in the focal group, who may lose rank and therefore lose further access to mating opportunities (Alberts et al., 2003; Altmann & Alberts, 2003)

Overall, for pregnant and lactating females, encounters are therefore likely to be costly, while for oestrous females, encounters may be beneficial. For males, and especially alpha males, the costs will usually be greater than the benefits because they cannot monopolize access to more than one female at a time (Baniel et al., 2016): encountering neighbours would not be beneficial when they are already engaged in a consortship in their own troop (a common situation given that alpha males have priority-of-access to fertile females). In addition, alpha males that previously originated from the neighbouring troop would have even less incentive to encounter this neighbouring troop because any associated mating opportunities or male transfers between troops might involve additional costs linked to inbreeding and/or competition with kin (Alberts & Altmann, 1995; Huchard et al., 2010; Nichols et al., 2015; Packer, 1979).

Finally, these individual-specific costs and benefits should be especially exacerbated when there is a female-biased operational sex-ratio in the focal troop. Indeed, in these periods extra-troop mating and/or the transfer of new immigrant males are more likely (Alberts & Altmann, 1995; Henzi et al., 1998; Packer, 1979; Rasmussen, 1979), and displays or herding behaviour by males are more frequent (Cheney & Seyfarth, 1977; Henzi et al., 1998; Kitchen et al., 2004).

B2. Troop members' knowledge of where to encounter neighbours and predictions on overlap

Regarding the expected knowledge of the neighbouring troop's home range, members of the focal troop who have never been members of the neighbouring troop (i.e. females and their offspring, and some males) should have either no knowledge or less knowledge of where the neighbouring troop usually ranges compared to immigrants originating from that neighbouring troop. Yet members native to the focal troop (i.e. females and their offspring) might still identify some parts of their own range as shared with a neighbouring troop through an association with more frequent inter-troop encounters in those areas (e.g. as recently suggested in a social bird in Ellison et al., 2020). Indeed, a previous study showed baboons troops could modulate their use of the shared overlapping parts of their home ranges (Markham et al., 2013), suggesting that avoidance could occur before direct perception of the other troop in these areas.

Females may therefore try to influence the collective movements of their focal troop either towards or away from the areas shared with neighbouring troops, depending on whether those females are in oestrus or pregnant/lactating, respectively. This predicts changes in overlap with the neighbouring area, but mostly within the shared part of adjacent home ranges rather than the exclusive part of the neighbouring home range. Importantly, females' influence may depend on the operational sex ratio (i.e. number of oestrous females per male) of their own focal troop. In the case of pregnant and lactating females, a more female-biased operational sex ratio could increase the adaptive costs of inter-troop encounters, due to the increased risk of male immigration and therefore infanticidal attacks. In contrast, for oestrous females, a more female-biased operational sex ratio could increase both the net benefits and ability to influence collective decisions: in the first case, the adaptive benefits may increase and costs decrease due to lower aggression from males in their troop (either because there are fewer males and/or because of dilution of aggression among a larger pool of oestrous females); in the second case, the opportunity to influence group movements may increase due to the relatively higher number of oestrous females and their common adaptive advantage (Conradt et al., 2009). However, if only females were influencing collective movements, we would not expect differences in patterns of overlap depending on the origin of the alpha male in the focal troop.

In contrast, if males are influencing the collective movements of the focal troop, we would expect a difference in overlap dependent upon the alpha male origin. Although we have suggested it would be in the interests of all alpha males to avoid encounters between their focal troop and a neighbouring troop, especially when the operational sex ratio of the focal troop is high, it is only those alpha males who immigrated from that neighbouring troop who would have the spatial knowledge to be able to do so. Thus, immigrant alpha males in a focal troop are predicted to reduce overlap with their neighbouring natal troop when the focal troop contains more fertile females per male, but no such pattern is expected for alpha males who have immigrated from other troops. Such males are likely to have even less knowledge of neighbouring troops' ranges than females, since they will have only recently joined the troop. This corresponds to our Prediction 2 in the main text.

B3. Further testing the net costs of encounters for males and the effects of inbreeding avoidance on overlap

Finally, as an alternative explanation to variation in overlap with neighbours, we also explored the possibility that alpha males in the focal troop might be more attracted to overlap with neighbouring troops when the latter contain a greater proportion of fertile females (i.e. potential extra-troop mating opportunities for males in the focal troop). We did so by incorporating the operational sex ratio of the neighbouring troop as another explanatory variable in our models of Overlap and testing its interaction with the Alpha Male Origin. We predicted however that the operational sex-ratio in the neighbouring troop should have weaker effects on the overlap with neighbours than the operational sex-ratio in the focal troop, for two reasons. First, as stated previously, males can only secure mating with one female at a time so the costs of mating competition should generally outweigh the benefits of assessing or gaining mating opportunities with females of neighbouring troops. This should be especially true for knowledgeable alpha males who were born in this neighbouring troop and therefore likely to be related to some of its fertile females, with whom reproductive opportunities would lead to inbreeding. Second, for males in the focal troop, the operational sex-ratio in the neighbouring troop should be more difficult to assess than the operational sex ratio in the focal troop.

Analyses exploring this possibility are introduced in Appendix S3, and the results presented in Appendix S4. In summary, as predicted, range overlap between the focal troop and neighbouring troop increased when the operational sex ratio of the neighbouring troop was higher, provided the alpha male of the focal troop was not an immigrant from the neighbouring troop. However, also as predicted, this model of range overlap received less statistical support than an alternative model based on the operational sex ratio of the focal troop. When both sex ratios were included in the same model of range overlap (using the residuals of the regression of the neighbouring troop sex ratio on the focal troop sex ratio, since the two were correlated) there was an increase in model fit, suggesting that these effects may be additive. However, this support was less robust to the different modelling choices (Appendix S4), so we did not report this effect in the main text.

Overall the finding that neighbour troop sex ratio has a weaker and inconsistent effect on overlap across alternative models supports our predictions (that males have less to gain from and/or lower abilities to assess reproductive opportunities in the neighbouring than in the focal, host troop), and therefore it also supports our decision to focus on focal troop sex ratio in the main section. In supporting our predictions, it also supports the view that inbreeding avoidance is not a major factor.

C. Familiarity effects of overlap

In addition to the above effects, knowledge of an area may increase the net adaptive benefits drawn from it through a "familiarity effect" (e.g., Wolf et al., 2009). In cases where troops venture far out into the neighbour's range and away from their own "core, traditional area", we may expect a reduced efficiency to find and/or acquire resources in less familiar areas (Wolf et al., 2009), and a higher risk to be displaced by other troops in unfamiliar areas (Crofoot, 2013; Markham et al., 2012; Radford et al., 2016). Overall, if such familiarity effects can have significant quantitative effects on adaptive interests, we would predict that overlap with the neighbouring area would be higher when the alpha male was born from this troop than when the alpha male was originating from another troop. This prediction received poor support in our data since overall the focal troop overlapped with the neighbouring troop at similar or lower levels when the alpha male in the focal troop was knowledgeable than when the alpha male was not knowledgeable (see Results main section).

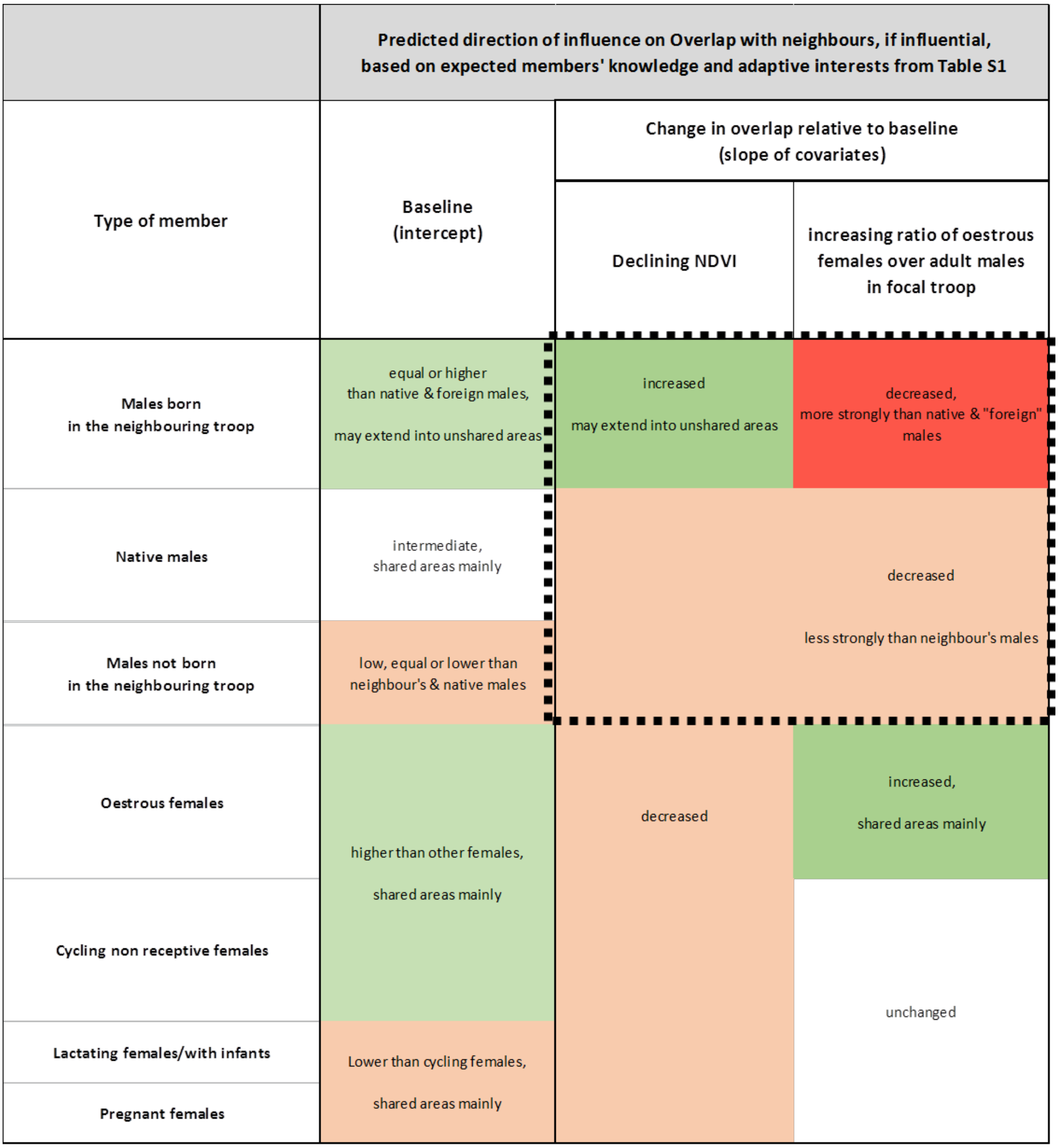
D. Synthesis

Overall, we expect that the costs and benefits of overlapping with the neighbouring range depend on both the composition of different types of group member and variation in either food availability in the environment and/or reproductive opportunities during between-troop encounters. In addition, we assume that, depending on their dispersal history, different group members will have different knowledge about the respective areas regularly used by different troops. We summarize the different adaptive interests as well as expectations of the potential states of knowledge of different group members in Table S1 below. The resulting predictions on expected overlap patterns, depending on which members of the troop are influencing collective movements, are summarized in Table S2. In the main text, we focus our analyses on testing the two most prominent predictions arising from the immigrant status of the alpha males (more overlap in periods of lower food availability and less overlap in periods of female-biased operational sex ratio in the focal troop).

Table S1: Expected knowledge (blue shades, darker blue indicates a relatively better state of knowledge; columns 2, 3), and expected adaptive costs and benefits of overlapping with the neighbouring range for different group members (columns 4-8). For the latter, we expected different group members could differ both in their "baseline" interests to overlap with neighbours (column 4) and/or in how their adaptive interests change with variation in either overall food availability (columns 5-6) or mating competition (columns 7-8). The colours in columns 4-8 thus refer to the expected contribution of each group member on the intercept (column 4) and/or slopes (columns 5-8) of the statistical model explaining variation in home range overlap (the response variable) in relation to food availability and mating competition (the predictors, assayed by NDVI and the operational sex ratio of the focal troop, respectively). The expected contributions assume that each member has perfect knowledge of all troops' ranges and is influencing the group's movement according to its needs (green shades indicate a net positive contribution, red shades a negative contribution, intensity of shading reflects the expected strength of the contribution). NDVI is a proxy for food availability in the environment comprising both home ranges; operational sex ratio refers to the number of sexually-receptive females over the number of adult males in the focal troop. Adaptive interests for males refer to those of any male in the troop; overall we expect adaptive costs and benefits in more dominant males to be less contrasted for foraging but more contrasted for mating opportunities, compared to those of less dominant males.

	Expected knowledge		Expected adaptive interests				
Type of member	Knowledge on focal troop home range	Knowledge on neighbouring troop home range	"Baseline" costs/benefits to overlap with neighbours (expected members' effects on intercept if knowledgeable and influential)	Change in costs/benefits of overlap relative to baseline (expected members' effects on covariate slopes if knowledgeable and influential)			
				change in costs/benefits of overlap with increasing NDVI	change in costs/benefits of overlap with decreasing NDVI	change in costs/benefits of overlap with increasingly female-biased operational sex ratio in focal troop	change in costs/benefits of overlap with increasingly male-biased operational sex ratio in focal troop
Males born in the neighbouring troop	(initially) low, except shared areas	high	Unknown, depends on interplay between relative foraging opportunities of the two home ranges, and relative effects of inbreeding avoidance, mating competition, and familiarity	likely unchanged, lower food competition may decrease costs of overlap, depending on relative foraging opportunities of the two home ranges	most likely unchanged or familiarity may increase benefits of overlap	increased avoidance (increased costs of mating competition for males)	likely unchanged or small benefits: benefits from mating opportunities with the neighbouring females may be counterbalanced by inbreeding costs
Native males	high	low except shared areas	Unknown, no familiarity benefits but no inbreeding costs compared to males born in other troop, depends on relative foraging opportunities of the two home ranges		likely unchanged or higher food competition may increase costs of overlap, depending on relative foraging opportunities of the two home ranges		increased benefits: mating opportunities in the neighbouring troop may reduce intra-troop male mating competition
Males not born in the neighbouring troop	(initially) low	low					
Oestrous females	high	low except shared areas	unknown but likely benefits from overlap (extra-mating opportunities) depending on relative foraging opportunities of the two home ranges			unchanged or increased benefits of overlap (mating opportunities with neighbouring males)	unchanged or increased costs of overlap (increased costs of mating competition for oestrous females)
Cycling non receptive females			unknown but likely neutral or benefits from overlap (short-term future mating opportunities) depending on relative foraging opportunities of the two home ranges				
Lactating females/with infants			most likely costs of overlap (risks of infanticide) depending on relative foraging opportunities of the two home ranges			unchanged or increased avoidance (increased risks of male immigration and infanticides)	unchanged
Pregnant females							

Table S2 : Predicted changes in home range overlap depending on which member is influential, under baseline conditions (expected effects on intercept) and under conditions of declining food availability (declining NDVI) and the relative availability of fertile females (operational sex ratio), accounting for both the adaptive interests and knowledge of the different types of group member (Table S1). Based on expected members' knowledge about surrounding troops (Table S1), we detail whether an increase in overlap would mainly concern the "shared area" common to both home ranges or could extend into the "unshared area" exclusive to the neighbouring home range. The quadrant of the table that generates the tested Predictions 1 and 2 for the immigrant-knowledge hypothesis is indicated by the bold dashed square.



	Predicted direction of influence on Overlap with neighbours, if influential, based on expected members' knowledge and adaptive interests from Table S1		
Type of member	**Baseline (intercept)**	**Change in overlap relative to baseline (slope of covariates)**	
		Declining NDVI	**increasing ratio of oestrous females over adult males in focal troop**
Males born in the neighbouring troop	equal or higher than native & foreign males, may extend into unshared areas	increased may extend into unshared areas	decreased, more strongly than native & "foreign" males
Native males	intermediate, shared areas mainly	decreased less strongly than neighbour's males	
Males not born in the neighbouring troop	low, equal or lower than neighbour's & native males		
Oestrous females	higher than other females, shared areas mainly	decreased	increased, shared areas mainly
Cycling non receptive females			unchanged
Lactating females/with infants	Lower than cycling females, shared areas mainly		
Pregnant females			

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Appendix S2. Data collection periods and attributes

Here we summarize the range of data collection periods that contribute data to this study across field seasons since 2005 (Table S3). Provisioning days refers to those periods when the baboons were provisioned with corn either during routine capture operations or as part of a large-scale feeding experiment; these occurred in blocks of consecutive days that we discarded from all analyses. Among the remaining days there could be incomplete data (defined as >2 hour gap in ranging data, or missing data among our explanatory variables), leading to the exclusion of more days. In particular, if both troops were not followed simultaneously, one of the two operational sex ratio variables could not be known; since both were required together as covariates in the expanded analyses presented below (Appendix S3 & S4), this led to the exclusion of further days. To facilitate comparisons between the models presented in the main paper and the expanded models presented in the supplementary information we used the same sample in both cases. This sample corresponds to the column "Number of 5-day periods used". The identity and origin (with reference to troops J and L) of the alpha males are shown next, with their used name and identity code in parenthesis.

Table S3: Data collection periods and attributes

Troop	Year	Start	End	Number of provisioning days	Number of full days of data left	Number of 5-day periods used	Alpha males	Alpha Male Origin
J	2005	29/05/2005	07/12/2005	33	81	7	(JM03)	Not J or L
J	2006	05/06/2006	25/11/2006	42	53	8	(JM03)	Not J or L
J	2007	NA	NA	NA	0	NA	unknown	NA
J	2008	30/08/2008	13/10/2008	0	37	3	Dave (LM05)	L
J	2009	18/05/2009	07/11/2009	0	155	31	Dave (LM05)	L
J	2010	15/05/2010	13/09/2010	42	62	12	Dave (LM05)	L
J	2011	24/07/2011	15/08/2011	0	19	NA	Dave (LM05)	L
J	2012	04/05/2012	13/10/2012	19	67	9	Cholera (LM07)	L
J	2013	04/05/2013	18/10/2013	48	94	16	Cholera (LM07) - Voltaire (JM37)	L - not J or L
L	2005	30/05/2005	06/12/2005	0	141	15	Chichi (HM23)	Not L or J
L	2006	06/06/2006	25/11/2006	49	26	3	Chichi (HM23)	Not L or J
L	2007	23/08/2007	29/11/2007	22	48	NA	Gland (HM28)	L
L	2008	16/07/2008	09/09/2008	0	39	3	Gland (HM28)	L
L	2009	19/05/2009	03/11/2009	0	144	30	Gland (HM28)	L
L	2010	16/05/2010	13/09/2010	64	36	5	Gland (HM28)	L
L	2011	18/06/2011	22/07/2011	0	25	NA	Gland (HM28)	L
L	2012	04/05/2012	14/10/2012	10	88	14	Porto Novo (JM17)	J
L	2013	03/05/2013	18/10/2013	40	96	15	Porto Novo, Accra, Limpopo, Darwin	All J

Appendix S3. Potential confounding factors and collinearity between explanatory variables

In this section (Appendix S3) and the next (Appendix S4) we report exploratory analyses to test alternative explanations to our results, using alternative methods and/or variables as a response in our statistical models; and/or using additional explanatory variables. We start Appendix S3 by defining the three additional explanatory variables and the alternative hypotheses they test (Section A). We then show the statistical relationships between all our explanatory variables (used in both the main text and supplementary information) and how we dealt with multi-collinearity structures (Section B). Finally, we present and define alternative methods and/or variables that were used to measure the extent to which a troop used the neighbouring home range (Section C). Appendix S4 reports the outcome of the statistical models using these extra variables.

A. Additional explanatory variables

Here we define three additional explanatory variables that were used to test alternative hypotheses to explain Overlap patterns with the neighbouring home range. These variables were: the operational sex-ratio in the neighbouring troop (*OSRneighbour*), the dominance-weighted average of all males' origins in the troop (AllMalesOri), and the difference in food scarcity between the two home ranges (DiffNDVI). Similar to the analyses reported in the main text, all three variables were calculated daily then averaged over a 5-day period (or a 2-day or 16-day period in alternative, sensitivity analyses).

OSRneighbour was defined as the number of fertile females divided by the number of adult males in the neighbouring troop. This variable was used to test the alternative hypothesis that overlap patterns may be driven by mating opportunities in the neighbouring troop: in periods of higher *OSRneighbour*, i.e. more female-biased sex ratio, encountering the neighbouring troop may be adaptive for males but not for females in the focal troop (see Appendix S1 for detailed arguments). Because the capacity to overlap with the neighbouring area during periods of increased *OSRneighbour*, as well as the adaptive value of such overlap, may depend on the origin and knowledge of the alpha male, we also tested for an interaction between *Alpha Origin* and *OSRneighbour*.

To define *AllMalesOri*, we assigned to each male in the troop a rank order from 1 for the lowest ranking male to *N* for the alpha male, *N* being the number of adult males in the troop. We then multiplied this rank score by -1 for all males that were not born in the neighbouring troop, summed these scores for all males, and divided the sum by *N*. This generated a dominance-weighted average of all males' origins. This variable was used to test the alternative hypothesis that all males and not just the alpha male could influence the collective movement process, although it assumed that higher ranking males would have a proportionately greater influence.

DiffNDVI was defined as the average NDVI values of pixels within the neighbouring troop's MASK minus the average NDVI values of pixels within the focal troop's MASK (see main text for definitions of MASKs, which roughly corresponds to a troop's core home range). A positive *DiffNDVI* value was thus taken to reflect that food was more abundant in the neighbouring area than in the focal area. We used *DiffNDVI* to test the alternative hypothesis that *Overlap* may be higher in periods of higher *DiffNDVI*, because food resources may be more abundant there.

B. Co-variation between explanatory variables

When two explanatory variables co-vary, their respective influence on the response variable can be confounded and difficult to disentangle in linear statistical models. The approach we used here to deal with this issue was that of "sequential" or "residual" regression, to minimize the overall R^2 of regressions between pairs of correlated variables. We first ran Anova tests for all pairs of explanatory variables (corresponding to a Pearson linear regression in most cases, except for pairs involving the variable *Alpha Origin* where this corresponded to t-tests) and extracted the corresponding R^2 and p-values (see Fig.S1).

Then we took the pair with the highest R^2 (*DiffNDVI* with *Alpha Origin*; Fig.S1) and calculated the residuals of the regression of *DiffNDVI* against *Alpha Origin* ("*resDiffNDVI*"), that by definition did not co-vary with Alpha Origin. These residuals could then be used as an explanatory variable instead of *DiffNDVI* directly to test for the effects of *DiffNDVI* that would be independent of those of Alpha Male Origin. We proceeded similarly with the next highest R^2 scores (*OSRneighbour* with *OSRfocal* to produce "*resOSRneighbour*"; *NDVI* with *Area* to produce "*resNDVI*"; and *AllMalesOri* with *Alpha Origin* to produce "*resAllMalesOri*") until we could not reduce further any R^2 scores without increasing another (see remaining patterns of co-variation in Fig.S2, all $R^2 < 0.07$, i.e. well below the threshold of 0.28 recommended in by Graham in 2003, reference cited in main text).

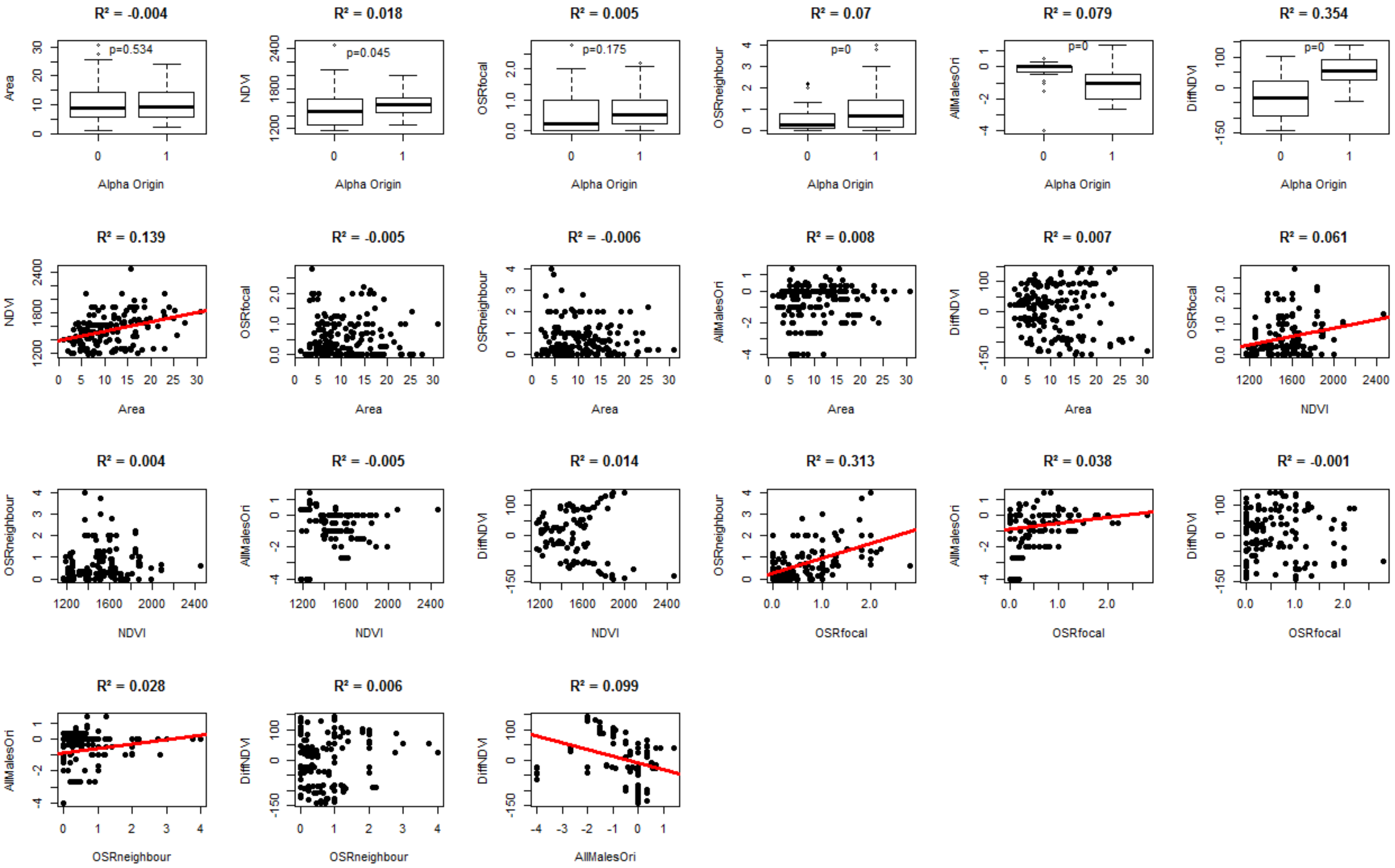

Figure S1: Co-variations between initial explanatory variables. P-values of t-tests from Anova models are reported for co-variations with *Alpha Origin* (value of 1= born in the neighbouring troop), for other pairs of variables regression lines are drawn only when the Pearson correlation was significant.

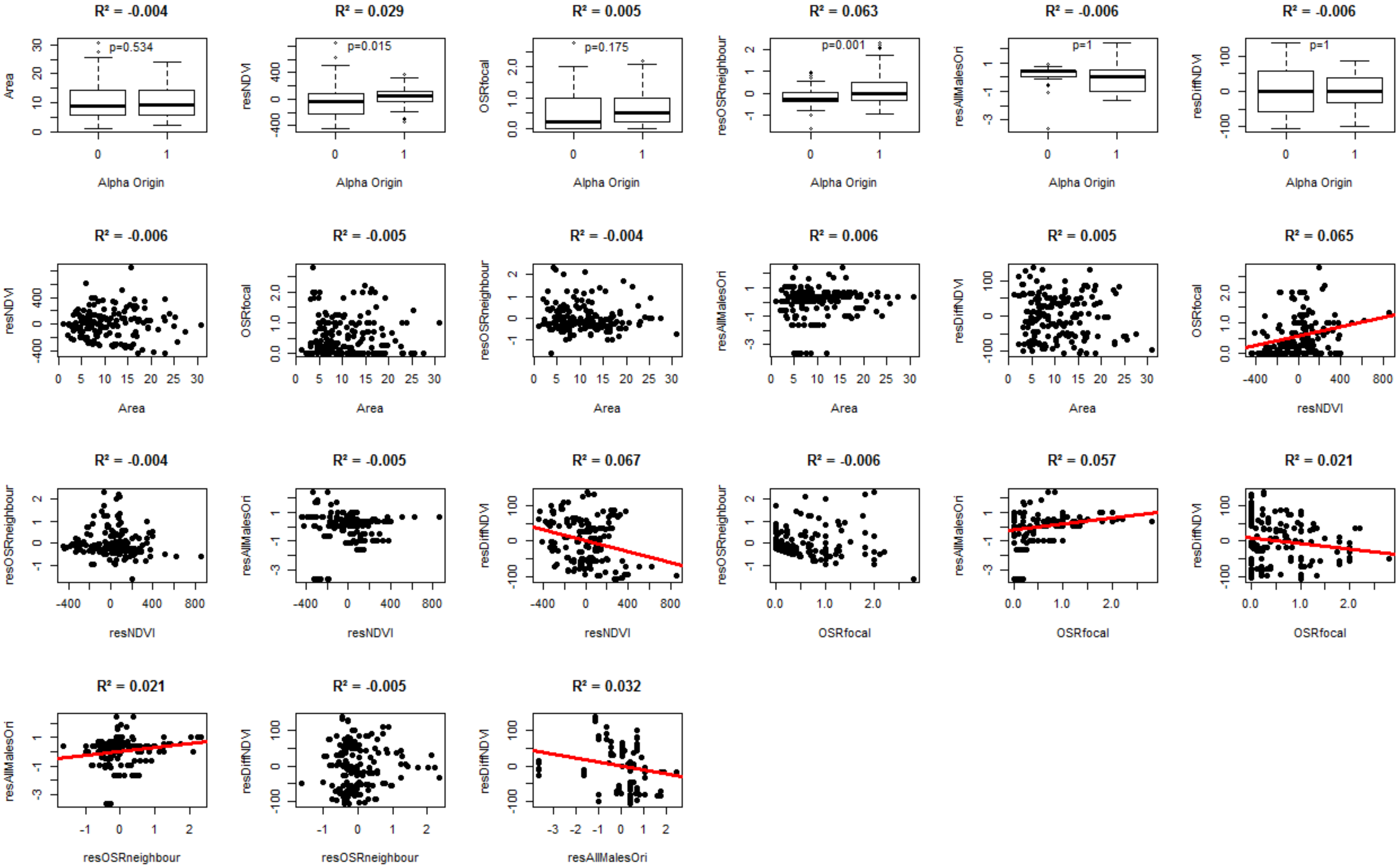

Figure S2: Co-variation between final explanatory variables after the collinearity correction procedure (see text). P-values of t-tests from Anova models are reported for co-variation with *Alpha Origin* (value of 1= born in the neighbouring troop), for other pairs of variables regression lines are drawn only when the Pearson correlation was significant.

The sequential regression approach requires a choice about which variable (“A”) in a pair will be regressed against the other (“B”) to obtain “resA”. This is implicitly giving more importance to the variable B than to the variable A. We chose to use the residuals of *AllMalesOri* regressed against *Alpha Origin*, and not the reverse, because it was easier (*Alpha Origin* being a categorical variable) and also because, as we detail in the main text, there was higher uncertainty around the reliability of *AllMalesOri* to test our hypotheses. We chose to use the residuals of *DiffNDVI* against *Alpha Origin* again for convenience, and also because *Alpha Origin* was used to test the main hypothesis of our study (i.e. the immigrant knowledge hypothesis), and because the difference in NDVI between the two MASKs seemed quantitatively small (~100 units) compared to the overall variance of NDVI (~1000 units) observed in the whole environment (e.g. see Fig.S1). We chose to regress *NDVI* against *Area* and not the reverse because, as explained in Appendix S1, we expected that *NDVI* could have either direct effects on *Overlap* or indirect effects through an overall increase in daily movement rates. The latter would increase *Area* and then by chance *Overlap*, which is exactly what the sequential regression is testing (i.e. we predict that if *NDVI* influences overlap directly there will be an effect of *resNDVI* on *Overlap*, whereas if it only affects movement rates there will be no effects of *resNDVI* on *Overlap*). Finally, we explored both options for Operational Sex Ratios, either regressing *OSRfocal* against *OSRneighbour* or the opposite (Appendix S4).

In Appendix S4 we ran all possible statistical models of *Overlap* including either the original explanatory variables or the collinearity-corrected explanatory variables (*resNDVI, resOSRfocal resOSRneighbour, resMalesOri, resDiffNDVI*) to confirm that our conclusions were robust to this statistical treatment. Overall, there was less support for a cumulative effect of the origin of other males in the troop than for alpha male origin, and low support for an additive effect of other males’ origins once accounting for the effects of alpha male origin. We think this may be due to large uncertainties in the reliability of our measure of other males’ origins and dominance rank, and advise great care before interpreting that as strong evidence for a low influence of non-alpha male members on overlap patterns or collective movements. Overall, there was lower support for an effect of the difference of food scarcity between the two MASKs compared to the effects of *Alpha Male Origin;* moreover, these effects suggested that *Overlap* increased when the neighbouring area was less productive. Taken together, we think these results strengthen the robustness of our conclusions of an effect of the origin and knowledge of alpha males on collective movements and patterns of overlap with the neighbouring troop.

C. Alternative methods and metrics for space use

In this section, we report on two points: our comparison of the Minimum Convex Polygon and 95% Utilisation Distribution approaches to describing troop MASKs and 5-day ranges, and our exploration of time spent in the neighbour’s MASK as an alternative measure to spatial Overlap.

Comparison of Minimum Convex Polygon and 95% Utilisation Distributions

As described in the main paper, for the purposes of describing the *Overlap* between one troop’s 5-day range and another troop’s MASK, we explored a suite of different approaches: (1) three different methods to define the MASK, namely 95% and 100% Minimum Convex Polygons (MCPs) and 95% kernels of Utilisation Distributions (UDs), and (2) two different methods to define the 5-day range, namely 100% MCPs and 95% kernel UDs.

Overall, the MCP and UD approaches produced similar patterns, although there were notable differences, which we illustrate here with reference to the troop MASKs. MCPs encompassing all recorded GPS locations during a field season gave the same weight to places visited once in a field season to those used intensively by the troop. As such, MCPs represented the full extent of places visited by a troop but also encompassed unvisited places between spatial outliers (Fig.S3), although note that this sensitivity to outliers is partially mitigated in this study by intersecting several MCPs. On the other hand, UDs based on kernels gave weights proportional to the intensity of space use, with 95% isopleths excluding those areas rarely used in a season. This approach may be better if males’ memories are also proportional to their intensity of winter space use. However, estimates based on kernels did exclude some places rarely visited during a given year even when those were consistently visited every year (Fig.S4), and may be more sensitive to artefacts of space use intensity created by irregular GPS recordings. Overall, these comparisons indicate that the shape and size of MASKs can vary depending on these definitions, but that this does not affect the qualitative trends of space use reported. Moreover, the findings that the 100% MCP and 95% kernel UD approaches produce comparable results (see below) indicate that our conclusions are robust to uncertainties linked to how we model males’ knowledge on a fine spatial scale.

In the main paper, we present the results of our analyses based on 95% kernel UDs throughout (i.e. for the assessment of both troop MASKs and 5-day ranges). However, we present the results of the same analyses using 100% MCPs in the Supplementary Information (Appendix 4). Since both approaches produce comparable results, we only use one method (100% MCPs) for the all the additional analyses presented in the Supplementary Information, unless otherwise stated.

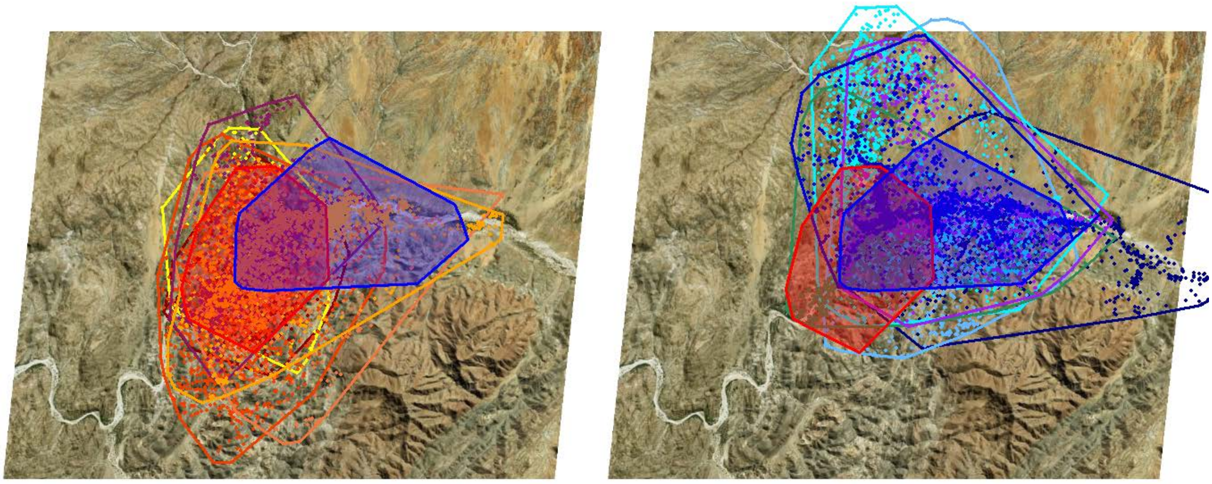

Figure S3: Defining MASKs from the intersection of each field season's Minimum Convex Polygon (MCP) based on 100% of locations, for J troop (left panel, orange shading) and L troop (right panel, blue shading). Solid lines indicate the MCP contours calculated from GPS locations (dots), each field season is represented with a different colour ; and the resulting MASKs of each troop are indicated with shadings. The MASKs for both troops are plotted on both figures (i.e., the MASK for L troop is included on the left, and the MASK for J troop is included on the right), to indicate the pattern of MASK overlap between the troops. Noticeably for both troops, each annual MCP covers areas that are rarely used (indicating sensitivity to outliers), but their intersection is much less sensitive to outliers. In addition, the MASK of troop L now encompasses the eastern portion of the riverbed that was left out by the kernel-based method (Fig.S1).

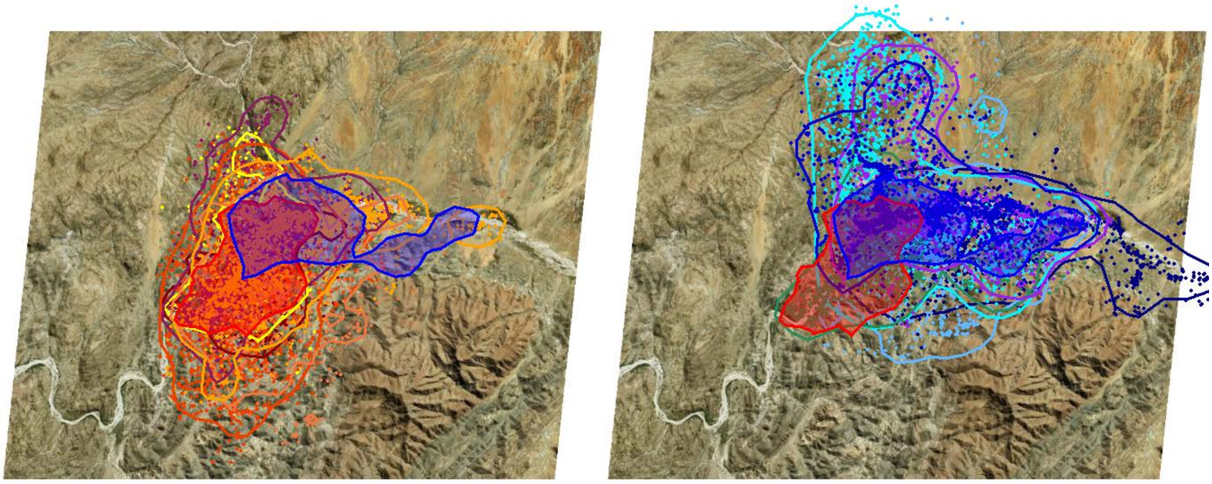

Figure S4: Defining MASKs from the intersection of each field season's 95% kernel-based Utilisation Distributions for J troop (left panel, orange shading) and L troop (right panel, blue shading). Solid lines indicate the 95% contours calculated from GPS locations (dots), each field season is represented with a different colour ; and the resulting MASKs of each troop are indicated with shadings. The MASKs for both troops are plotted on both figures (i.e., the MASK for L troop is included on the left, and the MASK for J troop is included on the right), to indicate the pattern of MASK overlap between the troops. Noticeably for L troop, the MASK avoids an eastern portion of the riverbed where the troop was still observed every year, and that is included in the MASKs defined using Minimum Convex Polygon intersections (Fig.S2).

Assessment of time spent in neighbour's MASK

To measure the proportion time spent in the neighbouring MASK rather than the extent of spatial overlap, we calculated the proportion of GPS points that fell within the neighbouring troop's MASK over each 5-day period. For this analysis, we excluded those GPS points that were additional to the regular locations taken at 30-min intervals throughout the day, i.e. those GPS records associated with troop encounters and alarm behaviour. Model selection outcomes are shown in Appendix S4, again showing that the same set of explanatory variables are selected as the best predictors.

Below we show the relationship between this proportion of GPS locations within the neighbouring MASK and spatial *Overlap* (Figure S5). This plot indicates that the proportion of time that troops spent in overlap areas (the proportion of locations within the neighbours' MASK) was positively correlated with the area of overlap, although there was substantial variation around this relationship at higher values, illustrating these two variables are not measuring exactly the same thing. Nevertheless, the fact that this temporal measure of overlap produces the same results as our spatial measure (Appendix 4) indicates that our conclusions on the immigrant knowledge hypothesis are robust to how we define the use of the neighbouring area.

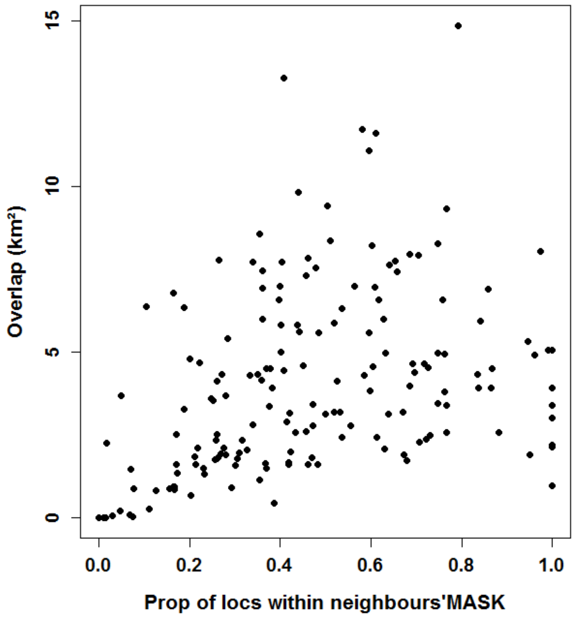

Figure S5: Relationship between observed *Overlap* and the proportion of locations in each 5-day period that are found within the neighbouring MASK, to help visualize the correspondence between spatial overlap and time spent within the neighbouring area.

Appendix S4. Model selection outcomes

In Appendix S4 and its associated Excel file, we present further details of the results presented in the main paper, plus a suite of additional analyses as described in Appendix 3, as follows:

[1] In the main paper we present an AICc-weighted average model computed from the set of all possible models including all or a sub-selection of the following variables and interaction terms: *Area*, *Alpha Origin*, *resNDVI*, *OSRfocal*. Here we present the details of these models from which the average was calculated. See 1st Excel worksheet ('Models averaged in main section').

[2] We test alternative hypotheses to those presented in the main paper, involving a fuller set of models including additional explanatory variables. See 2nd Excel worksheet ('Fuller models (add. expl. var.)').

[3] We provide sensitivity analyses in three areas:

(i) The temporal scale of analyses, i.e. 2-day or 16-day periods instead of the 5-day periods reported in the main text. See 3rd Excel worksheet ('Time-scale').

(ii) The definitions of MASKs and 5-day ranges, i.e., comparing the use of Minimum Convex Polygon and 95% kernel Utilisation Distribution methods. See 4th Excel worksheet ('MCP or kernel').

(iii) The definition of *Overlap* with the neighbouring MASK, i.e. using an alternative temporal measure. See 5th Excel worksheet ('Proportion of loc in MASK').

In all of these models, [1] to [3], the interaction between *Alpha Origin* and *OSRfocal* receives high support (generally included in all top-ranking models). This highlights that our main conclusions on the immigrant knowledge hypothesis, and the importance of mating competition on range overlap, are very robust to the alternative hypotheses, methods and time-scale of analyses as described in Appendix S3 and in the main text. However, the effects of *resNDVI* reported in our paper, and the potential effects of *OSRneighbour* (see below) are more sensitive to the definitions being used, suggesting weak or non-significant influences on home range overlap.

Regarding the effects of *OSRneighbour*, our models explored its role additively to those of *OSRfocal.* The OSR correlated between troops (Appendix S3), so we used the residuals of *OSRneighbour* regressed against *OSRfocal*. We found less support for the effects of *resOSRneighbour* than for the effects of *OSRfocal* on range overlap, but more support for models including the effects of both. Moreover, these effects of *resOSRneighbour* also depended on the origin of the alpha male: they were minimal for alpha males born in the neighbouring troop, but when the alpha male was not born in the neighbouring troop there was greater overlap when the *resOSRneighbour* was more female-biased than the *OSRfocal.* This is consistent with our previous review (Appendix S1) that alpha males who originated from the neighbouring troop will have little interest in reproductive opportunities in that troop due to inbreeding avoidance, but alpha males who were born in another troop will be interested in such opportunities, especially when they exceed those in his present troop.

Appendix S5. R packages and associated references

Geographical projection of data :

sp 1.2-3:

Pebesma, E.J., R.S. Bivand, 2005. Classes and methods for spatial data in R. R News 5 (2), http://cran.r-project.org/doc/Rnews/.

Roger S. Bivand, Edzer Pebesma, Virgilio Gomez-Rubio, 2013. Applied spatial data analysis with R, Second edition. Springer, NY. http://www.asdar-book.org/

proj4 1.0-8

Simon Urbanek (2012). proj4: A simple interface to the PROJ.4 cartographic projections library. R package version 1.0-8. http://CRAN.R-project.org/package=proj4

MCP (and kernel) calculations

adehabitatHR 0.4.13

Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, *197*(3–4), 516–519. doi: 10.1016/j.ecolmodel.2006.03.017

NDVI spatial value extraction

raster 2.5-2

Robert J. Hijmans (2015). raster: Geographic Data Analysis and Modeling. R package version 2.5-2. http://CRAN.R-project.org/package=raster

Geometrical overlap calculations

rgeos 0.3-8

Roger Bivand and Colin Rundel (2014). rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-8. http://CRAN.R-project.org/package=rgeos

Satellite images

OpenStreetMap 0.3.2

Fellows, I., & Stotz, J. P. (2016). OpenStreetMap: Access to Open Street Map Raster Images (Version 0.3.3). Retrieved from https://cran.r-project.org/web/packages/OpenStreetMap/index.html

Statistical modelling

lme4 1.1-7

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1–48. doi: 10.18637/jss.v067.i01

Model averaging

MuMIn 1.13.4

Bartoń, K. (2013). MuMIn: Multi-model inference. R package version 1.9.13. *The Comprehensive R Archive Network (CRAN), Vienna, Austria*.

Appendix S6: Discussion of collective decision-making mechanisms in chacma baboons

In the main text, we do not discuss in depth how alpha males exert their influence on the focal troop's ranging behaviour. However, to have confidence in the conclusions of our study, it is necessary to show that our interpretation is consistent with the social behaviour and collective decision-making processes of chacma baboons. Here we provide a brief review of the rich scientific literature on this subject, and further consider the implications of our findings for future research in this area.

A. Movement initiations

In chacma baboon troops, individuals can initiate movements in a particular direction when the troop is stationary, and initiations by certain individuals elicit more followers and thus have a greater influence on group movements than other individuals. This type of leadership has been demonstrated in a number of troops across different chacma baboon populations. Here we summarize previous results on the matter, with more details than space allowed in the Introduction in the main text.

In chacma baboons, alpha males have been observed to elicit more followers, and thus to have a greater influence on group movements, than other individuals (Kaplan et al., 2011; King et al., 2008, 2011; Sueur, 2011). The greater influence of alpha males in movement decisions is thought to occur because these individuals occupy the most central positions within the troop's social networks. Therefore, when alpha males initiate a movement they tend to have more and closer affiliates that follow them (Kaplan et al., 2011), compared to movements initiated by individuals that are peripheral in these networks. The influence of alpha males on group movements has also been shown by foraging experiments conducted in two different populations of chacma baboons. Troops repeatedly visited artificial food patches that only the alpha male was able to exploit, while all other troop members had to wait (Kaplan et al., 2011; King et al., 2008). In these experiments, subordinates incurred a 'consensus cost' (in terms of lost foraging opportunity) as a result of these 'despotic' group decisions (Conradt & Roper, 2003).

Adult males often have a similarly large influence on group decisions in other closely related species of baboons (see review in Montanari, 2019, synthetized here). For instance, in a population of olive baboons (*Papio anubis*), the highest ranked male was most likely to determine the direction and timing of group movements (Ransom, 1981); in a population of hamadryas baboons (*Papio hamadryas*), males exclusively initiated group movements (Kummer, 1968); and in a population of

Guinea baboons (*Papio papio*), the majority of group departures were initiated by adult males (Montanari et al., 2019). Nevertheless, there are also instances where males play a less influential role. Female leadership has also been reported in a population of yellow baboons (*Papio cynocephalus*: Norton, 1986), and in another population of olive baboons (where the majority of the adults and sub-adults in the troop were fitted with high resolution GPS collars), decision-making was equally shared among all group members and the alpha male did not have greater influence on troop movements (Strandburg-Peshkin et al., 2015). Decisions of baboon troops when 'on the move' (King & Sueur, 2011), rather than decisions regarding when and where to move after rest periods, is less well studied. In these contexts, the probability for males and especially dominant males to be at the front, at the middle or at the back of the moving troop seems highly variable across studies in various populations and species (see review in Montanari, 2019).

We do not fully understand why different studies on various baboon species and populations vary in their findings of decision-making and leadership roles, but it is very likely that collective movement processes depend on the socio-ecological environment, and may therefore change within social groups across time and contexts. Unfortunately, it is often difficult to assess the influence of such environmental conditions. In the aforementioned olive baboon study by Strandburg-Peshkin et al. (2015), for instance, the work was conducted over a short time period (weeks) with little information on the wider ecological context (e.g. the distribution and abundance of food, reproductive status of females, and influence of nearby neighbouring troops). Our results in the present study, and those reported by Markham et al. (2013), suggest that these socio-ecological contexts and (linked) individual interests are likely to be key in determining individual contributions to group movements through time. Indeed, when all troop members have similar interests, any individual might lead (Conradt & Roper, 2005). In contrast, where resources incentivise certain individuals to lead (and they have the social influence to do so), then more unshared leadership is expected. Experimental manipulation of food resource quality and distribution in two baboon populations confirms this (Kaplan et al., 2011; King et al., 2008).

The results of the present study are consistent with the idea that the respective contribution of different members to collective movement may vary within social groups according to the socio-ecological context, as well as to the knowledge of different group members. Yet, at least in the case of chacma baboons, there is another potential challenge to consider in understanding how alpha males might influence troop movements in periods of female-biased sex ratios in their troop. Indeed, such periods might be particularly challenging for the leadership roles of alpha males, as we will argue in the next subsection.

B. Consortships and troop movements

Female sexual state can also affect male behaviour and therefore troop movements. Chacma baboon males engage in prolonged mate-guarding relationships, or ‘consortships’, with one sexually-receptive female at a time (e.g., Baniel et al., 2016). During such consortships, males closely follow their consorts and may therefore have less opportunities to initiate and actively lead troop movements over sustained periods (King et al., 2008). This is especially true for alpha males, who have privileged access to fertile females in their troop, and so are more often engaged in consortships than other males (Baniel et al., 2016). We have not controlled for the consortship status of alpha males in this study, to avoid multiple testing with our limited sample size. Nevertheless, such analyses may generate further insights into the dynamic influence of males, since consortships change the alpha male’s movement patterns (King et al. 2008). Chacma baboon males can also coercively influence the behaviour of group-mates through previous acts of aggression (Baniel et al., 2017), and in some cases alpha males may herd their troop away from certain directions, as observed during inter-group encounters (Henzi et al., 1998). This may provide a more time-effective solution for males than initiating and subsequently maintaining movements in a particular direction, although it may cost them more energy. In a final complication, it’s also the case that when the operational sex ratio becomes female-biased, within-troop male mating competition may decrease as more males can engage in consortships (Baniel et al., 2016). In these cases, the costs of temporarily leaving a female mate more loosely guarded may be relatively lower than the costs of encountering a neighbouring troop. Clearly, the potential influence of all these mechanisms needs to be explored further, but thus far have remained outside the scope of most recent empirical studies of collective behaviour in baboons (although see King et al., 2008, for an exception).

C. Conclusions and perspectives for future studies

Overall, our results in the present study support the hypothesis that the collective-decision making processes will vary within and across social groups according to variation in socio-ecological contexts (e.g. changes in food resources, or mating competition). This hypothesis could be tested at a ‘fine-scale’ by examining individuals’ influences on group-mates’ movements with respect to individual motivations and phenotypes, ideally combined with study of the large-scale emergent home ranging patterns and dynamics (as we have explored here). Indeed, here we focused on the interests of alpha males for the sake of testing the immigrant knowledge hypothesis, but other predictions arising from our synthesis (Appendix S1) could be investigated regarding the influence of other troop members (e.g. pregnant and lactating females). Likewise, our modelling of the spatial knowledge of different group members may be further refined. For instance, one explanation for the absence of support between NDVI and Alpha Origin in our results is that immigrant males may quickly update their spatial knowledge of food patches within their focal troop range. If this is the case, accounting for the time since immigration may thus reveal further insights into the influence of males, since our Prediction 1 in the main text may be more likely to be observed soon after immigration than after several weeks or months. In conclusion, while our sample size limited the number of hypotheses we could investigate in our model, we think our approach opens up promising new perspectives for future studies.

D. References to Appendix S6

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Kummer, H. (1968). Social organization of hamadryas baboons: A field study. The University of Chicago Press.

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