

Passive segregation and multi-scale space-use adjustments to socio-ecological variables in western gorillas

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1 **Passive segregation and multi-scale space-use**
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3 **western gorillas**
4

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21 **Abstract** | Understanding what are the proximate mechanisms shaping species' space-use dynamics,
22 and at which scale, can provide insights into species socio-ecology. This is crucial information for both
23 applied (e.g., conservation) and theoretical questions (e.g. individuals' coexistence/segregation). Yet,
24 longitudinal views of the space-use dynamics of animal species are generally lacking. Taking
25 advantage of an unprecedented long-term data set (up to 8 years) on ranging patterns of wild western
26 gorillas (*Gorilla gorilla*), we investigated the dynamics of home ranges in relation to socio-ecological
27 variables in five habituated groups in Central Africa. First, we looked at the scale at which their
28 ranging movements are stationary. Second, we studied how space use is shaped by (i) foraging and
29 intra-group constraints (e.g., diet, group size, presence of offspring) by focusing on group daily path
30 lengths, and by (ii) inter-group competition (direct or indirect), by quantifying static and dynamic
31 interactions in neighbouring group-dyads. We found that gorilla groups shifted the barycenter of their
32 home range 0.17 per year by a distance larger than the mean home range radius. Movements within
33 the home range were highly dependent on an ecological factor (seasonal diet) and on the group
34 composition, particularly on the presence of dependent infants. Repeatedly visited sites were also
35 used the longest, but their locations differed seasonally, suggesting use of mnesic abilities for foraging.
36 There was little overlap between the home ranges of neighbouring groups that did not tend to move
37 away from each other more than expected at random. Groups also ventured into, and slept in, the
38 central part of the home range of a neighbouring group. Overall, this highlights the absence of
39 territoriality and suggests that spatial segregation should be the simple consequence of avoidance of
40 depleted areas. This study shows how social and ecological constraints may shape space-use patterns
41 at different scales in a non-territorial species. It also raises questions on the cognitive mechanisms
42 underlying high foraging efficiency in environments shared with competitors.

43 **Keywords:** Daily path length - *Gorilla gorilla* - Home range - Indirect competition - Overlap - Site
44 fidelity - Spatial segregation

45 **Word Count:** 7588

47 INTRODUCTION

48 An animal moves to find food, mates or flee a predator (Nathan et al. 2008; Shaw 2020). Its movement
49 is shaped by its physiological state (e.g., poor/good body condition, Goossens et al. 2020) and abilities
50 (e.g., locomotor or cognitive abilities, Fagan et al. 2013), and by the ecological challenges it faces (e.g.,
51 landscape attributes, such as food distribution, Bartumeus et al. 2005). For animals living in group,
52 movement is also shaped by social factors, such as intra-group cohesion or interactions with other
53 groups (Shaw 2020). These different facets of animal movement illustrate the plethora of space-use
54 strategies (Teitelbaum and Mueller 2019).

55 In most mammalian species, individuals restrict their movements within limited areas called home
56 ranges, which are much smaller than expected based on their movement abilities alone (Burt 1943;
57 Börger, Dalziel, and Fryxell 2008; Powell and Mitchell 2012). The space-use dynamics at the home
58 range scale varies in terms of site fidelity (e.g., Morrison et al. 2021), and in terms of “neighbourhood
59 interactions” and space-use exclusion (e.g., Pearce et al. 2013). Large differences may exist even in
60 closely related species. For example, chimpanzee (*Pan troglodytes*) communities show little home
61 range overlap (Herbinger, Boesch, and Rothe 2001) and conduct intense patrolling at the periphery
62 of their home range to defend it (Langergraber et al. 2017; Watts and Mitani 2001), while bonobo
63 (*Pan paniscus*) groups have undefended home ranges that largely overlap with those of neighbouring
64 groups (Samuni, Wegdell, and Surbeck 2020). Consequently, highlighting the space-use dynamics is
65 essential for a broader understanding of each species socio-ecology (Börger, Dalziel, and Fryxell
66 2008), hence of population dynamics (Morales et al. 2010; Barraquand and Murrell 2012; Riotte-
67 Lambert et al. 2017), and for providing key knowledge for their conservation.

68 Site fidelity generally enhances familiarity with the environment (Piper 2011). It is therefore
69 associated with improved foraging efficiency (Riotte-Lambert, Benhamou, and Chamaillé-Jammes
70 2015) and reduced risk of predation (Gehr et al. 2020). However, site fidelity may be disrupted

71 because of changes in environmental conditions (e.g., food availability), which is well illustrated by
72 migratory behaviour (Avgar, Street, and Fryxell 2014). This may also be a consequence of social
73 factors, for example, specific reproductive strategies, which is well illustrated by dispersal at sexual
74 maturity (Bowler and Benton 2005).

75 Site-fidelity benefits depend from possible exclusive use of the area. Animals may possibly defend it,
76 which is then called a territory, to attempt to have exclusive access to food and/or mates. The territory
77 may correspond to the entire home range or only a part of it. Territoriality (Burt 1943; Grant,
78 Chapman, and Richardson 1992) usually involves asymmetric interactions between the owner of the
79 territory and other conspecifics. In gregarious species such as primates, securing exclusive use of
80 space is a 'collective action problem' (Willems et al. 2015) and is therefore reflected in the movement
81 pattern of the whole group. In territorial species, because of the need to display some patrolling, the
82 daily path length is expected to increase with the home range size and, for a given home range size,
83 to be larger than in non-territorial species (Mitani and Rodman 1979).

84 In all mammalian species, food is a key determinant of movement. For example, in mountain gorillas,
85 the daily path length is related to resource availability and group size (the latter being used as a proxy
86 of energy intake and food accessibility for the group, Caillaud et al. 2014; Ganas and Robbins 2005).
87 Exclusive space use may then occur passively as a by-product of spatial memory-based foraging
88 optimization, as this involves avoidance of areas depleted by neighbouring conspecifics (Riotte-
89 Lambert, Benhamou, and Chamaillé-Jammes 2015; Aarts et al. 2021; Ranc, Cagnacci, and Moorcroft
90 2021).

91 Interestingly, the two site exclusion mechanisms, social and ecological, are central to the existing
92 literature on primate cognition. On the one hand, the positive correlation between home range
93 overlap and brain size (Grueter 2015) has been considered as supporting the hypothesis that
94 intergroup interactions should shape selection towards higher cognition (*Napoleonic Intelligence*

95 *Hypothesis*, Ashton, Kennedy, and Radford 2020). On the other hand, patterns of food availability
96 should imply weak to intensive selection towards higher cognition, depending on whether the
97 distribution is homogeneous or heterogeneous in space and time (*Ecological Intelligence Hypothesis*,
98 Milton 1981; Rosati 2017). Thus, the characterisation of socio-ecological factors affecting the
99 dynamics of space use can also provide helpful insights into the discussion of the evolution of animal
100 cognition (e.g., see Janmaat and Chancellor 2010). Yet, studies providing a joint synthetic view of both
101 social and ecological drivers of space-use in primates remain rare (e.g. Isbell 1991). Such a complete
102 picture was only recently offered by Seiler et al. (2017; 2018), who showed that mountain gorillas
103 (*Gorilla beringei*) favour the previously used most productive areas, while avoid those used by
104 neighbouring groups.

105 Western gorillas (*Gorilla gorilla*) are much less studied than mountain gorillas. They are much more
106 frugivorous, and their groups include a single adult male (Forcina et al. 2019; Masi et al. 2015; Seiler
107 et al. 2017). To date, most studies have focused separately either on the social or the ecological factors
108 of space use either indirectly (via camera traps, Morrison et al. 2020) or directly on groups still under
109 habituation to human presence (Cipolletta 2003, 2004), based on a relatively limited set of spatial
110 metrics based (e.g., daily path length, Doran-Sheehy et al. 2004). There is no doubt that ecological
111 factors strongly influence their space-use patterns (Remis 1997; Goldsmith 1999; Cipolletta 2004;
112 Seiler and Robbins 2020) due to their seasonal frugivory diet (Masi, Cipolletta, and Robbins 2009;
113 Masi et al. 2015). This seasonally-dependent diet has been shown to affect their travel patterns, with
114 longer travel times, and therefore greater distances travelled and areas covered, during periods of
115 high fruit abundance (Remis 1997; Goldsmith 1999; Cipolletta 2004; Masi, Cipolletta, and Robbins
116 2009; Seiler and Robbins 2020). On the other hand, social interactions between groups are also likely
117 to shape large-scale movements as these encounters can lead to infanticide and/or the transfer of
118 females (Harcourt and Stewart 2007). However, the interactive roles played in western gorillas by

119 the social and ecological factors remain unclear, leaving questions about ape space-use strategies and
120 evolution unanswered.

121 Space-use patterns in western gorillas may result from both individual needs, food distribution and
122 cognitive abilities (e.g., spatial memory), as well as interactions with other conspecific groups. To
123 better understand the respective roles played by these different factors, we benefited from a unique
124 long-term monitoring of five habituated groups in central Africa, including two neighbouring dyads.
125 We investigated various space-use variables (daily path length, home range size, site fidelity,
126 recursion and intensity distributions, space-use overlap between neighbouring groups) to address
127 the following questions:

- 128 • To what extent do home range size (a proxy for space defensibility), group size (a proxy for
129 energetic requirements and food competition) and season (a proxy for environmental
130 complexity) influence gorilla daily path length?
- 131 • To what extent are western gorillas faithful to an area and what factors are associated with
132 site fidelity disruption?
- 133 • To what extent do neighbouring western gorilla groups segregate in space, and what
134 mechanisms are likely to drive the level of space sharing?

135 **METHODS**

136 **Study sites and gorilla study groups**

137 This study was carried out from three field research stations within the Sangha Tri-National
138 Landscape (known by its French acronym TNS, Figure 1): Bai Hokou (N 2° 52', E 16° 28'), Mongambe
139 (N 2° 55'; E 16° 23'), both in the Dzanga-Ndoki National Park in the south-western part of the Central
140 African Republic (CAR), and Mondika (N 4° 39'; E 18° 56') in the periphery of the Nouabalé-Ndoki
141 National Park in the Republic of Congo (RC). The TNS environment has a seasonal climate with a dry

142 season (< 100 mm monthly rainfall) in December-February and a peak of rainy season in September-
143 October (Mehlman and Doran 2002; Lilly, Mehlman, and Doran 2002; Masi, Cipolletta, and Robbins
144 2009). The region is characterised by a largely pristine tropical rainforest which is a mosaic of
145 primary monodominant *Gilbertiodendron* forest and mixed forest, including secondary *Marantaceae*
146 forest patches, swamps and natural forest clearings. Data were collected on five habituated groups of
147 wild western gorillas. (13 to 14 individuals), and RC2 (6 to 11 individuals) at Mondika, CAR1 (7
148 individuals) at Bai Hokou, and CAR2 (9 to 10 individuals) at Mongambe were fully habituated groups,
149 while CAR3 (8 to 9) at Bai Hokou was in the latest stage of habituation individuals), tolerating human
150 presence within 10 to 15 m. Group composition and its possible changes during the study period are
151 provided in Supplementary Material Table S1. In the analyses including the group size (see below),
152 1- to 4-year-old infants (following Breuer et al. (2009)'s age classification) were ever counted as they
153 could contribute to the energetic need of the group, albeit less intensively than adults. We refitted the
154 models including "group size" both with and without < 1-year-old infants, who are fully nutritionally
155 dependent on mothers and whose energetic needs greatly differ from those of adults, to see how this
156 may affect the results.

157 **Data recording**

158 From sunrise to sunset, gorilla groups were followed daily at less than 10 m by the observers. CAR1
159 was first tracked from February 2003 to August 2004, and then from January 2009 to September
160 2014 (totalling 1904 days) and CAR2 from January 2008 to August 2014 (totalling 2194 days; > 1-
161 month gaps occurred due to data loss in both groups; see Figure 3). During this first tracking period,
162 locations were recorded based on a grid-system made of 250 m side-quadrats, with the help of a
163 compass and an extensive network of mapped trails (*grid data set*; see Cipolletta 2003, 2004). During
164 a second tracking period, from June 2016 to November 2017, CAR1, CAR2 and CAR3 were
165 simultaneously GPS-tracked (thanks to handheld GPS receivers carried by people staying in close

166 proximity to the group) for 469, 380 and 337 days, respectively. In Republic of Congo, RC1 and RC2
167 were simultaneously GPS-tracked using handheld GPS receivers from October 2012 to January 2015
168 (596 and 523 days, respectively). However, in this *GPS data set*, CAR groups were tracked using the
169 continuous track-log setting, involving a location recorded about every 18 m, whereas RC group
170 locations were recorded every 20 min.

171 During gorilla tracking, we also daily collected information about the group composition (presence
172 of newborn or immigrating individuals, deaths or emigrations of individuals) and interaction with
173 other social units (other groups or solitary males) based on (i) direct observations (visual or auditory)
174 of other gorillas, (ii) alert reactions from group members (e.g., hand clapping, screaming, running
175 away etc.) and/or silverback (chest beating and/or hooting, slap on ground/tree), and (iii) presence
176 of traces from other gorillas (particularly at the nest sites).

177 **Data analyses**

178 Data processing and analyses were implemented in the *R* environment (v.4.1.2, R Core Team 2020).
179 Except for the *base* package, directly available within *R* software, all *R* packages used are cited where
180 appropriate. Additionally, the *Rcpp* package (Eddelbuettel and François 2011; Eddelbuettel 2013;
181 Eddelbuettel and Balamuta 2018) was used to implement some homemade C++ functions. The
182 different metrics calculated in this study are shown in the Supplementary Material Figure S1.

183 **Locational stationarity**

184 Home range behaviour involves locational stationarity (absence of significant changes in mean
185 location and/or variance in location across time), due to repeated visits to the same restricted set of
186 places. If the location time series over a large temporal extent (e.g., several years) is stationary, a long-
187 term home range can be defined. Additionally, irrespective of whether the series is stationary or not
188 in the long-term, it may be piecewise stationary (i.e., made of phases that are stationary over shorter

189 periods). Each stationary phase then corresponds to a temporary (e.g., seasonal) home range
190 (Benhamou 2014), which can then be highlighted on a biological basis rather than based on an
191 arbitrary (e.g., monthly) segmentation basis, as classically done. For each gorilla group, we looked at
192 possible global stationarity, and at piecewise stationarity with phases > 30 days using the
193 “segmentation” function of the *segclust2d* package (Patin et al. 2020), in time series of easting (x) and
194 northing (y) coordinates. For the *grid data set*, they corresponded to the coordinates of the quadrat
195 centre (see Figure 2 for example) with a time-stamp defined only on a daily basis. For the *GPS data*
196 *set*, we kept a location every 2 hours between 8 am to 4 pm (i.e., five locations a day, as keeping more
197 locations resulted in computer memory issues). The output of the segmentation of the location time
198 series obtained from the *GPS data set* is shown in Supplementary Material 3.

199 To quantify the overall tendency of a group to change its home range (shift or change in size,
200 corresponding to the breakpoints in the piecewise stationary series of locations), we calculated the
201 Simpson (1949) index, which ranges between 0 and 1, on the relative time lengths of each stationary
202 phase as $ST = \sum_i t_i^2 / t^2$ where t_i is the duration of stationary phase i , and t is the total duration of the
203 time series. A ST value larger than 0.25 is assumed to indicate the occurrence of a dominant stationary
204 phase but, with our data, this index has to be interpreted with caution for two reasons. It may be
205 biased by the occurrences of time gaps (i.e., period without gorilla tracking) > 30 days because the
206 group was lost (which happened only for the *grid data set*; Figure 2; for the *GPS data set*, time gaps
207 were always lower than 22 days)). Furthermore, the ST index is also affected by the arbitrary
208 beginning and end of the tracking period, as the first and last stationary phases could last longer than
209 their apparent durations.

210 Home ranges, space-use fidelity, and shifts

211 We assessed the Utilization Distribution (UD) for each stationary phase. With the *grid data set*, the
212 UDs were obtained simply by counting the number of times the various quadrats were visited and the

213 home ranges were defined by the set of quadrats visited at least twice (corresponding to cumulative
 214 isopleths of 88% to 97%). With the *GPS data set*, we used a movement-based kernel density
 215 estimation approach (BRB/MKDE; Benhamou (2011); program freely available at
 216 www.cefe.cnrs.fr/fr/recherche/bc/dpb/216-simon-benhamou), with parameters $T_{max} = 30$ min (i.e., two
 217 successive relocations separated by a larger delay were not linked), $L_{min} = 30$ m (successive
 218 relocations with 30 m of each other were considered corresponding to the same place, to filter out
 219 GPS noise), no-movement filtering (the time spent on the spot was not considered to focus on
 220 prospection time) and $h_{min} = 100$ m (corresponding to the kernel smoothing value). The home ranges
 221 areas and core areas were then determined as the minimum areas encompassed within the 95% and
 222 50% cumulative isopleths of the UD, respectively.

223 We assessed space-use fidelity by computing the overlap between all pairs of UDs of the same group
 224 (separately for the *grid* and *GPS data sets*), using Bhattacharyya (1946)'s coefficient (see Fieberg and
 225 Kochanny 2005), which ranges from 0 (no overlap) to 1 (identical UD):

$$226 \quad BC_{i,j} = (U_i U_j)^{-0.5} \sum_{q=1}^N (u_{i,q} u_{j,q})^{0.5}$$

227 where N is the total number of quadrats involved (corresponding to the actual quadrats for the *grid*
 228 *data set*, and to virtual quadrats for the *GPS data set*), $u_{i,q}$ and $u_{j,q}$, are the fractions of UD
 229 encompassed in quadrat q for stationary phases i and j , and U_i and U_j are the total UD fractions
 230 encompassed in the home ranges ($U_i = U_j = 0.95$ for the *GPS data set*, but could take other values for
 231 *grid data set*). A time-weighted average value of spatial fidelity was obtained for each gorilla group
 232 (for the *grid* and *GPS data sets* separately) as

$$233 \quad \bar{BC} = \sum_{i>j} \sqrt{t_i t_j} BC_{i,j} / \sum_{i>j} \sqrt{t_i t_j}$$

234 Furthermore, we computed the distances between successive home range barycentres. We
235 considered that a large home range shift occurred when this distance was larger than the radius of
236 the circle that has an area equal to the mean home range area (computed using the *GPS data set*). We
237 also visualised the space-use dynamics along time by computing the Bhattacharyya coefficient for all
238 pairs of 2-month UD's with a 1-month overlap (to allow sufficient smoothing, analogously to
239 Kranstauber et al. 2020).

240 Intra-group space-use pattern

241 These analyses, which require a high spatial and temporal resolution, could be conducted only on the
242 *GPS data set*.

243 Recursion and Intensity distributions

244 For each stationary phase, in addition to the UD, we computed the Recursion Distribution (RD, i.e.,
245 the distribution of the number of revisits to any location within the home range) and the Intensity
246 Distribution (ID, i.e., the distribution of the mean visit duration, Benhamou and Riotte-Lambert 2012,
247 see Supplementary Material 4). Any given location was considered visited when the resident group
248 spent at least 12 min within 100 m of it. A new visit to this location was counted each time the group
249 came back within 100 m of it after having left this area for at least 2 hours (the revisit to the area after
250 a shorter delay was considered the same visit, and the additional time spent there was included in the
251 duration of the visit). Given the gorilla travelling speed (0.42 km/h estimated from the *GPS data set*
252 on CAR groups that were tracked in continuous mode), the 12-min threshold corresponded to the
253 minimum time required to cross the area through its centre. The 2-hour threshold corresponded to
254 the minimum time required to ensure that the group really left the neighbourhood of the location
255 considered before coming back. To assess whether a group tended to spend more time per visit at the
256 places they revisit more often, we computed the overlap between ID and RD using the Bhattacharyya
257 coefficient. We then looked at whether this value depended on the resource seasonality,

258 distinguishing between the high fruit (June-September), and low fruit season (November-April, Masi,
259 Cipolletta, and Robbins 2009; Masi et al. 2015).

260 Daily path length (DPL)

261 We looked at how DPL, for each group, varied with the high and low frugivory season (s , dummy
262 coded; transitory months between those two seasons, May and October, were discarded), the group
263 size (z), and the home range area (A) using a linear mixed Gaussian regression (Zuur et al. 2009)

$$264 \quad \text{DPL}_{d,g} = \beta_0 + \beta_1 s_d + \beta_2 z_{d,g}^2 + \beta_3 z_{d,g} + \beta_4 \sqrt{A_{d,g}} + \beta_5 \ln(c_{d,g}) + \sum_{j=1}^{G-1} \gamma_j x_j + \sum_{n=1}^{11} \alpha_n m_n + \epsilon_{d,g}$$

265 where $c_{d,g}$ is a control variable, accounting for the tracking duration of the day d considered of the
266 group g among the G groups, x_j and m_n are the indicator functions (dummy variable) being equal to
267 1 for $j = g$ and $n = d$ respectively, or 0 otherwise, for accounting for possible effects of the variable
268 amount and repetition of data for the different groups and months. $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4$ (fixed effects), γ_j
269 and α_n (random effects) are the parameters to be estimated by the model, and $\epsilon_{d,g}$ is the error term.
270 As years of study were completely separated between groups, we could not include the year as a
271 covariate. Details on statistical implementation are available in the **Statistical model implementation**
272 section.

273 We considered a quadratic effect of group size since we expect a larger group to have larger energetic
274 requirements. Yet, the bigger the group, the bigger the “inertia,” and thus, we expected a decrease in
275 travel distance at too high group sizes.

276 We considered the “group” a fixed factor to control for differences stemming from a “population”
277 effect and/or location sampling frequency (i.e., continuous vs 20-min tracking in CAR vs RC,
278 respectively), and from group composition (e.g., number of adult or subadult males/females,
279 adults/sub-adults/juveniles etc.). We did not consider it as a random factor to avoid assumption

280 violation of residuals normality and homoscedasticity (see Supplementary Materials 6 and 7). As the
281 variations in sampling effort (e.g., in some days, gorillas may have been tracked only for a couple of
282 hours) induced model instability, we considered DPL values only for days for which gorillas were
283 tracked for at least six hours (64% of the 1453 observation days). Furthermore, we filtered out
284 potential upper outliers (DPL > 6 km), which represented about 1% of the remaining observation
285 days, to minimise leverage effects that rendered the model less meaningful. The initial distribution of
286 DPL, as well as that obtained after filtration, are presented in Supplementary Material Figure S4. For
287 further details on model implementation, see **Statistical model implementation** below.

288 Group interactions

289 To evaluate the potential occurrence of territory defence in gorillas, for each stationary phase
290 corresponding to a home range, we calculated the Mitani and Rodman (1979) territoriality index,
291 $MR = \overline{DPL} / \sqrt{A/\pi}$, and the expanded version of this index by Lowen and Dunbar (1994), $LD =$
292 $\pi N_s \overline{DPL} / (4A)$, where \overline{DPL} is the mean daily path length, A is the home range area, N is the number of
293 independent moving parties, which for cohesive species such as gorillas is one, and s is the mean
294 “detection” distance of other groups, set to 500 m as in Lowen and Dunbar (1994). Both indices are
295 related to the probability of animals bouncing against the boundaries of their home range based on a
296 gas diffusion model (Lowen and Dunbar 1994) and, for LD, patrolling along the borders. In this
297 approach, the whole home ranges are assumed to correspond to territories.

298 To analyse further the extent to which two neighbouring groups may interact with each other, we
299 computed the UD overlap between neighbouring dyads, namely RC1-RC2 and CAR1-CAR3 (Figure 1),
300 with the Bhattacharyya coefficient computed for periods during which two corresponding stationary
301 phases overlapped in time. The time-weighted mean overlap (i.e., pondered to account for the length
302 of common duration of used home ranges) for a pair of neighbouring groups was then computed as

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$$\bar{BC} = \frac{\sum_p (t_p BC_p)}{\sum_p t_p}$$

where BC_p is the Bhattacharyya coefficient for a given period of time overlapping p whose duration is t_p . We additionally computed the fraction of UD of one group encompassed in the area currently used by the neighbouring group, $FUD_{1,2}$ and $FUD_{2,1}$ for any pair of neighbouring groups 1 and 2 (Smith and Dobson 1994; Benhamou et al. 2014). The dissymmetry in space use was computed as $D = |FUD_{1,2} - FUD_{2,1}|$. We also computed the time-weighted mean value \bar{D} in the same way we computed \bar{BC} .

We also aimed at assessing the intensity with which a group may have used the central part of the home range of a neighbouring group. In the present study, the central part could not be assimilated to the core area (i.e., the minimum area within the 50% cumulative isopleth of the UD), which was highly fragmented, with many subparts occurring within the home range periphery (Figure 1). Consequently, we defined the central part of the home range as the area within the 50% cumulative isopleths of the home range based on the elliptical home range model (Jennrich and Turner 1969; Mazurkiewicz 1969). It corresponds to a single elliptical area centred on the home range barycentre. We then calculated the number and average duration of visits of a group to the central part of its neighbour's home range. A visit was counted as soon as the group entered this area. The number of visits was calculated for every month including at least ten tracking days. The average number of visits for each group was obtained using Poisson regressions. To determine whether the tendency of a group to enter the centre of a neighbouring group's home range varied across the year, we fitted a Poisson model (see **Statistical model implementation**). We compared the Akaike Information Criterion (AIC, Burnham and Anderson 2002) of models of the form

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$$n_{m,g} = \exp \left[\beta_0 + \beta_1 \cos((m - 1 + k)\pi/6) + \sum_{j=1}^G \gamma_j x_j + \ln(o_{m,g}) + \epsilon_{m,g} \right]$$

326 where $n_{m,g}$ is the number of visits for group g during the month m (“January” = 1; etc.) and k is a shift
 327 parameter set to an integer value in the range $[0, 11]$ to test varying locations for the mode of the
 328 cosine function, $\ln(o_{m,g})$ is the associated offset term (logarithm of the number of monitored days
 329 that month for the group considered), x_j is an indicator function (dummy variable) being equal to 1
 330 for $j = g$, and 0 otherwise (random effect), and $\epsilon_{m,g}$ is the associated error term. The best-fit value for
 331 k was given by the model with the lowest AIC.

332 Finally, we considered the possible occurrence of dynamic interactions, i.e., the tendency of the two
 333 groups to move together or to avoid each other, or to move independently of each other, when they
 334 were simultaneously within a shared area. For this purpose, we computed the dynamic interaction
 335 index (“IAB” function of the *wildlifeDI* package, Long et al. 2014), between two groups $I(t) =$
 336 $\exp[-0.5d(t)/c]^2$ (Benhamou et al. 2014) where $d(t)$ is the distance between the two groups at
 337 time t and c is the critical distance, which separates distances for which an interaction effect is
 338 assumed to be small or large. We tested whether the mean value of this index was significantly higher
 339 (attraction) or lower (repulsion) than expected under the null hypothesis of independent movements.
 340 To do so, we used a time permutation procedure that maintains the correct chronology of locations
 341 of both groups (see Benhamou et al. 2014 for details). We considered three critical distances: 200,
 342 500 m and 1000 m, approximating critical distances expected for visual, olfactory and auditory cues.

343 Statistical model implementation

344 Statistical models were fitted with the *lme4* package (mixed Gaussian models, Bates et al. 2015) or
 345 otherwise the *glmmTMB* package (Brooks et al. 2017). The singular effect of each variable was
 346 assessed by comparing model likelihood with and without the variable using a maximum likelihood

347 ratio-test with the “drop1” function, while, if multiple (DPL model), their synergic effect was assessed
348 by comparing the *full* model, including all descriptive variables, with a *null* model, including only
349 control variables. The “conditional” variance explained by the model (i.e., including fixed and random
350 effects) was calculated using the “r.squaredGLMM” function from the *MuMIn* package (Barton 2020).
351 To ease model interpretability, continuous control variables were reduced and centred (i.e., shifted
352 and rescaled to have a null mean and unit variance, Schielzeth 2010).
353 After fitting, we checked the necessary assumptions depending on the model family, using Q-Q plots,
354 residuals vs. fitted values scatter-plots and histograms of residuals distribution (Zeileis and Hothorn
355 2002) based on the *DHARMA* package (Hartig 2022). The deviations obtained were reasonable (see
356 Supplementary Material 6). We did not find overdispersion in the Poisson model. If several predictors
357 were considered (“DPL” model), we also assessed the Variance Inflation Factor (VIF, Field 2005) using
358 the “vif” function of the *car* package (Fox and Weisberg 2019), which pinpointed several correlation
359 issues (max VIF > 3; “DPL” model) because some groups consistently had a higher weekly group size
360 combined with low variance. The directions of average estimates were nonetheless robust: only
361 significance was affected. For the “DPL” model, when possible, we also checked model sensitivity to
362 outlier points and random levels, using a series of statistical indices (Cook’s distance and dfBetas,
363 Quinn and Keough 2003; Zuur et al. 2009). This was done using the *influence.ME* package
364 (Nieuwenhuis, Te Grotenhuis, and Pelzer 2012), which did not highlight major issues (Supplementary
365 Material 7). We also considered the influence of the group identity by comparing model output
366 (estimate and significance) with and without one group (Supplementary Material 7).

367 RESULTS

368 Site fidelity and space-use adjustment

369 All study groups but CAR3 shifted the location of their home range at some point. This occurred on
370 average 0.72 times per year (range: [0,1.8], Figure 3) per year, sometimes to re-occupy an area
371 previously used (see CAR2 group in Supplementary Material 3).

372 Ten shifts out of 19 (six out of nine in the *grid data set*, and four out of ten shifts in the *GPS data set*)
373 were larger than 1600 m, corresponding to the radius of a circular area equal to the average home
374 range size in this study (ca. 8 km²). The *grid data set* provided further evidence that large spatial shifts
375 occurred after long periods of stability and were often followed by periods of instability characterised
376 by frequent “small” shifts (see CAR2 group after 2012, right panel, Figure 2) or by a drifting period
377 with a gradual shift with no consistent spatial direction (see CAR1 group between 2010 and 2012;
378 left panel, Figure 2).

379 The Simpson index was on average 0.43 for the *grid data set* (range: [0.36,0.43]) and 0.51 (range:
380 [0.25,1]) for the *GPS data set*, indicating that western gorillas spent most of their time exploiting a
381 single area corresponding to their main home range. For the four study groups out of five that used
382 multiple home ranges, site fidelity was moderate to high, (Bhattacharyya coefficients for *grid data set*:
383 0.36 and 0.39; for *GPS data set*: mean = 0.44, range = [0.24,0.73]). The size of the home range (mean
384 = 7.96 km², range = [1.65, 13.48]; calculated from the *GPS data set* only) was positively correlated
385 with its duration (Spearman correlation: $r = 0.56$, $N = 15$, $p = 0.034$).

386 Small (< 1600 m) or large (> 1600 m) home range shifts were not less or more frequent in the high-
387 fruit season than expected by chance (observed: 0.16 (CI95% = [0.03,0.4]) vs. expected: 0.33, $N = 19$,
388 $p = 0.143$). We further looked at whether shifts (both small and large) may have had a possible
389 biological explanation in the three study groups for which we had associated behavioural data (CAR1,

390 RC1 and RC2). Among the six large shifts done by CAR1 and RC1 (RC2 did only small-scale shifts), five
391 (83%) were associated with a particular event (i.e., interaction with another gorilla group for three
392 of them, long heavy rain in the previous days for one of them, and visit to distant aquatic areas for
393 another one). Interestingly, eight out of nine (89%) of the small-scale shifts occurred when gorillas
394 had an interaction with another social unit (on the same day or/and one or two days before the shift
395 date). In addition, all shifts happened distantly in time from the birth/arrival, or death/departure of
396 group members (minimum absolute time distance of 35 and 28 days from a birth/arrival, or a
397 death/departure).

398 **INTRA-GROUP SPACE-USE PATTERN**

399 **Space-use and resource seasonality**

400 The UD_s have a mean “flatness” (ratio between the size of the core area and the home range size
401 depicting how evenly is space-used) of 0.25 (CI_{95%} = [0.22,0.28]), close to the flatness of a bivariate
402 Gaussian distribution (ca. 0.23). However, contrary to a bivariate Gaussian distribution, the core area
403 was not central but fragmented over the whole home range area (Figure 1).

404 Overall, highly revisited sites were also visited for the longest (mean overlap between ID and RD:
405 0.94, CI_{95%} = [0.91,0.95]; Supplementary Material Figure S3 and S4). No difference was observed
406 between the low-fruit season, when gorillas relied more on mature/young leaves and stems, and the
407 high-fruit season, when they mostly fed on fruits (paired Wilcoxon signed rank test: $V = 12$, $p = 0.461$,
408 Supplementary Material Figure 2; median difference of -0.01, with high-fruit season taken as
409 reference). Note however that the high overlap values (Bhattacharyya coefficient) between the ID and
410 RD within a given season are in part because both distributions are restricted to the same area (for
411 comparison, the overlap between a bivariate Gaussian distribution, and the inverted distribution
412 centred on the same location is close to 0.82).

413 In periods where the home range spanned over several seasons, the sites highly used varied across
414 seasons: the inter-season ID/RD overlap (using the average overlap of the ID of one season and the
415 RD of the other) was clearly lower than the intra-season ID/RD overlap (using the average overlap of
416 the ID and RD of the same season; paired Wilcoxon signed rank test: $V = 36$, $p = 0.008$, Supplementary
417 Material Figure S2; median difference (with within season take as a reference) of 0.45).

418 **Energetic and foraging constraints shape daily path length**

419 Variation in DPL was significantly explained by some of the tested predictors (*full vs null* model
420 comparison: $\chi^2 = 21.54$, $df = 4$, $p < 0.001$; pseudo- $R^2 = 0.52$). This variation was basically driven by a
421 seasonal effect, as gorillas travelled more during the high-fruit season (with low-fruit season taken as
422 reference, est. = 79.55, $CI_{95\%} = [689.81, 747.84]$, $\chi^2 = 21.07$, $df = 1$, $p = 0.002$, Table 2, Figure 5). Home
423 range size had no effect on the DPL ($\chi^2 = 1.73$, $df = 1$, $p = 0.188$, Figure 5). The effect of group size was
424 significant ($\chi^2 = 8.16$, $df = 1$, $p = 0.004$). This took the form of an inverted bell shape (negative estimate
425 of squared terms, Table 2). This shape was flattened when < 1 -year-old dependent infants were not
426 considered (Figure 5, Supplementary Material Figure S6). As a note side, RC groups travelled less than
427 CAR groups (Table 2).

428 **INTER-GROUP SPATIAL RELATIONSHIPS**

429 **Territorial indices**

430 The two territoriality indices were highly correlated (Spearman correlation: $N = 15$, $r = 0.91$, $p <$
431 0.001). They were lower than the traditionally considered, yet empirically established, threshold of
432 territoriality (MR-index: mean = 0.17, $CI_{95\%} = [0.13, 0.2]$, the threshold is 1; LD-index: mean = 0.01,
433 $CI_{95\%} = [0, 0.02]$, the threshold is 0.08; Supplementary Material Figure S1).

434 Neighbouring home range overlaps

435 The average overlap between neighbouring UD (Bhattacharyya coefficient) was very low in both the
436 CAR dyad (mean = 0.08, range = [0,0.2]) and RC dyad (mean = 0.04, range = [0,0.19]). The level of
437 overlap was unrelated to the duration of the temporal overlap (Spearman correlation: $r_s = -0.49$, $N =$
438 10 , $p = 0.153$). In both dyads, a group did not occupy the shared area more than its neighbour: $\bar{D} =$
439 0.03 for both dyads (values close to 0 indicate symmetry in space use).

440 A group ventured into the central part of the neighbouring group's home range on average 0.59 times
441 a month (varied from 0.31 to 1.58 among groups, see Supplementary Material Figure S1 for group-
442 level value), with a maximum frequency just before the start of the high-fruit season (April; lowest
443 AIC for the model including for $k = 4$; $\chi^2 = 3.76$, $df = 1$, $p = 0.052$, Supplementary Material Figure 5).
444 No group visited this central area of the other group more frequently than the other dyad (paired
445 Wilcoxon signed rank test with continuity correction: CAR dyad, $V = 23$, $p = 0.683$, RC dyad, $V = 22$, p
446 $= 0.205$). The mean duration of these visits was 115 min (CI95% = [46,286]). Two visits out of 41
447 lasted more than 12 h, during which the gorillas stayed overnight within the neighbouring group's
448 central area. Within the RC dyad, neither group visited the central part of the home range of the other
449 group for a longer time than the other (Welch's t-test: $N = 16$, $t = 0.8$, $df = 13.71$, $p = 0.435$). Within
450 the CAR dyad, the CAR1 group visited the central part of the home range of CAR3 for a significantly
451 longer time than the CAR3 visited the CAR1 central area (mean difference of 262.5 min, CI95% =
452 [28.9,496.1], $N = 25$, $t = 2.39$, $df = 15.08$, $p = 0.03$; Residuals were normally and homogeneously
453 distributed, see Supplementary Material 8).

454 Dynamic interactions

455 Two neighbouring groups were rarely within 500 m of each other. This occurred only around 5.11
456 times a year for each dyad. At their closest, groups were observed at 150 m (RC dyad) and 288 m

457 (CAR dyad) of each other. When the two groups were simultaneously within a shared area, they
458 tended to move independently of each other (permutation test of locations, most p-value > 0.05, Table
459 2). Avoidance was statistically observed only once (with the parameter threshold separating short
460 and long inter-group distances set to 200 m; N = 708, observed vs. expected interaction 0.052
461 vs. 0.048, one-tailed p = 0.477). Attraction was statistically observed once (with the parameter
462 threshold separating short and long inter-group distances set to 200 m; N = 333, observed
463 vs. expected interaction 0.016 vs. 0.024, one-tailed p = 0.372).

464 **DISCUSSION**

465 In this study, we provided an integrated longitudinal picture of the dynamics of space use by wild
466 western gorillas. In particular, we illustrated how the scale of the response depended on the nature
467 of the stimuli (social vs. ecological). In western gorillas, ecological factors, such as diet choice, had a
468 major influence on day-to-day space-use, whereas social factors, such as male reproductive strategies
469 and subsequent (risk of) intergroup interactions, tended to shape broader (spatial) and longer
470 (temporal) patterns, such as home range dynamics. Yet, neighbouring home ranges overlapped little
471 and the shared areas were rarely used simultaneously, although groups ventured, and even could
472 nest, in the central part of the neighbouring group's home range. To add, groups did not show
473 ownership, patrolling or asymmetric interactions (i.e., dominance of one group over the other). This
474 suggests that western gorillas are an illustrative example of passive segregation (i.e. without
475 territoriality) between groups which should take root in their cognitively-driven foraging strategy
476 and scrambling competition with neighbouring groups.

477 **Spatial shifts and socio-ecological factors**

478 In all groups studied, gorillas tended to stay in the same area, as evidenced by the high average
479 pairwise overlap between UDs of the same group. Overall, gorilla home ranges were generally less

480 than 13 km², while gorillas moved around 1.42 km per day (median value). Site fidelity appears to be
481 a ubiquitous trait in primates (Janmaat et al. 2009; Ramos-Fernandez et al. 2013; Campos et al. 2014;
482 Wartmann, Juárez, and Fernandez-Duque 2014; Cheyne et al. 2019; Belle and Estrada 2020; José-
483 Domínguez, Savini, and Asensio 2015; Caillaud et al. 2014). This is probably because of the advantages
484 of greater familiarity with the environment, which is particularly useful when feeding on spatio-
485 temporally heterogeneous foods or to avoid predation (Powell and Mitchell 2012). Nevertheless,
486 gorilla groups occasionally readjusted their home range location, either locally (small shifts < 1600
487 m) or more widely (shifts > 1600 m). We observed this in all study groups but the one that was tracked
488 for the shortest time (1.5 years). However, this group too has recently shifted its home range, by
489 crossing the border with the Republic of Congo and residing there (Bai Hokou station long-term
490 monitoring data). It is worth noting that the onset of large shifts was followed by periods of instability
491 in space use, involving frequent small shifts over a few years, presumably to readapt to new ecological
492 (e.g., food distribution/availability) and social (e.g., presence of other gorilla groups/solitary males)
493 conditions. Such a strategy, which may allow gorillas to gain information on a new environment, was
494 also observed in mangabeys that become less cohesive, move more and venture into larger areas per
495 day when settling into a new area (Janmaat and Chancellor 2010).

496 Although the activity budget, diet and movement patterns of western gorillas are strongly influenced
497 by seasonal changes in fruit availability (Remis 1997; Goldsmith 1999; Cipolletta 2004; Doran-Sheehy
498 et al. 2004; Masi, Cipolletta, and Robbins 2009; Masi et al. 2015), home range shifts (small and large)
499 did not follow the same pace, leading to high variability in home range duration. However, our
500 behavioural observations indicate that large shifts might be related to social interactions and long
501 and heavy rains. Although gorillas are less active during rains (e.g., DPL is reduced, Ganas and Robbins
502 2005), they may also be more vulnerable to attacks from other males as hearing is difficult (thus, we
503 could have missed some potentially auditory interactions too).

504 On the other hand, small shifts may be mainly related to male reproductive strategies, as observed
505 for a former group of western gorillas in CAR, who moved its home range to acquire a sub-adult female
506 before returning to its original range after she joined the group (Cipolletta 2004). In western gorillas,
507 females are known to disperse when they reach maturity (Stokes, Parnell, and Olejniczak 2003) but
508 over shorter distances than males (Masi et al. 2021). Males (solitary or in groups) could therefore
509 move to attract potential dispersing females from other groups or to prevent their females from
510 dispersing by avoiding the other group's home range (Breuer, Robbins, and Robbins 2016; Cipolletta
511 2004). Although we did not observe shifts related to female acquisition (or loss), the vast majority of
512 small shifts occurred after interacting with other social units, risky events in which other males may
513 lead to infanticide or female appropriation/transfer (Stokes, Parnell, and Olejniczak 2003; Baudouin
514 et al. 2019; Manguette et al. 2020).

515 **Ecological factors shape within-home range movements**

516 Overall, we observed a large variability in the daily path lengths, especially between groups.
517 Specifically, the CAR groups seemed to travel more than the RC groups, but this is simply the result of
518 the difference in tracking methodology (discussed in McCann et al. 2021). Indeed, subsampling the
519 CAR data to match the RC protocol (a location recorded every 20 min) resulted in reduced a daily path
520 length estimate reduced by 638 m (± 162 ; see Supplementary Material Figure S6), which is close to
521 the mean difference observed between the CAR and RC groups (DPL model with infants, Table 2).
522 Controlling for this by including a "group" effect, we were then able to compare the relative effect of
523 several proxies related to ecological or social factors.

524 Movement decisions should be based on current and/or future environmental conditions, as well as
525 metabolic and nutritional needs (Nathan et al. 2008), which may vary by season and group size. We
526 found that only these two factors (but not the home range size, here used as a proxy of defensibility)
527 affected the daily path lengths. This is consistent with previous evidence that dietary changes shape

528 gorilla activity and travel time or distances (Remis 1997; Goldsmith 1999; Cipolletta 2004; Doran-
529 Sheehy et al. 2004; Masi, Cipolletta, and Robbins 2009).

530 The effect of dietary season was largely preponderant over the positive effect of group size (Figure
531 5). Indeed, finding sufficient food for maintaining nutritional and energetic balance in a seasonal
532 environment is an important challenge for western gorillas (Masi et al. 2015). In particular, gorillas
533 tended to travel more in the high-fruit season, compared to the low-fruit season, echoing previous
534 observations (Remis 1997; Goldsmith 1999; Cipolletta 2004; Doran-Sheehy et al. 2004; Seiler and
535 Robbins 2020; Masi, Cipolletta, and Robbins 2009). This suggests that more than energy *per se*, the
536 variation in movement patterns might be the result of variation in the challenge of locating resources
537 such as fruit, which are usually patchier and more ephemeral than herbaceous/foilage resources
538 (Milton 1981; Janmaat et al. 2016).

539 The effect of group size depended on whether or not fully dependent infants (< 1-year-old) were
540 included in the calculations. When included, the group size had a significant quadratic effect (Figure
541 5 and Table 2). In addition to infanticide risk forcing the group to travel more to avoid conspecifics,
542 the presence of infants is likely also associated with a higher energy demand for breastfeeding
543 mothers (Masi, Cipolletta, and Robbins 2009; Lodwick and Salmi 2019). This should lead to larger
544 daily path length to find more food. Yet infants may also contribute to slowing down the group, which
545 should lead to shorter daily path length. The observed quadratic relationship highlights this trade-off.
546 In mountain gorillas, such a quadratic pattern was also observed when weaned individuals were
547 removed (Grueter et al. 2018). This pattern was explained as being the combined result of within-
548 group competition (leading to an increase in daily path length) and inter-group competition (leading
549 to a decrease in daily path length). When infants were removed in western gorillas, group size and
550 daily path length were no longer correlated. This is because our study groups of intermediate size
551 both had the largest number of infants (see Supplementary Material Figure S7) and travelled more
552 than the groups of equivalent size without infants. Thus, the disappearance of the quadratic pattern

553 when infants were removed may imply that within-group competition outweighs inter-group
554 competition in western gorillas as opposed to mountain gorillas. As we discuss below, direct and
555 indirect interactions between groups are indeed low in western gorillas. On the contrary, in mountain
556 gorillas increased population size led to closer proximity and exacerbation of aggressive behaviour
557 between neighbouring groups (Caillaud et al. 2020).

558 **Exclusive space-use: the consequence of a passive segregation**

559 The benefits of a home range behaviour in terms of knowledge about the current food distribution
560 may be limited when space is shared with conspecifics (Powell and Mitchell 2012). In this framework,
561 limiting spatial overlap with neighbours should minimise resource depletion by competitors. We
562 showed that gorillas tended to use exclusive space, as we observed little or no overlap between home
563 ranges of known neighbouring groups (though the actual set of neighbouring groups was likely larger
564 than that considered here).

565 The exclusive use of space by western gorillas raises questions about the underlying factors that may
566 drive it: direct aggressive behaviour (i.e., territoriality) or indirect passive segregation (Riotte-
567 Lambert, Benhamou, and Chamaillé-Jammes 2015). Based on data obtained with camera traps,
568 Morrison et al. (2020) recently suggested that western gorillas are a good example of animals with a
569 notion of “ownership” (i.e., territoriality): the areas most used by one group (i.e., core areas) being
570 avoided by others. However, we highlighted that groups ventured into the central area of the
571 neighbouring group’s home range 0.59 times per month. They potentially then spent considerable
572 time there (median duration of visits: 156 min), even staying overnight (two out of 41 visits). Many
573 groups of western gorillas frequently visit the same large clearings (Magliocca, Querouil, and Gautier-
574 Hion 1999), which likely implies crossing other groups’ home ranges. All this underlines that gorillas
575 are not fierce defenders of space, and suggests that they do not consider places further away from
576 their own home range centre as riskier than others. Accordingly, we did not observe patrols, and the

577 daily path length was lower than expected for a territorial animal that would attempt to defend an
578 area of an equivalent size. Furthermore, there were no asymmetric relationships, as would be
579 expected in the case of direct competition. The spatial behaviour of neighbouring dyads was very
580 similar despite the different group sizes (used here as a proxy for group strength): groups occupied
581 the home range of the neighbouring group equally, exploited the same locations in shared areas
582 equally intensively, and ventured into the neighbour's home range equally frequently and for equal
583 periods of time. In contrast, larger groups of mountain gorillas had exclusive use of more than 50%
584 of their home range, while smaller groups had less than 20% (Caillaud et al. 2014). However, for
585 larger differences in group size we cannot exclude asymmetric space use may exist also in western
586 gorillas, as group size affects diet choice in this species (Fuh et al. 2022).

587 Like other apes (Trapanese, Meunier, and Masi 2019), western gorillas are known to be “cognitive”
588 foragers (Salmi et al. 2020). As illustrated here, sites exploited for the lengthiest times are also the
589 most visited and varied seasonally (Supplementary Material 4). These observations converge on the
590 prevalence of long-term spatial memory shaping the foraging decision. It is therefore likely that the
591 memorization of depleted areas by others contributes to the observed pattern of passive spatial
592 segregation (i.e., without territoriality Riotte-Lambert, Benhamou, and Chamaillé-Jammes 2015).
593 Potentially, long-range multimodal signalling, such as with vocalisations or odour (Salmi and Doran-
594 Sheehy 2014; Masi and Bouret 2015), should promote fast identification of known opponents, thus
595 long-range avoidance. This study thus highlights the absence of territoriality in western gorillas (as
596 opposed to Morrison et al. 2020), and suggests that spatial segregation should be the simple
597 consequence of passive avoidance due to the memorization of depleted areas. This underlines the
598 need for caution when interpreting static interactions to infer dynamic interactions.

599 In conclusion, this study highlighted how food affected directly (by changes in spatio-temporal
600 distribution) and indirectly (because of inter-group scramble competition) the space-use strategy of
601 a frugivorous species. In addition, fruit is a particularly rare and limited resource (Janmaat et al. 2016)

602 and several species may compete for it. For example, the diet of western gorillas largely overlaps with
603 that of chimpanzees (Tutin and Fernandez 1993; Head et al. 2011) and forest elephants (White, Tutin,
604 and Fernandez 1993). In birds, inter-species competition for food translates into territoriality among
605 species (Stiles and Wolf 1970; Drury, Cowen, and Grether 2020). Thus, space use may not be only
606 narrowed by conspecifics but any potential competitor. Promising avenues hence lie in considering
607 multi-species dynamics to better understand the patterns of species segregation and space use.

608 **ETHICS**

609 All research protocols adhered to the ethics rules of the local country at time of the study where it
610 was conducted (Central African Republic and Republic of the Congo). Research permits were
611 provided by the Ministries in Central African Republic and Republic of the Congo under the support
612 of World Wide Fund for Nature (WWF) and Wildlife Conservation Society (WCS), respectively.

613 **DATA AVAILABILITY**

614 Data will be accessible upon reasonable requests to TB for the RC data set, and to ShM and TF for the
615 CAR data set. Analytic codes will be provided by BR upon request afterwards.

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633 **CONFLICT OF INTEREST**

634 The authors declare having no conflict of interest.

635 **AUTHORS' CONTRIBUTION**

636 BR conceived the study with SB and ShM, BR cleaned and analyzed the data, and wrote the first draft.
637 ASM, AT, CC, EOB, GB, SiM, ShM, and TF collected the data. SB, ShM and TB primarily revised the
638 article. SB and ShM subsequently revised it several times. All authors revised and finally approved the
639 final version.

640

641 Table 1: Comparison of observed and expected values of dynamic interactions using a randomization procedure |
 642 Comparisons were computed for RC and CAR dyad separately for each period during which home-range overlapped
 643 (periods of overlap with few simultaneous tracks within the overlapping area were discarded). The p-values
 644 correspond to a one-tailed test. Observed interaction values significantly lower and larger than the expected values
 645 means avoidance and joint movements, respectively.

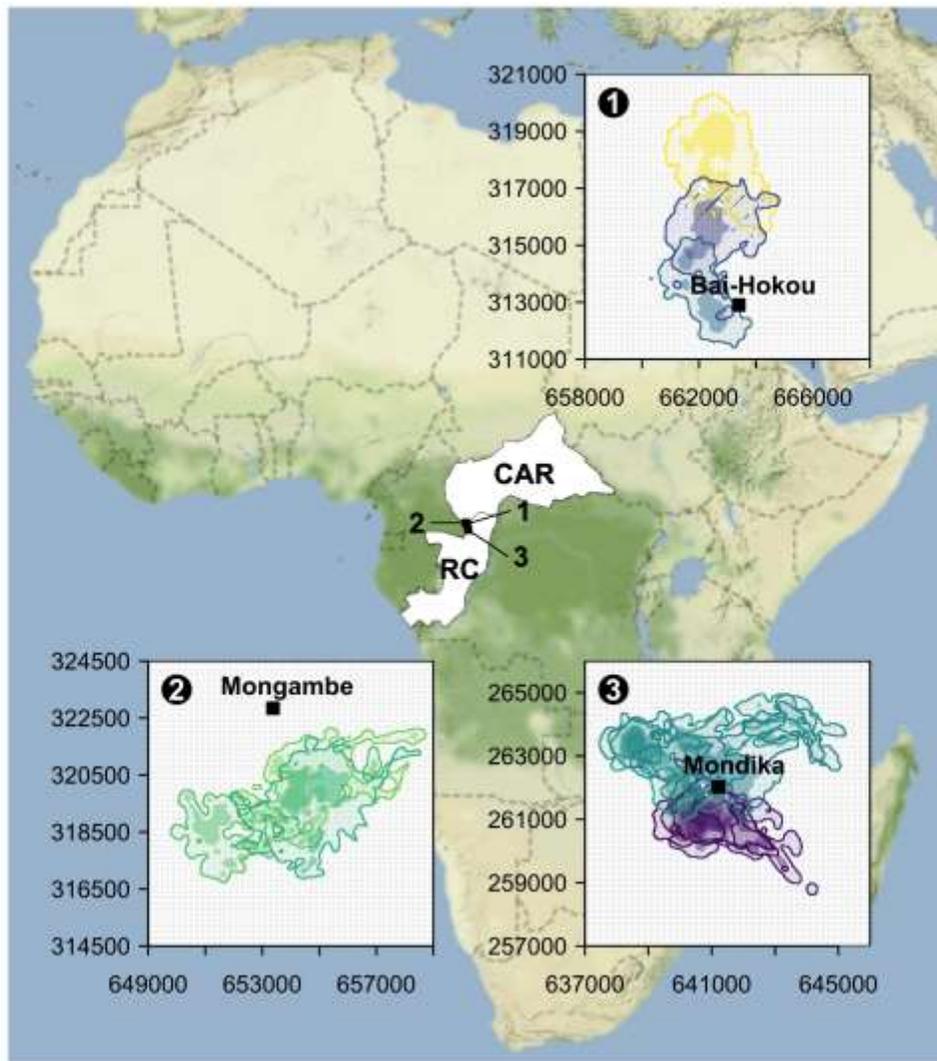
Critical distance	Synchronized relocation number	Interaction (observed)	Interaction (expected)	p-value
RC dyad (1st common period)				
c=200	510	0.153	0.204	0.361
c=500	510	0.538	0.632	0.206
c=1000	510	0.826	0.876	0.09
RC dyad (2nd common period)				
c=200	333	0.016	0.024	0.372
c=500	333	0.26	0.255	0.402
c=1000	333	0.552	0.533	0.468
CAR dyad				
c=200	708	0.052	0.048	0.477
c=500	708	0.395	0.255	0.01
c=1000	708	0.748	0.599	0.001

646

647 **Table 2: Summary of the generalized linear regressions | The model name is self-explicit and indicated with the**
648 **intercept. Est.=Estimate, Se=Standard error, CI95\%=the 95\% confidence interval, Df=Degree of freedom,**
649 **Chisq=Chi-squared statistics. Absent values or those with no meaning are not displayed (i.e., '-' symbol). The level**
650 **for categorical variables is indicated between parentheses. Scaled continuous variables are indicated as such, their**
651 **initial mean and sd are depicted in footnotes. Duration of the day was scaled in the DPL model. Prior to**
652 **transformation, mean = 8.46, sd = 0.95**

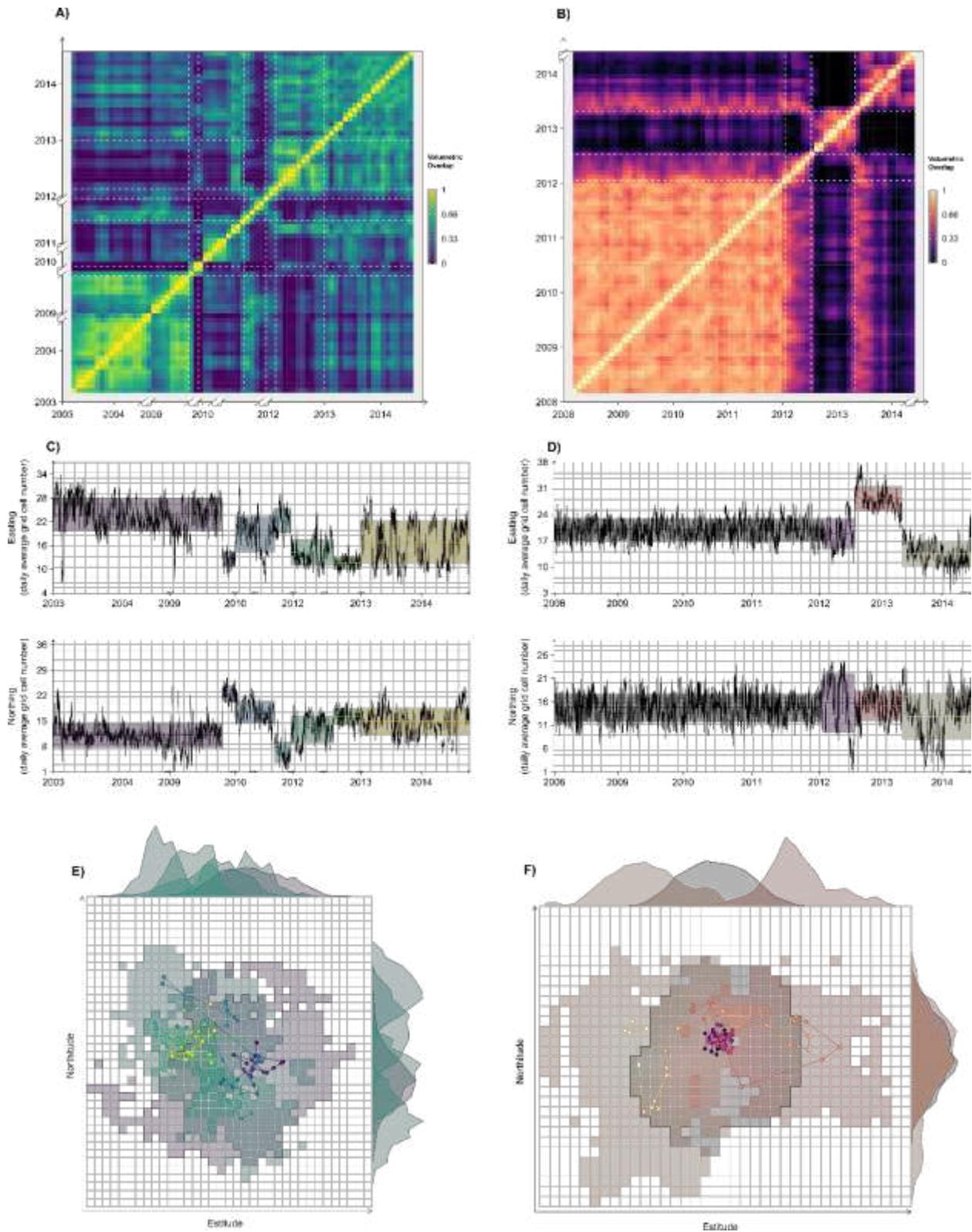
Variable	Est.	Se	CI95%	Df	Chisq	p-value
Model Visit Core Area: (N = 71)						
Intercept	-3.69	0.31	[-4.29,-3.09]	-	-	-
cos(month + best phase)	0.43	0.23	[-0.01,0.87]	1	3.76	0.052
Model DPL (with infants): (N = 1188)						
Intercept	254.25	655.65	[-1014.56,1541.6]	-	-	-
Home range size (sqrt)	79.55	60.44	[-38.2,197.12]	1	1.73	0.188
Season (Frugivory)	520.28	113.34	[302.39,739.16]	1	21.07	0.002
Group size (squared)	-22.25	7.79	[-37.34,-6.9]	1	8.16	0.004
Group size	378.9	140.43	[102.24,651.07]	1	7.28	0.007
Duration of the day (log and scaled)	175.58	25.74	[125.08,225.66]	1	46.54	<0.001
Group name (CAR2)	194.69	122	[-45.17,431.64]	4	76.97	<0.001
Group name (CAR3)	1321.89	106.34	[1113.76,1529.16]	4	76.97	<0.001
Group name (RC1)	-435.52	249.23	[-924.91,49.19]	4	76.97	<0.001
Group name (RC2)	-837.73	112.25	[-1056.57,-618.16]	4	76.97	<0.001
Model DPL (without infants): (N = 1188)						
Intercept	1412.96	472.63	[501.53,2341.34]	-	-	-
Home range size (sqrt)	47.6	63.48	[-75.6,171.55]	1	0.56	0.454

Season (Frugivory)	504.68	113.16	[287.15,723.21]	1	19.89	0.002
Group size (squared)	-4.6	6.29	[-16.76,7.81]	1	0.54	0.464
Group size	109.75	103.48	[-95.07,309.57]	1	1.12	0.289
Duration of the day (log and scaled)	169.43	26.15	[118.1,220.3]	1	41.98	<0.001
Group name (CAR2)	111.85	119.64	[-122.29,345.13]	4	74.49	<0.001
Group name (CAR3)	1342.21	99.75	[1146.96,1536.62]	4	74.49	<0.001
Group name (RC1)	- 1136.16	249.81	[-1623.85,- 647.76]	4	74.49	<0.001
Group name (RC2)	-972.35	117.63	[-1200.17,- 740.45]	4	74.49	<0.001



654
 655 **Figure 1: Study sites and study groups' home ranges | The home range areas and the corresponding core areas**
 656 **(within the 95% and 50% cumulative isopleths the UDs, respectively) are shown with light and dark colour,**
 657 **respectively. Camp sites are indicated by black squares. They are ca. 30 km away from each other, on each side of**
 658 **the border between the Central African Republic (CAR) and the Republic of the Congo (RC).**

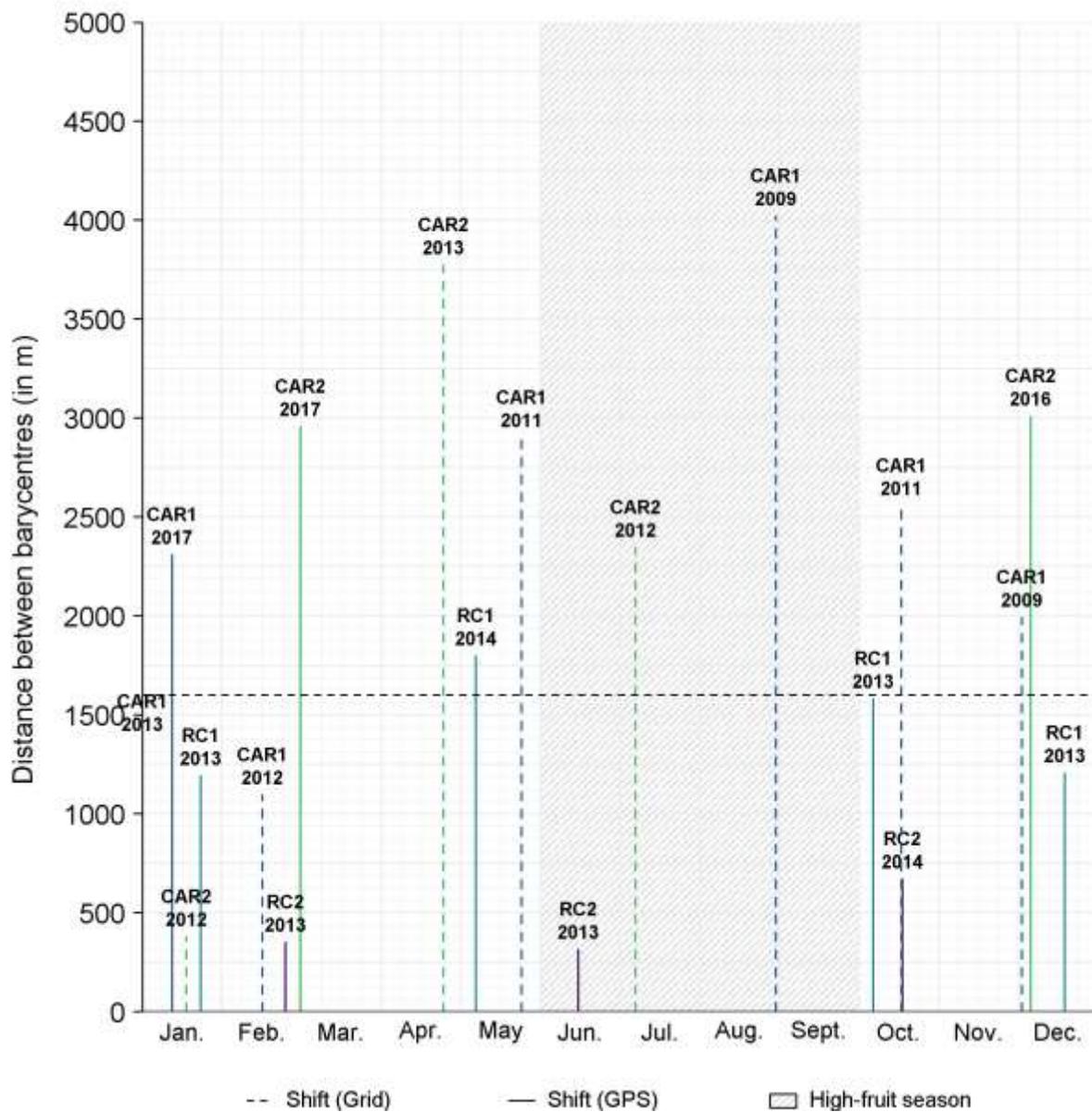
659



660
 661 **Figure 2: Shift occurrences and associated patterns based on the grid data set, which were available for CAR1 (left)**
 662 **and CAR2 (right). Bhattacharyya coefficients measuring overlap between UDs over 4-month periods were**
 663 **computed between periods along a sliding window re-centred every 2 months. In (A) and (C), the label for the year**
 664 **"2011" is not displayed for readability. (A, B) Dissimilarity matrix of overlaps. Lighter colours indicate higher**

665 values. White dashed lines indicate the occurrence of significant spatial shifts identified by the segmentation
666 procedure. Time gaps > 1 month are indicated by the axis break signs. (C,D) Locational time series. The different
667 stationary phases are identified by the corresponding mean location (plain horizontal line) and associated
668 standard deviation (bandwidth) of different colours. (E,F) For clarity, only new home ranges following a large
669 spatial shift are indicated (i.e., distance between barycentres > 1 600 m, see Methods). The spatial location of the
670 4-month barycentre, calculated every 2 months, is also indicated by the points that are linked by a plain line to
671 emphasise the sequence order which is highlighted by colour changes (lightest colours for the most recent dates).

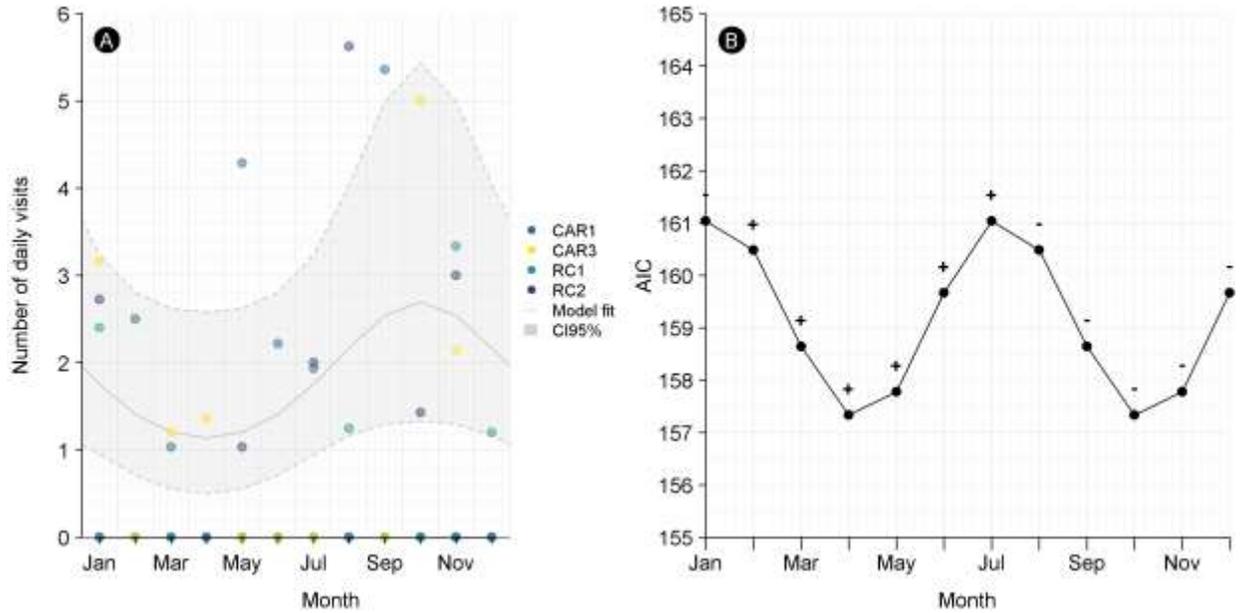
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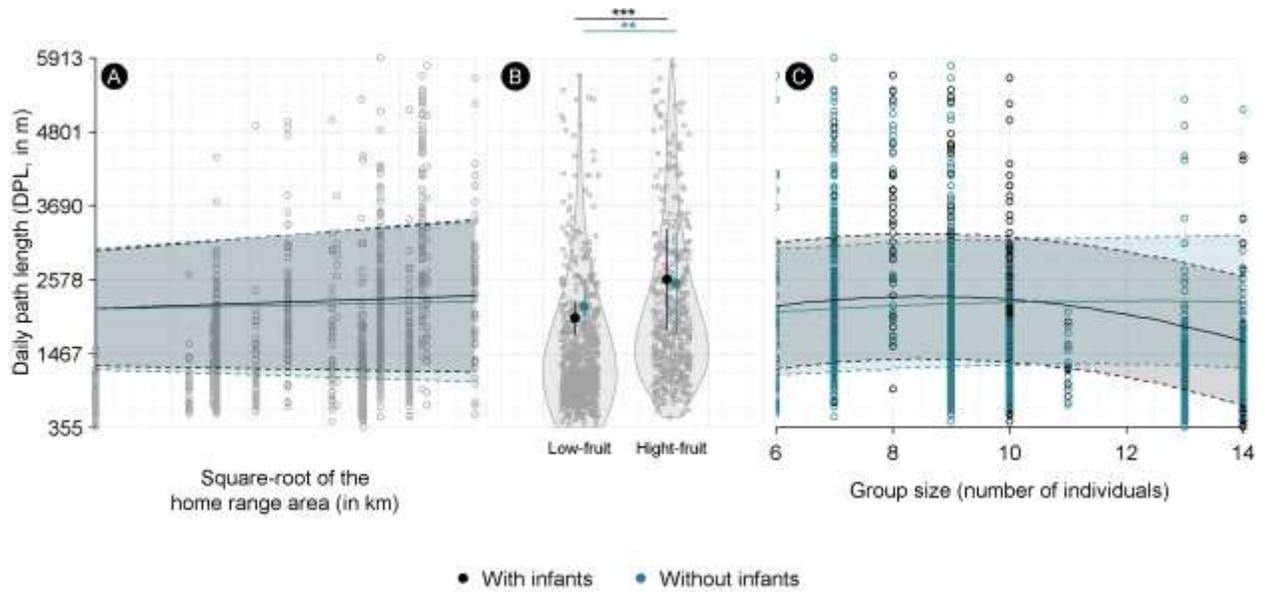
674 **Figure 3: Small and large shift occurrences |** The period of high-fruit season indicates the period in which gorillas
 675 **have a dominant frugivorous diet (Masi, Cipolletta, and Robbins 2009; Masi et al. 2015).** The distance between the
 676 **barycentres of two successive home ranges is indicated by the height of vertical bars.** Plain and dashed vertical bars
 677 **indicate values derived from the GPS and grid data sets.** The name of each group is shown above the corresponding
 678 **shifts.** The dashed horizontal line indicates the threshold to distinguish between small and large home range shifts.

679



680
 681 **Figure 4: Number of daily visits to the central area of the neighbouring group's home range | (A) Distribution of the**
 682 **number of daily visits for each month, year and group. The best-fit model (based on the selection of the phase of the**
 683 **cosine), holding the effect of other covariates/offset term at their average, is indicated by the plain grey line, while**
 684 **the associated 95% confidence interval is indicated by the grey background bordered with dashed lines. (B) AIC of**
 685 **generalised linear mixed models for visit number within the central area of the neighbouring group's home range**
 686 **as a function of the month. The signs close to the dots indicate the sign of the estimated regression slope associated**
 687 **with the month.**

688



689
 690 **Figure 5: Effect of home range size (A), dietary season (B) or group size (C) on daily path length | As the effect of one**
 691 **predictor is conditional of other predictors values, we plotted the predictor of interest's effect when the effect of**
 692 **any other predictor was averaged. For the group identity, we did so by averaging predictions for each group. The**
 693 **result is indicated by the plain line. The confidence interval is plotted with a coloured background for continuous**
 694 **variables or with vertical bars for categorical variables. The models presented here either include less than 1-year-**
 695 **old infants (black and white colours), or not (blue). Similarly, raw data are indicated by points, with grey points. In**
 696 **B), the background density estimation of data distribution ('violin' plot) is either prior (black) or after (coloured)**
 697 **dependent infants have been removed. In C), confidence intervals were obtained using the 'predictInterval'**
 698 **function of the merTools package (Knowles and Frederick 2020).**

699

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