

1 We present data on spatial organization and patterns of interaction in the striped hyena, a
2 species which is essentially unstudied. We show that striped hyenas are behaviorally
3 solitary, but live in stable 'spatial groups' consisting of multiple males and a single adult
4 female. These data describe a new social organization not exhibited by any other species
5 within the Carnivora. Further, this form of spatial grouping is not predicted, for this or
6 any other species, by any hypothesis for the evolution of grouping behaviors and
7 sociality. Our findings beg the questions of whether and how any particular aspects of
8 pre-existing theory can account for grouping behavior as found in this species. Overall,
9 the formation and function of spatial groups in striped hyenas seem best explained by an
10 unanticipated interactive relationship between diet, foraging behaviors, and the influence
11 of female territory size on the ability of males to defend access to females.

1 **Spatial Grouping in Behaviourally Solitary Striped Hyenas (*Hyaena hyaena*)**

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16 ABSTRACT

17

18 We investigated spatial organization and patterns of interaction in a population of striped
19 hyenas *Hyaena hyaena*, a species about which very little is known. We use the resulting
20 data to test hypotheses of group formation which predict that female striped hyenas will
21 be solitary in response to over-dispersion of food resources and males will be solitary in
22 response to female over-dispersion. Based primarily on anecdotal or historical
23 information, striped hyenas have been described as solitary. We show that, as predicted,
24 striped hyenas of both sexes are behaviourally solitary. However, they form stable,
25 polyandrous spatial groups composed of multiple males and a single female. We suggest
26 that male coalition formation may be the result of male strategies to optimize trade-offs
27 between the number of female ranges defended and the effectiveness of that defence
28 when females are solitary and maintain large territories. Nevertheless, the joint male
29 defence of a territory (of any size) containing only a single female would not be predicted
30 by any major hypothesis for the evolution of group living, in this or any other species.

31

32 *key words: Hyaena hyaena, social evolution, resource dispersion, polyandry, spatial*
33 *ecology, sociality*

34 Diet and the dispersion of food resources are widely recognized as the key determinant of
35 group formation (Crook 1965; Alexander 1974; Wilson 1975; Gittleman 1989; Mills
36 1989)—the distribution of food and methods of obtaining food play strong roles in
37 determining whether grouping carries costs or provides benefits. For most carnivores, the
38 benefits of grouping do not outweigh the associated costs. Consequently, 80-95% of
39 carnivore species are solitary (Bekoff *et al.* 1984). However, a disproportionately small
40 effort has been devoted to studying these species and it is unlikely that their full value has
41 been realized in identifying factors that influence the evolution of social systems.
42 Specifically, data from incipiently social species can tell us as much about the
43 mechanisms and evolution of group formation and sociality as data purely from highly
44 social species (Johnson *et al.* 2001; Waser 1981; Waser & Jones 1983) because the
45 realized benefit(s) of grouping in social species may be a consequence of grouping, and
46 not the force that initially favoured its evolution (Waser 1981; MacDonald 1983). Thus,
47 the origins of sociality cannot be resolved purely from studying its current functions in
48 social species (Waser & Waser 1985; Packer *et al.* 1990). Rather, the ideal condition for
49 evaluating hypotheses about social evolution is to study groups of closely related species
50 with variation in group size and social organization (Rood 1986; Johnson *et al.* 2002).

51

52 The Hyaenidae show great inter- and intra-specific variability in diet and social
53 organization, making them useful for studies of carnivore social evolution (Mills 1989).
54 Seminal studies relating social organization to the distribution of resources have
55 successfully drawn on inter-specific comparisons of three of the four extant hyena

56 species: spotted hyenas *Crocuta crocuta*, brown hyenas *Parahyaena brunnea*, and
57 aardwolves *Proteles cristatus* (e.g. Kruuk 1976; MacDonald 1978; Mills 1978a, 1989 &
58 1990). The aardwolf is a highly specialized forager on termites that lives in socially
59 monogamous, territorial pairs with only their most recent dependent offspring
60 (Richardson 1987; Richardson & Coetzee 1988), and the aardwolf's diet is thought to
61 have constrained the evolution of social groups (Mills 1989). Brown hyenas live in small,
62 female-bonded social groups that share and defend a common territory (Owens & Owens
63 1979a & 1979b; Mills 1978b & 1989). They feed on carcasses and small prey that tend to
64 be rare, widely dispersed, and provide food for only one individual (Owens & Owens
65 1978; Mills 1989 & 1990; Frank 1996). Because of their diet, foraging is primarily
66 solitary and this behaviour may have constrained the development of larger social groups
67 (Mills 1983 & 1989). Spotted hyenas live in matrilineal, territorial social groups of up to
68 one hundred individuals (Kruuk 1972). They specialize in feeding on relatively large prey
69 items that provide enough food for more than one individual and the benefits of
70 cooperative foraging (being greater than the costs of feeding competition) are considered
71 to be the initial selective pressures favouring group formation in the species (Frank 1996;
72 Van Horn *et al.* 2004).

73

74 In contrast to these well studied hyenids, the striped hyena *Hyaena hyaena* is
75 largely unstudied (Mills & Hofer 1998) and the basic biology of the species in most
76 contexts is very poorly understood. Consequently, our understanding of social
77 organization within the hyenids remains incomplete. In this paper, we present data from a

78 multi-year study of spatial organization and patterns of interaction in a striped hyena
79 population and consider how resources may have influenced social evolution in the
80 species. Based on the principle that food type and size is generally correlated with
81 spacing patterns in carnivores and the influence of food resources is expected to be
82 greatest on females, Wrangham & Rubenstein (1986) proposed a series of questions that
83 should be addressed to understand the evolution of a species' social system. Briefly, does
84 the nature of (food) resources permit or promote group foraging, group travel, or group
85 living (among females)? And (how) does the resulting distribution of females limit male
86 distribution options? Here we use our data on striped hyena behaviours to address these
87 questions. A priori, we had limited scope to explicitly test hypotheses regarding the
88 regulation of specific aspects of striped hyena social ecology, because most aspects of
89 their ecology were not yet described. However, we can still expect striped hyenas to
90 follow the principles regulating group formation as described by the dominant hypotheses
91 of carnivore social evolution. Accordingly, we use our data to test fundamental
92 predictions stemming from this body of socio-ecological theory on the expected
93 influences of resources and resource utilization on social organization.

94

95 To understand and test hypotheses of group formation, it is useful to distinguish
96 factors that allow group formation by lowering costs (which we term *permitting*
97 conditions), from the factors that actively favour grouping and sociality by providing
98 benefits (*promoting* conditions). In general, the distribution, abundance, and renewal of
99 resources (primarily food) set the limits under which the factors promoting group living

100 operate. Once resources permit groups to form at little cost, the benefits of other
101 behaviours such as group hunting, defence against predators, and defence against con-
102 specifics, are more likely to exceed the costs of sharing resources (MacDonald 1983;
103 Creel & Creel 1995). Selection pressures can then promote the evolution of sociality and
104 group formation, group living, and cooperation through increased offspring production
105 (Gittleman 1989; Sandell 1989), predator defence (Rasa 1986; Rood 1986), exploitation
106 of food and other resources (Kruuk 1972; Schaller 1972; Caraco & Wolf 1975;
107 Lamprecht 1981; MacDonald 1983; Creel & Creel 1995), defence of resources (Owens &
108 Owens 1984; Packer 1986), mating success (Gittleman 1989; Sandell 1989), or high costs
109 of dispersal relative to costs of natal philopatry (MacDonald 1983; Lindstrom 1986;
110 Blackwell & Bacon 1993; Johnson *et al.* 2002).

111

112 In part because dominant selection pressures may differ among species, times,
113 and ecological circumstances, there is no single theory unifying all of the permissive and
114 promoting conditions underlying social evolution. Nevertheless, many studies have
115 identified conditions that may initially facilitate group formation or subsequently favour
116 sociality itself (Wrangham & Rubenstein 1986) and Macdonald's (1983) Resource
117 Dispersion Hypothesis (RDH) encapsulates the underlying logic by predicting that the
118 resource-related costs of group size are determined by the distribution and abundance of
119 resources (Johnson *et al.* 2002). The RDH cannot account for all circumstances of group
120 formation based on resource characteristics (e.g. rapid resource renewal rates: Waser
121 1981), but the RDH is inclusive of many hypotheses and, as in other studies, we are

122 primarily concerned with the widely applicable set of hypotheses ‘of what may be
123 broadly called the Resource Dispersion Hypothesis’ (Carr & MacDonald 1986).

124

125 RDH models predict overlapping home-ranges when resources can be shared with
126 little reduction in foraging success (a permissive condition) (MacDonald 1983; Waser &
127 Waser 1985). When home-ranges overlap, social groups may form if promoting
128 conditions exist, but sociality is not a necessary consequence of sharing space. Some
129 species form ‘spatial groups’ within which group members have highly congruent and
130 overlapping home-ranges, but group members remain behaviorally solitary within the
131 shared range (Macdonald 1983). The abundance and distribution of resources is expected
132 to determine the resource-related costs of group size (Macdonald 1983; Johnson *et al.*
133 2002). In particular, temporal or spatial variation in resource abundance within defended
134 territories can act as the primary factor permitting group formation because the minimum
135 viable range for a pair may also support a group. For instance, if resources occur in
136 patches and production within those patches is asynchronous, an animal might require
137 access to several patches (so that patch dispersion determines territory size), but any one
138 patch that is productive at any one time may be able to support multiple users (so that
139 mean patch quality determines group size). In this way, spatial groups can form even with
140 very weak selection pressures to directly promote group formation or social interaction
141 (MacDonald 1983; MacDonald & Carr 1989; Johnson *et al.* 2002).

142

143 Here we present data on striped hyena spatial and social ecology. We consider
144 how resource requirements and resource dispersion may interact to influence social
145 organization as found in striped hyenas. We remain primarily concerned with the
146 mechanisms of, or constraints on, spatial group formation (permissive conditions) and not
147 sociality (although the former is expected to be a precondition for the evolution of the
148 latter). We also use these data to test predictions of RDH. In general, we can expect
149 striped hyenas to follow RDH principles regulating group formation:

150 (1) Diet (through effects of resource abundance and dispersion) should influence
151 group size and individual distribution.

152 (2) If ranges are shared, group structures and social interactions should reflect a
153 balance between fitness costs and payoffs to behaviours such as the formation of
154 cooperative coalitions of males to defend access to mates (Caro 1994) or cooperative
155 hunting groups (Creel & Creel 1995).

156

157 Although direct observations of striped hyena foraging and feeding behaviour are
158 extremely limited, it is known that their diet includes a wide variety of hunted small food
159 items (e.g. small vertebrates, invertebrates, fruits), as well as rare scavenged items (e.g.
160 lion *Panthera leo* and spotted hyena kills) (Ilani 1975; Kruuk 1976; Macdonald 1978;
161 Leakey *et al.* 1999; Wagner 2006; Wagner *in press*). With a food resource base
162 consisting of predominantly rare, uniformly distributed, and small prey items, RDH
163 models predict that female striped hyenas will be strictly solitary. If the distribution of
164 females drives the distribution of males, RDH models also predict that males will be

165 solitary in response to female over-dispersion. If the distribution of females is a response
166 to the distribution of food, then this prediction is reinforced because the distributions of
167 both food and females would predict that males should be solitary.

168

169

METHODS

170 Details on the study area and protocols for trapping, animal handling, and radio tracking
171 are given in Wagner (2006). Briefly, the study was conducted from August 2000-October
172 2003 on private and communal ranch lands in Laikipia District, Kenya. Although we
173 conducted research throughout north-central Laikipia, the core study area was centred on
174 the Loisaba ranch and wilderness reserve (see Fig. 1). Unless explicitly indicated
175 otherwise (as in Fig. 1), we refer in this manuscript to data from the Loisaba study area,
176 where the broad patterns apparent in data collected throughout Laikipia were more
177 intensively investigated.

178

179 We caught striped hyenas in soft-catch foot-hold traps. For most of the study
180 period, we set traps opportunistically at locations where striped hyenas had recently been
181 seen. To compliment this opportunistic trapping, beginning January 2003, we used
182 spatially systematic trapping, radiating outward from the centre of the study area. At each
183 trap site, we set traps for a minimum of three nights. If any previously unmarked hyenas
184 were caught, we kept traps active until no new hyenas were caught for two consecutive
185 nights. At each capture, we anesthetized trapped animals, recorded body and tooth
186 measurements, and retrospectively assigned each animal to an age class based on known

187 dates of birth or estimates from body measurements, weight, and tooth wear (cub: < 6
188 months, juvenile: 6mos to 1year, young adult: 1 to 3 yrs, adult: 3+ yrs). We fit all adult
189 and young adult hyenas caught with VHF radio collars (Telonics, Inc or SirTrack).

190

191 Radio Tracking & Spatial Data

192 Striped hyenas move and forage throughout the night and usually move little
193 during the day. Because the terrain was too rugged to allow off-road following of hyenas
194 from a vehicle at night, we could directly observe hyenas only on foot and only in the
195 daytime (0630-1829 hours). Consequently, radio-tracking was our primary tool for
196 inferring night-time locations and activity patterns. We based night-time (1830-0629
197 hours) locations on triangulation of radio-collar signals taken from a vehicle, typically
198 restricted to roads and tracks. For each location, we also scanned for the frequencies of
199 all other hyenas to determine if any were in the area. We located all collared hyenas at
200 least once per month (in 2003, at least once per week).

201

202 Based on highly overlapping home-ranges and field observations of direct
203 interactions throughout Laikipia, we identified distinct spatial groups with stable
204 membership (Fig. 1). Complimenting the radio-tracking described above, on Loisaba, we
205 selected six focal hyenas from three spatial groups (see Fig. 2) for more intensive radio-
206 tracking from February to November 2003 (one male and one female from each of the
207 Northern, Eastern, and Western groups). For each focal hyena, we recorded locations for
208 every hour of the day according to a randomized (by time and individual) schedule with

209 no more than one daytime and one night-time location recorded for each individual
210 within a 24-hour period. For every location, we checked the frequencies of all other
211 hyenas and, if detected, triangulated the positions of those hyenas. We also used daytime
212 walk-ins to record sightings of known/unknown hyenas in the immediate vicinity. We
213 repeated this cycle seven times, from a new randomized schedule each time, yielding
214 locations and activity patterns with seven observations for each individual in each of the
215 24 hours ($7 \times 6 \times 24 = 1008$ total observations taken on this schedule).

216

217 Home-ranges & Space-use

218 We determined the minimum number of locations needed to reliably estimate
219 home-range size based on the asymptote in the relationship between calculated home-
220 range size and the number of locations considered. For each of three males and three
221 females with ≥ 150 locations, we identified the asymptote using a bootstrap routine
222 (Seaman *et al.* 1999) to select locations, in steps of 10 locations, up to the maximum
223 number of locations available divisible by 10 (e.g. if 139 locations were available, only
224 13 sets of iterations were conducted). We randomly selected each set of points for each
225 sample size ($N = 10, 20, 30 \dots$) from the full data set(s), using the Bootstrap file creator in
226 the ArcView Animal Movement 2.0 extension (Hooge & Eichenlaub 1997), in 30
227 iterations with replacement between iterations. We determined a home-range for each
228 iteration by the 95% fixed-Kernel method using the Home Range Extension for ArcView
229 (Rodgers and Carr 1998). We then calculated the mean and variance of the home-range
230 size (km^2) for each individual at each sample size. We used the point at which the home-

231 range size estimate and variance changed little with any increase in sample size (80
232 locations, see Results) as the minimum number of locations required to calculate home-
233 range size. For those with enough locations (i.e. ≥ 80), we calculated fixed-Kernel home-
234 range size for 50, 75, and 95% isopleths. For animals with less than 80 locations, we did
235 not determine home-ranges, but where possible included them in analyses of social
236 organization using distributions of point locations and any observed incidents of
237 interaction as indicators of general areas of space use and group residency for each
238 animal.

239

240 Spatial Patterns of Association

241 We calculated levels of association for all dyads (pairs) of individuals that
242 overlapped spatially and temporally. Here, we define ‘association’ as the proportion of
243 observation periods in which a pair of hyenas was together. We calculated association
244 levels as the number of occasions (nights or days) that the pair of hyenas was known to
245 be together (resting at the same site or travelling together), divided by the total number of
246 occasions at which the presence/absence of both hyenas was known. We did not need to
247 know the exact location of both hyenas at each observation to classify them as located but
248 not together: all that was required in this case was to confirm that the second member of
249 the dyad was not in the same location as the first (confirming that an animal is not in a
250 specific location is easier than fixing its true location). We calculated association
251 independently for observations made in the night-time and made in the daytime. For
252 daytime observations, we considered hyenas ‘together’ if we saw both hyenas

253 simultaneously or found them within 50 meters of each other. At night, direct
254 observations were not possible and hyenas we considered ‘together’ if their triangulated
255 locations were within 200 meters of each other (because hyenas were usually moving at
256 night, we used a larger distance to indicate co-location). We did not restrict night-time
257 locations to those observations taken after hyenas had clearly begun moving or foraging.
258 Thus, there are some night-time observations in which hyenas were considered together
259 that represent a delay in separation for the night rather than actively joining together
260 while foraging. We further evaluated association by the characteristics of the dyad: male-
261 male or male-female. Because adult females did not share ranges (see Results),
262 association for female-female dyads was zero.

263

264 Temporal Patterns of Association

265 To evaluate differences in levels of association during the night-time and daytime
266 and for male-male dyads and male-female dyads, we used bootstrap simulations
267 implemented with PopTools 2.6.2 (Hood 2003). We used bootstrap simulations to avoid
268 pseudo-replication: the observations of association are repeated measures, but they are
269 nested within dyads, rather than individuals, so that the common method of including
270 individual identity as a random effect cannot be employed. Because some individuals
271 appear in more of the dyads than others, different dyads with one individual in common
272 cannot be considered independent, and the distribution of the observed data was non-
273 normal. To test for differences between day and night-time association for male-female
274 dyads, we randomly assigned each observed level of association as either a day or night-

275 time observation and calculated the mean level of association for those assigned to day
276 and night-time. This random assignment and mean calculation was iterated 1000 times.
277 We then compared the observed difference between night-time and daytime mean levels
278 of association to the distribution of the simulated differences. We used the proportion of
279 the frequency distribution for the simulated data more extreme than the observed
280 difference to evaluate the significance of the observed difference. If <5% of the simulated
281 values were more extreme than the observed difference ($\alpha=0.05$), we considered that
282 difference to be significant. We repeated this bootstrap simulation for all dyads (male-
283 male and male-female dyads considered together). For male-male dyads alone, however,
284 there were only seven dyads of individuals to consider. With seven observations that can
285 be assigned to two different categories (night and day), there are only 2^7 , or 128, possible
286 combinations. Rather than using a Monte Carlo method of assigning the observations to
287 day and night (repeating many combinations many times), we simply considered each of
288 the possible 128 arrangements once because any valid randomization procedure would
289 converge on this distribution.

290

291 To evaluate the difference between levels of association in male-male dyads and
292 male-female dyads, we conducted a similar bootstrap simulation in which we randomly
293 classified each observed level of association as either a male-male or male-female. In
294 1000 simulations, we calculated the male-male and male-female mean levels of
295 association. We compared the observed difference between male-male and male-female
296 levels of association to the frequency distribution of the simulated differences in the

297 means. Again, we used the percentage of simulated values more extreme than the
298 observed to evaluate the significance of the observed difference.

299

300 Overlap in Space-Use

301 For those individuals with enough locations to calculate accurate home-ranges,
302 we calculated the proportions and area of 50% and 95% fixed-Kernel home-ranges that
303 overlapped between individuals living in the same spatial group and between those living
304 in adjacent spatial groups. We only considered spatial overlap for dyads of individuals
305 with fixes that overlapped temporally. The percentage of spatial overlap for any two
306 individuals is a relative measure and changes when calculated as a proportion of the
307 home-range size of each of the two individuals being considered. Consequently, we used
308 a full matrix to represent percent overlap relative to each individual. This was not
309 necessary for area of overlap (km²), an absolute measure.

310

311 RESULTS

312 Trapping

313 In total, we caught 16 individual adults and 9 subadults (i.e. all cubs, juveniles,
314 and young adults) in the 240, 192, 432, and 1865 trap-nights (i.e. the number of
315 individual traps set multiplied by the number of nights each trap was active) of each of
316 the respective calendar years of the study. In addition, we caught five cubs at den sites
317 without the use of traps. We caught no new adults in 2003, despite a substantial increase
318 in trapping effort, indicating that we had captured, identified, and sampled most adults in

319 the population. With only six captures, adult re-captures in 2003 were below
320 expectations. Hyenas that had been captured in previous years may have learned to avoid
321 traps by this time. However, habituation is not likely to have affected hyenas that had
322 never been trapped. Subsequent paternity and maternity analysis confirmed that mothers
323 and fathers could be identified for the sampled population of young hyenas, which further
324 indicates that the majority of adult hyenas were sampled within the main study area
325 (Wagner 2006, Wagner *et al. in press*). Seven adults either died during the course of the
326 study or were lost and not recaptured. Hyenas were lost due to either collar failure or, as
327 suggested by the fact that they were not recaptured or resighted, emigration.

328

329 Home-ranges & Space-Use

330 In general, the fixed-Kernel method was robust to changes in the number of
331 locations used. The mean and variance of hyenas' 95% fixed-Kernel home-range sizes
332 stabilized when 70 or more locations were used (Wagner 2006). However, we chose 80
333 as a stringent minimum number of locations needed from each individual to estimate a
334 home-range. Note that we distinguish 'home-ranges' from 'space used'. Our use of the
335 former is restricted to those individuals with ≥ 80 locations, while the latter is a more
336 general term used to describe the broad ranging patterns of any individual.

337

338 We determined 50, 75, and 95% fixed-Kernel home-ranges for ten individual
339 adults (males: $N = 4$, females: $N = 6$) that had 80 or more locations (Fig. 2), including one
340 female (F21) from outside the Loisaba study area. The respective mean \pm SE 50%, 75%,

341 and 95% fixed-Kernel home-range sizes were 14.15 ± 1.0 , 30.3 ± 2.7 , and $68.9 \pm 7.8 \text{ km}^2$
342 with no significant difference detected between sexes (two-sample t-tests — 50%: $p =$
343 0.56 , $\bar{x}_{\text{females}} = 13.6 \pm 1.5$, $\bar{x}_{\text{males}} = 14.9 \pm 1.3$; 75%: $p = 0.63$, $\bar{x}_{\text{females}} = 29.1 \pm 3.6$, \bar{x}_{males}
344 $= 32.0 \pm 4.7$; 95%: $p = 0.49$, $\bar{x}_{\text{females}} = 64.2 \pm 9.8$, $\bar{x}_{\text{males}} = 76.0 \pm 13.8$), though 95%
345 male home-ranges were estimated to be 19% larger than those of females.

346

347 Spatial & Temporal Patterns of Association

348 Individual home-ranges (Fig. 2) clearly demonstrate spatial grouping, with high
349 spatial overlap within groups and low overlap between groups, but these patterns do not
350 reveal whether individuals interacted with one another within the shared range. Overall
351 rates of association within spatial groups were very low: group members were alone more
352 than 90% of the time (Table 1). This is similar to the levels of association found in the
353 other behaviourally solitary carnivore that form spatial groups (e.g. red fox *Vulpes*
354 *vulpes*: Macdonald 1983).

355

356 Males rested with other males at only 4% of day locations and with females at 8%
357 (Table 2). At night (when foraging and other activity occurs), males were never found
358 together, and were found with females at 8% of locations. Thus a clear picture emerges of
359 largely independent movements and solitary foraging and feeding within a shared range.

360

361 From the bootstrap simulations, we detected no significant differences in levels of
362 association in the daytime vs. the night-time for males with males, females with males, or

363 all individuals pooled (Table 2). These results should be viewed with caution, however,
364 as individuals were categorized as ‘together’ during the day only when they were seen or
365 found together from a close observation distance. At night, individuals were classified as
366 ‘together’ whenever the triangulated positions from each radio-collar were within 200
367 meters. If a finer spatial scale could have been applied to the night-time observations,
368 night-time levels of association might have been lower, which would further reinforce the
369 conclusion that striped hyenas typically forage alone within their shared ranges. Further
370 bootstrap simulations showed that males were more likely to associate with females than
371 with other males (bootstrap $p = 0.029$). We were not able to isolate periods of male-
372 female association that may have fallen during mating periods, but we attribute the higher
373 levels of association for inter-sexual dyads to reproduction.

374

375 Overlap in Space-use

376 Within Loisaba, 95% fixed-Kernel home-ranges overlapped across adjacent
377 groups by an average of $22 \pm 2 \%$, $N = 24$ or $17.17 \pm 2.11 \text{ km}^2$, $N = 12$ (Table 3) for those
378 adjacent groups where overlap was non-zero (Northern-Western and Eastern-Western), or
379 by $13 \pm 2 \%$ for all adjacent groups. The mean overlap of 95% home-ranges for group-
380 mates was $85.26 \pm 3 \%$, $N = 14$ or $59.52 \pm 6.08 \text{ km}^2$, $N = 7$. 50% fixed-Kernel home-
381 ranges (home-range ‘cores’) of individuals in adjacent groups did not overlap, but
382 overlap in the core ranges of group-mates averaged $73 \pm \text{SE} = 2 \%$, $N = 14$ or $11.07 \pm$
383 0.59 km^2 , $N = 7$.

384

DISCUSSION

385

386 Group Sizes & Individual Distributions: Responding to Food Resource Abundance &

387 Dispersion

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Sociality and group-living can be understood in the contexts of space-use, feeding, foraging, or breeding (Gittleman 1989). Current hypotheses of group formation predict that female striped hyenas should be solitary in each of these respects as a consequence of a varied diet that depends on small, often rare, and uniformly distributed foods. Solitary *foraging* should be favoured in (male and female) striped hyenas because with this diet there are no benefits to group foraging to offset local feeding competition (grouping not promoted). *Feeding* group size is linked to foraging group size and varies with prey size (Gittleman 1989). When prey items or patches are small, solitary feeding is favoured due to the depletion of food items or patches that would result from large feeding groups (grouping not permitted). Our data are compatible with predictions for foraging and feeding group sizes of male and female striped hyenas, and for spatial group sizes among females: in the Laikipia population, striped hyenas form stable, spatially associated groups of one adult female and up to three adult males (Figs 1 & 2) with very low levels of overall inter and intra-sexual association (Table 1) and strictly solitary foraging and feeding (Tables 1 & 2). In contrast, the spatial grouping by males that we detected would not have been predicted by existing hypotheses for grouping in carnivores.

406 Although spatial grouping by males requires explanation, differences in the sizes
407 of different functional group types are not unusual and are broadly compatible with RDH
408 predictions. Spatial group size is not necessarily expected to correlate with foraging
409 group size because different factors affect the two. Spatial group size is limited by prey
410 availability (Waser 1981; Macdonald & Carr 1989), while foraging group size is linked to
411 the ability to successfully locate, pursue, and kill prey (Gittleman 1989). Differences in
412 the sizes of feeding and foraging groups can occur when large prey items or rich food
413 patches permit formation of feeding groups exceeding the size of foraging groups (e.g. in
414 spotted hyenas: Kruuk 1972; Mills 1989, brown hyenas: Owens and Owens 1978, lions:
415 Kruuk 1972; Schaller 1972; Mills 1989 & 1990, Kinkajous *Potos flavus*: Kays &
416 Gittleman 2001). However, striped hyenas do not form large feeding groups even when
417 large prey items are available. Similar to European badgers *Meles meles* at large feeding
418 sites (rich earthworm patches in ploughed fields: Kruuk 1978), several striped hyenas
419 may visit the same carcass over a long period, but temporal spacing maintains solitary
420 feeding (Wagner 2006). For example, during this study, a giraffe *Giraffa camelopardalis*
421 killed by lions in the zones of overlap for the Eastern and Western groups was scavenged
422 repeatedly over a period of six weeks by at least three adult and three juvenile striped
423 hyenas. The three related juveniles visited the carcass at the same time on several
424 occasions, but we never detected two adults at the carcass simultaneously.

425

426 This observation contrasts to feeding group formation recorded for striped hyenas
427 at spatially fixed, temporally predictable human-provisioned feeding stations in Israel

428 (Macdonald 1978). Based on those observations, striped hyenas were specifically cited as
429 a case where a large and clumped food resource may have allowed for large feeding
430 groups and those feeding groups may then lead to formation of larger spatial groups
431 (Macdonald 1978; Mills 1989; Gittleman 1989). This determination was based, in part,
432 on Kruuk's (1976) limited observations that striped hyenas in East Africa were
433 omnivorous scavengers that were strictly solitary with respect to space-use, foraging, and
434 feeding. Our observations of spatial grouping in a different East African population do
435 not disprove Macdonald's thesis, but do demonstrate that clumped resources did not
436 produce social foraging under more natural circumstances, despite the existence of spatial
437 groups.

438

439 Male Coalitions: Responding to Female Distributions

440 In evaluating hypotheses regarding group formation, different sub-sets of the
441 population are not necessarily predicted to behave similarly, react to the same resources,
442 or face the same selection pressures (Mills 1978a; von Schantz 1984; Van Orsdol *et al.*
443 1985; Gittleman 1989; Revilla 2003). While female distributions are argued to reflect
444 selection pressures arising from access to food resources, the spacing pattern of males is
445 adapted to the distributions of both food and females (Jarman 1974) because males
446 compete for access to mates, while females generally do not (MacDonald 1983; Johnson
447 *et al.* 2002). Our data suggest that females remain solitary, reflecting a lack of permissive
448 and promoting conditions for grouping due to resource constraints. Our data also support
449 the generally accepted idea that male distributions are influenced by female distributions,

450 but the way in which males respond to females (multiple males monopolizing single
451 females) is both unique and surprising.

452

453 The distinction between spatial and social groups is clear for striped hyenas, as in
454 some other ‘proto-social’ carnivores such as white-tailed mongooses *Ichneumia*
455 *albicauda* and slender mongooses *Herpestes sanguineus* (Waser & Waser 1985; Waser *et*
456 *al.* 1994). Low levels of association within a group do not support a view of striped hyena
457 groups as the highly organized, interactive social units typical of some social carnivores
458 (e.g. African wild dogs *Lycaon pictus*, dwarf mongooses *Helogale parvula*, meerkats
459 *Suricata suricatta*, lions, spotted hyenas, and wolves *Canis lupus*). This distinction is
460 important when differentiating the selection pressures that might favour the initial
461 evolution of group living from the selection pressures that operate once grouping is
462 established. To our knowledge, the essentially polyandrous spatial organization of striped
463 hyenas, combined with little direct social interaction, is unique among the Carnivora (for
464 comparisons to other species, see Wagner *et al. in press*; Wagner 2006). Male-group
465 formation in carnivores has been explained by the benefits of male cooperation in
466 defending or providing access to several females. Females should establish the minimum
467 defendable territory with enough resources to provide food for herself and her offspring
468 (Jarman 1974). In response, males, alone or in groups, generally either establish larger
469 fixed ranges and attempt to monopolize a number of females, or roam and compete with
470 other males for mating with several females in heat (Sandell 1989). Accordingly,
471 exclusive male territories have been predicted (outside of monogamous systems) only if

472 multiple females can be defended simultaneously (Macdonald 1983; Sandell 1989;
473 Johnson *et al.* 2002). After male coalitions in slender mongooses were detected in areas
474 with high female densities that allowed groups of males to successfully defend a number
475 of females, it was identified as being of particular interest to know if male coalitions form
476 only in areas with high female densities and not in areas where females are more highly
477 dispersed and therefore less defensible (Waser *et al.* 1994). In striped hyenas, defence of
478 multiple females is not necessary for male coalition formation: groups of males cooperate
479 to defend a territory containing a single female. No explanation for this pattern has
480 previously been needed, because it has not been described (or predicted) for any other
481 carnivore species.

482

483 Potential Costs & Benefits of Spatial Grouping for Males

484 Males must optimize the trade-off between the number of females defended and
485 the effectiveness of their defence. Constraints on this optimization problem occur when
486 1) the species' diet results in solitary foraging and feeding, so that males cannot simply
487 employ a mate guarding strategy, and consequently must defend the entire territory and
488 2) breeding is not seasonal—seasonal roaming is not a viable option and the ability of
489 males to restrict defensive behaviours to short time periods is limited, particularly if the
490 costs of establishing a defended territory are higher than maintaining them. Both of these
491 conditions exist in striped hyenas (Rieger 1979 & 1981; Wagner 2006; Wagner *in press*).

492

493 Under these conditions, sharing a female with a coalition (particularly of
494 relatives) may yield greater fitness to an individual male than attempting to defend a
495 female alone and failing. Hypothetical male territories encompassing more than one
496 female may not be economically defensible, particularly when female home-ranges are
497 large (Brown 1964). Moreover, if males expand their territories to include multiple
498 females, with increasingly poor defence of an increasing number of females, at some
499 point these males would effectively become nomads. On the other hand, even one female
500 territory may not be 100% defensible. If a resident male cannot effectively defend a
501 female territory against encroachment by solitary bordering males on each of four sides,
502 for example, he would be competing for mating opportunities with four males. However,
503 if a coalition of two males can maintain exclusive use of the territory (which is the same
504 as defending one female effectively), each resident male is only competing with one other
505 resident for mating. Consequently, the way in which the diet of striped hyenas affects
506 female territory size and foraging behaviour may result in guarding of females by solitary
507 males to be only a marginally effective strategy. This then could favour males who
508 tolerate additional males guarding the same female territory, where one solitary male
509 cannot.

510

511 Why should male ranges overlap completely with one female and not partially
512 with several females, as in felids and mustelids? The latter strategy offers little protection
513 of mating opportunities from intrusion by nomadic males (common in the aardwolf:
514 Richardson 1987; Richardson & Coetzee 1988, and brown hyena: Mills 1982). In

515 essence, trade-offs between the extent and effectiveness of defence appears to favour
516 localized and joint mate defence in striped hyenas. A counter argument might be that the
517 dispersion of females determines male range sizes, but the 'value' of a female determines
518 the number of males using her range. However, given that the number of striped hyena
519 females per range is always one, this seems to be a weak argument. Nevertheless, it
520 remains possible that variation among females in reproductive value could be great
521 enough to offset the costs of shared mate access when multiple males share a territory. To
522 be influential, that mechanism only requires an ability in males to assess female age or
523 other indicators of female reproductive value.

524

525 Potential Costs & Benefits of Spatial Grouping for Females

526 Though changes in group size do not necessitate changes in territory size under
527 the RDH, primary territory holders should expand their territory size to compensate if
528 resources become depleted (Johnson *et al.* 2003). In solitary species, strong inter-sex
529 competition over food resources is minimized by space-use patterns characterized by a
530 mosaic of exclusive, large male home-ranges overlapping a separate mosaic of smaller
531 female home-ranges, because female territories need only support a fraction of each
532 additional (male) user, while males can effectively maximize mating ranges (Carr &
533 Macdonald 1986). This pattern is typical of most mustelids (e.g. European pine martens
534 *Martes martes* and fishers *Martes pennanti*: Powell 1994), felids (e.g. caracal *Felis*
535 *carcal*: Avenant & Nel 1998), and the white-tailed mongoose (Waser & Waser 1985;
536 Admasu *et al.* 2004). Striped hyenas raise interesting questions about interactions

537 between male and female group sizes and territory sizes because, in contrast to these
538 species, female striped hyena ranges must support the whole of each additional male user.

539

540 In striped hyenas, it is reasonable to consider only the female (and her offspring)
541 as the primary territory holder (following the logic that resources determine female
542 distribution which, in turn, determines male distribution). Alternatively, one could also
543 consider the first male on a territory as a primary resident. The immigration of additional
544 males is likely to reduce the resources available to the primary resident(s). Consequently,
545 female territory size would need to increase to compensate unless female-defended food
546 resources can support several males in addition to herself and her offspring, without cost.
547 For males, equilibrium will be reached where increasing within-group competition for
548 resources and mates is offset by the benefit of excluding non-group males more
549 effectively. The equilibrium point might differ for females, because mate-defence is not a
550 benefit to females, and this creates the possibility of inter-sexual conflict over group
551 structure.

552

553 If female striped hyenas are 'forced' to maintain larger home-ranges because of
554 the number of males within their territories, females should be intolerant of resident
555 males (and possibly more accepting of non-resident males as mates), unless resident
556 males provide some offsetting fitness payoff to females. In terms of excluding competing
557 females, resident females are unlikely to accrue benefits from tolerating multiple males
558 because males are unlikely to exclude additional encroaching females. It remains

559 possible, however, that stability in resident males may reduce the chances of infanticide
560 by immigrating males, as it does in lions (Whitman *et al.* 2004) and perhaps brown bears
561 *Ursus arctos* (Swenson *et al.* 1997), but infanticide has not been reported for this species
562 in captivity or the wild. Females could also benefit from the presence of multiple males if
563 they protected females from harassment by non-resident males (Wittenberger & Tilson
564 1980). However, this hypothesis does not fully explain female tolerance of resident males
565 outside of breeding periods, when harassment is unlikely, and male harassment has not
566 been reported for *Hyaena*.

567

568 When one sex invests more in the care of offspring, the other sex will compete for
569 the first (e.g. males typically will compete for females in the absence of paternal care)
570 (Trivers 1972). Females having access to multiple resident and non-resident males, as
571 they do in striped hyenas, can allow for female mate choice and the demanding of
572 rewards or pay-offs in exchange for tolerance and mating opportunities (Waser & Waser
573 1985). In studies of primate social evolution, this is known as the ‘food for sex’
574 hypothesis. Male payoffs could take the form of feeding or guarding offspring, but
575 striped hyena males do not spend significant periods of time at den sites (Davidar 1990;
576 Wagner *in press*). Consequently, there appears to be both the conditions and the
577 opportunities for males to contribute to offspring care in striped hyenas, but there is as yet
578 no evidence that common forms of paternal care occur, beyond territorial defence.

579

580

Conclusion

581 In striped hyenas, males and females form spatial groups, but not foraging or
582 social groups. Male coalition formation occurs despite providing for the defence of only a
583 single adult female's range. This pattern of coalition and spatial group formation is not
584 expected under any major model for the evolution of group living. Even if spatial and
585 social organizations in other striped hyena populations differ from those of this
586 population, adequate hypotheses of group formation should predict all naturally occurring
587 forms of social and spatial organization. Conventional explanations for group formation
588 and social evolution have probably correctly identified the influential factors involved
589 here, but the interaction between those factors has resulted in unexpected and
590 unanticipated association patterns. Overall, the relationships between resources, spatial
591 patterns, and grouping in this striped hyena population appear to be best explained by diet
592 determining female group size, the number of males neighbouring a females' territory
593 determining male group size, the number of guarding males determining female territory
594 size, and female territory size determining male territory size. A key test of our
595 hypotheses in this regard would come from additional data on striped hyenas in areas
596 having higher female densities. As female densities increase, defendability of females by
597 individual males would increase, and either lone males should defend single females or,
598 if female densities are particularly high, males should form coalitions to defend multiple
599 females. Whether such patterns exist will only be known once data on space use become
600 available from other striped hyena populations.

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601

602

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610

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MS# 10718 revisions

Dear Dr. Blumstein,

Thank you for your letter of 18 May 2007 with the reviews of our manuscript, which we have revised accordingly. We found the suggestions very useful and addressed all of the issues presented by the reviewers and the subject editor, as noted below (line numbers used below refer to the revised manuscript).

We addressed the bulk of the editor's and reviewers' comments through an extensive rewrite of the introduction and discussion sections. The critical concerns can be readily summarized as 'the original manuscript was too long and detailed and the hypotheses being tested were not clearly stated'. To address these concerns, the introduction was heavily revised and shortened. Our changes focus the paper more immediately and directly on the primary data and hypotheses being tested. The discussion section was also heavily revised, but the reduction in length was not as dramatic because our unexpected results demand explicit consideration of what benefits striped hyenas might accrue by living in spatial groups. As reviewer #2 notes, it was also important to explicitly consider how the different sexes might accrue different benefits.

For the most part, the revised manuscript does not contain any new information. Instead, in our reorganization of the paper, we pulled to the surface and highlighted many of the key points that were previously too buried to be apparent to the reader. The revised manuscript was constructed around, and now highlights, those main messages.

Responses to Editor's general comments (in the order that they appeared in the review):

- 1) 'concerned about the lack of direct hypotheses being tested': We have made substantial changes to the introduction and discussion to clarify the specific hypotheses we address in the paper (e.g. lines 150-155, 161-167). As the editor notes, the original manuscript contained so much detail that the 'main messages' about which hypotheses we were addressing were lost.
- 2) 'eliminating some tables': We have eliminated three of the tables, as suggested by Reviewer #1.
- 3) 'generate some non-trivial and generalizable aims': Mainly via our revisions to the introduction (as in #1, above), we have clarified that the main aims of this study were to use data from an unstudied species *to test specific hypotheses on the evolution of grouping and sociality*.
- 4) 'cut your methods': We have cut the methods by more than 1/3. The bulk of what remains describes the somewhat complex analytical methods we employed. Unlike details on field methods, these analytical methods are specific to this manuscript only and did not lend themselves to any substantial reductions in length.
- 5) 'rewrite the discussion based on revisions to the introduction': We revised the discussion based on the suggestion of the editor that we should first evaluate the predictions presented in the introduction and then introduce hypotheses that could explain the observed patterns. We kept the discussion as short as possible. However, in order to address many of the concerns raised (particularly by Reviewer #2, e.g. separate male vs

female perspectives), the discussion contains several sub-sections and we could not reduce the length of that section as substantially as we did for the introduction.

- 6) 'keep clear the differences between male and female perspectives': Our revised discussion explicitly keeps male and female perspectives separate by considering each under different sub-sections.
- 7) 'think more about the benefits to the female of tolerating more than one male': This is explicitly considered in the sub-section of the discussion that begins on line 686 ("Female Tolerance of Multiple Males").

Responses to Reviewer #1's general comments:

- 1) 'far too long and no clear hypotheses being tested': We have cut the paper by more than 1/3, with much of that reduction coming from changes to the introduction and discussion. Explicit statements of the hypotheses being tested are on lines 150-155 and 161-167.
- 2) 'too much said about the benefits of sociality in terms of foraging and breeding': Much of this information, which was contained in the introduction in the original manuscript, was removed in the revised manuscript.
- 3) 'abstract...not based on results': We rewrote the abstract to more directly address the hypotheses tested in the manuscript, the data considered, and our interpretation of the results.
- 4) 'a number of tables could be removed': We removed the tables as suggested.

Responses to Reviewer #2's general comments:

- 1) 'keeping the male and female perspectives separate': As noted above, we explicitly consider the benefits of spatial grouping from both male and female perspectives in separate sub-sections of the discussion.
- 2) 'any hard evidence for prey being sparse and evenly distributed': These data are already considered in other manuscripts and we cite those publications.
- 3) 'costs and benefits of grouping to males vs. females': We have broken up the discussion to allow explicit consideration of possible benefits to each sex. Also, the reviewer notes here that "...these solitary foragers actually associate when not foraging". This is incorrect, or at least somewhat misleading. Levels of association when not foraging are extremely low and the hyenas are essentially behaviourally solitary in every respect.

1

TABLES

2

3 Table 1. Temporal and spatial overlap among resident adults

4

ID1	ID2	Overlapping Days	Day			Night			Overall
			Total obs	Together	Assoc.	Total obs	Together	Assoc.	
F09	M10	715	77	3	0.04	8	2	0.25	0.06
F09	M11	547	55	2	0.04	7	0	0.00	0.03
F09	M26	414	61	1	0.02	1	0	0.00	0.02
M10	M11	547	49	3	0.06	7	0	0.00	0.05
M10	M26	695	99	5	0.05	8	0	0.00	0.05
M10	F48	288	64	10	0.16	26	3	0.12	0.14
M11	M26	246	31	0	0.00	0	-	-	0.00
M26	F48	86	17	3	0.18	8	0	0.00	0.12
F14	M23	409	49	4	0.08	0	-	-	0.08
M18	F35	352	53	8	0.15	26	2	0.08	0.13
M17	F43	500	76	10	0.13	31	3	0.10	0.12
M17	M42	501	61	1	0.02	17	0	0.00	0.01
F43	M42	501	68	2	0.03	21	0	0.00	0.02

5

6 Table indicates dyads of individuals that overlapped spatially and temporally in the study

7 area with the number of days for which their space-use overlapped, the total number of

8 occasions (Total obs) at which the individuals were known to be together or apart, the

9 number of those occasions for which those individuals were together, and the resulting

10 levels of association ($\text{Assoc.} = \frac{\text{Together}}{\text{Total obs}}$) for each dyad for those observations

11 recorded in the daytime and night-time, and the overall level of association (Overall =

12 $\frac{\text{Together day} + \text{Together night}}{\text{Total day} + \text{night obs}}$). There were no simultaneous night-time locations

13 available for the M11-M26 and F14-M23 dyads.

14 Table 2. Levels of association among resident adults

15

	<u>Day</u>		<u>Night</u>		Obs. Night – Day Assoc.	Percentile of the Randomized Distribution
	Mean assoc.	n	Mean assoc.	n		
All dyads	0.068	13	0.062	11	-0.006	0.227
Male-male	0.038	4	0	3	-0.038	0.070
Male-female	0.083	9	0.078	8	-0.004	0.277

16

17 Mean levels of association are given for adult male-male, male-female, and all dyads of
18 individuals that overlapped spatially and temporally within the study area (n = # dyads
19 considered). The observed difference between mean levels of night and daytime
20 associations (= Night Mean assoc. – Day Mean assoc.) was compared with the frequency
21 distribution of the differences in the mean night and daytime associations from bootstrap
22 simulations. The percentile of the frequency distribution where the observed differences
23 fell indicate levels of association were not significantly different (at $\alpha=0.05$) between
24 night and day for male-male, male-female, and all dyads. In each of the three cases, >5%
25 of the simulated values were less than the observed difference.

26 Table 3. Proportion of overlap in 95% fixed-Kernel home-ranges within and between
 27 spatial groups

28

	F09	M26	M10	F48	M18	F35	M17	F43
F09	-	0.96	0.88	**	0.00	0.00	0.40	0.27
M26	0.64	-	0.72	0.87	0.00	0.00	0.25	0.16
M10	0.82	1.00	-	0.98	0.00	0.00	0.29	0.19
F48	**	0.91	0.74	-	0.00	0.00	0.22	0.14
M18	0.00	0.00	0.00	0.00	-	0.79	0.15	0.07
F35	0.00	0.00	0.00	0.00	0.88	-	0.14	0.09
M17	0.40	0.37	0.31	0.31	0.18	0.15	-	0.93
F43	0.36	0.16	0.27	0.26	0.11	0.13	0.82	-

29

30 Outlined box contents indicate same spatial group members. Although both F48 & F09
 31 lived in the Eastern group with M10 & M26, the two females were successive, not
 32 contemporary, residents. Outlines indicate within group overlaps, by group. The full
 33 matrix is needed as overlap must be evaluated relative to each individual considered.

FIGURE LEGENDS

1

2

3 Figure 1. Simplified representation of spatial group orientations and membership
 4 observed throughout north-central Laikipia District. Solid outlines indicate well sampled
 5 and well known groups. Dashed outlines indicate groups in which group membership was
 6 less certain because of low sampling effort in these areas. Individual IDs are given within
 7 each spatial group. Over the course of the study, membership in some groups changed
 8 due to deaths of group members and/or immigration/emigration. Changes in group
 9 composition are indicated by horizontal dotted lines. Sets of individuals separated by
 10 horizontal lines within a range were present in non-overlapping time periods. Background
 11 map indicates property boundaries. The Loisaba study site is indicated by the shaded and
 12 dashed-outlined area in the upper-right of the base map.

13

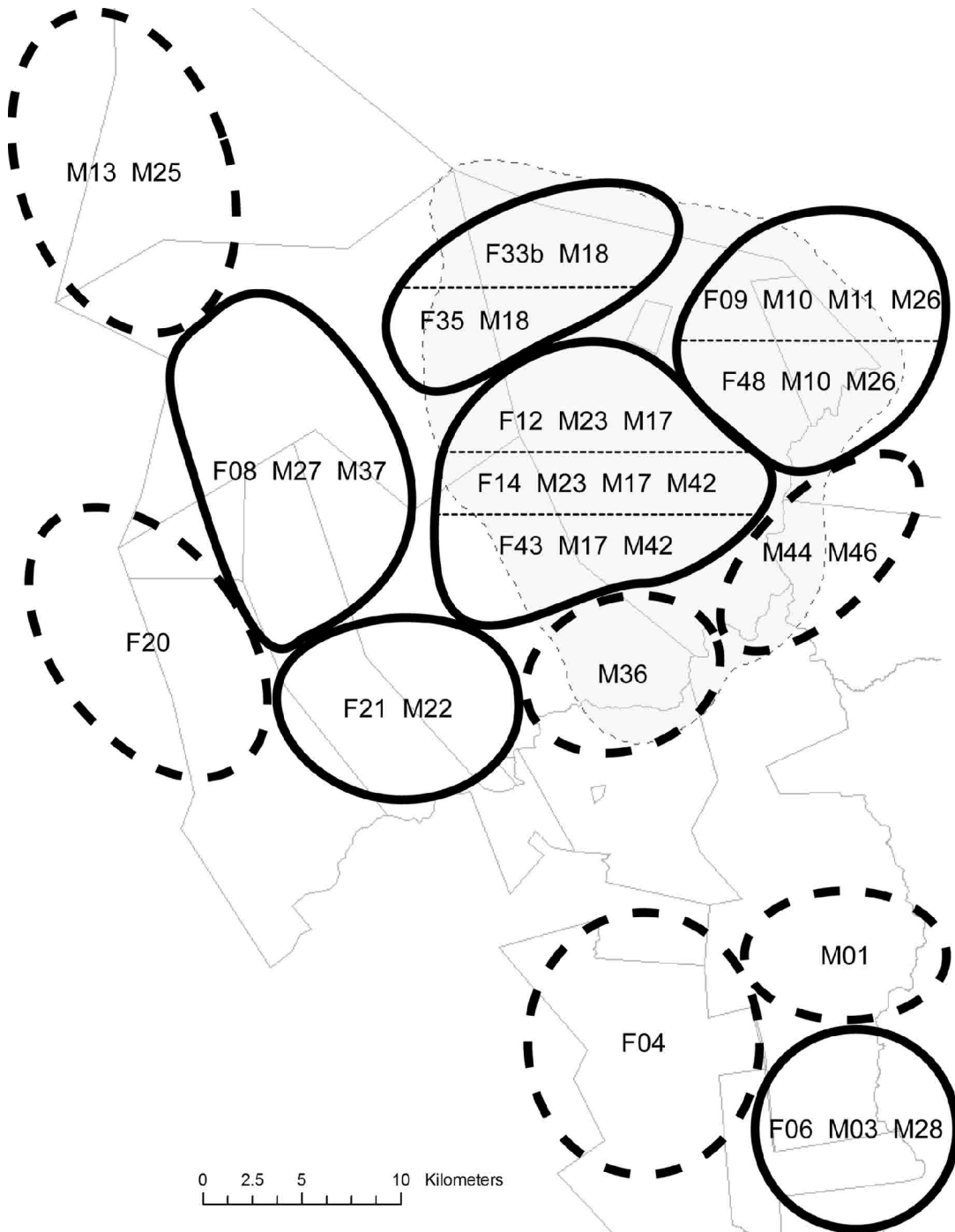
14 Figure 2. 95% fixed Kernel home-ranges for individual adults with ≥ 80 locations within
 15 the Loisaba study area. Figure key indicates the individual IDs and the shaded (males) or
 16 outline (females) colour patterns used for each. Locations for other residents having
 17 fewer than 80 observations are included as points. Note that this figure does not account
 18 for time and, while many males did share ranges, no two females lived in the same range
 19 at the same time (see Fig. 1, Table 1).

20

FIGURES

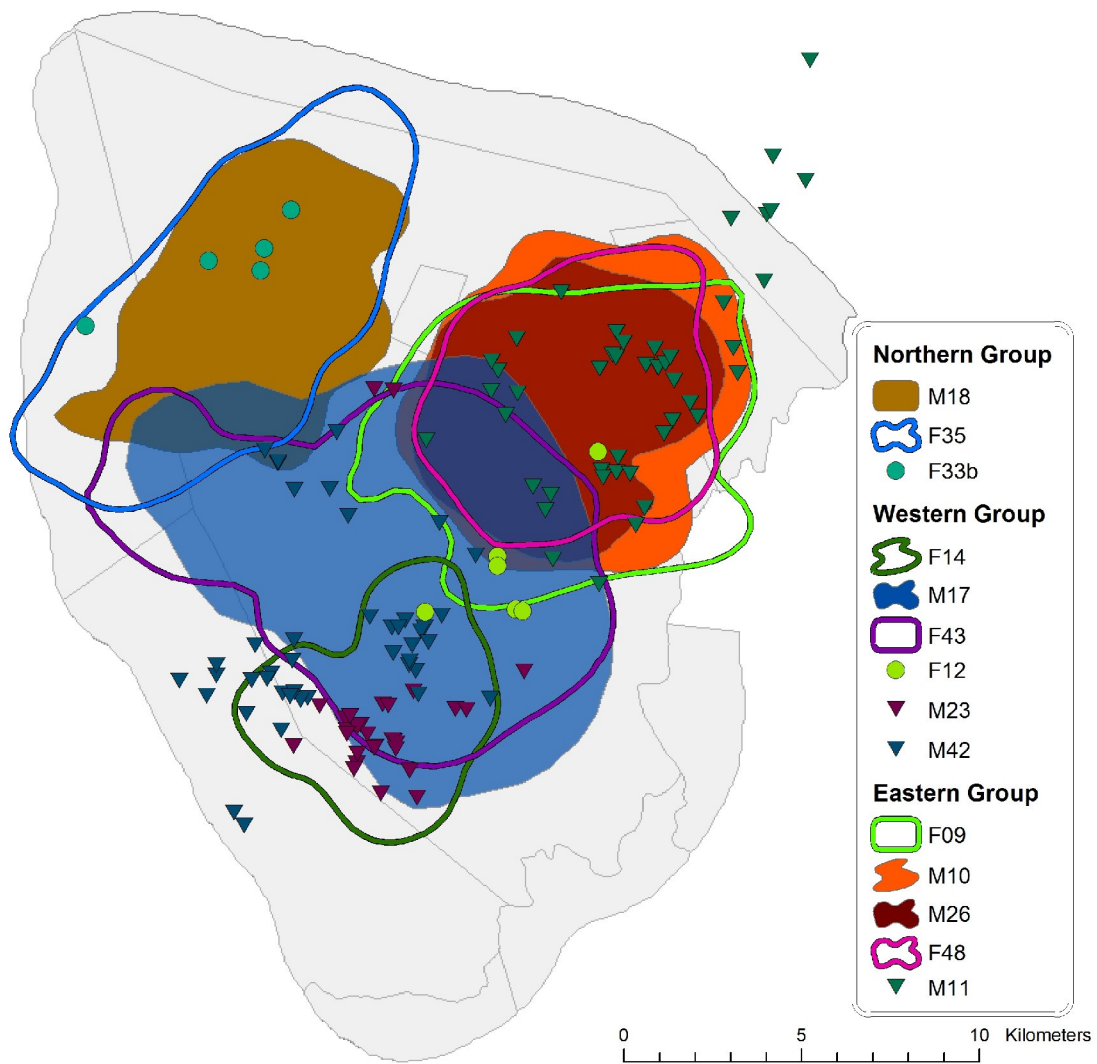
21

22 Figure 1.



23

24 Figure 2.



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26