Life as a bachelor: quantifying the success of an alternative reproductive tactic in male blue monkeys

Su-Jen Roberts, Marina Cords

In species that live in one-male groups, resident males monopolize access to a group of females and are assumed to have higher reproductive success than bachelors. We tested this assumption using genetic, demographic, and behavioral data from 8 groups of wild blue monkeys observed over 10 years to quantify reproduction by residents and bachelors and compare the success of the two tactics. We used maximum-likelihood methods to assign sires to 104 offspring born in the study groups, 36 of which were sired by extra-group males, i.e., residents of neighboring groups and bachelors. Among these extra-group males, high-ranking males (many of whom were neighboring residents) were more likely to sire offspring than low-ranking males, but the time these visiting males spent in the mother's group when she conceived (male presence) did not predict their relative success. When bachelors competed for reproduction with other bachelors, neither rank nor male presence during the mother's conceptive period affected the probability of siring an offspring, suggesting that highly opportunistic mating with conceptive females is important in bachelor reproduction. In a second analysis, we used long-term data to estimate resident and bachelor reproductive success over the long term, and particularly to determine if there are any circumstances in which a typical bachelor may sire as many offspring as a typical resident during one or two periods of residency. Our findings generally support the assumption of a resident reproductive advantage because in most circumstances, a lifelong bachelor would be unable to sire as many offspring as a resident. However, a bachelor who performs at the average rate in the average number of groups for several years may have similar lifetime reproductive success as a male whose reproduction is limited to one short period of residency, especially in a small group. Our findings suggest that one should not assume a resident reproductive advantage for males in one-male groups in all circumstances.

1   TITLE: Life as a Bachelor: Quantifying the Success of an Alternative Reproductive Tactic

2   in Male Blue Monkeys

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14   ABSTRACT

15   In species that live in one-male groups, resident males monopolize access to a group of

16   females and are assumed to have higher reproductive success than bachelors. We tested

17   this assumption using genetic, demographic, and behavioral data from 8 groups of wild

18   blue monkeys observed over 10 years to quantify reproduction by residents and bachelors

19   and compare the success of the two tactics. We used maximum-likelihood methods to

20   assign sires to 104 offspring born in the study groups, 36 of which were sired by extra-

21   group males, i.e., residents of neighboring groups and bachelors. Among these extra-

22   group males, high-ranking males (many of whom were neighboring residents) were more

23   likely to sire offspring than low-ranking males, but the time these visiting males spent in

24   the mother's group when she conceived (male presence) did not predict their relative

25   success. When bachelors competed for reproduction with other bachelors, neither rank

26   nor male presence during the mother's conceptive period affected the probability of siring

27   an offspring, suggesting that highly opportunistic mating with conceptive females is

28   important in bachelor reproduction. In a second analysis, we used long-term data to

29   estimate resident and bachelor reproductive success over the long term, and particularly

30   to determine if there are any circumstances in which a typical bachelor may sire as many

31   offspring as a typical resident during one or two periods of residency. Our findings

32   generally support the assumption of a resident reproductive advantage because in most

33   circumstances, a lifelong bachelor would be unable to sire as many offspring as a

34   resident. However, a bachelor who performs at the average rate in the average number of

35   groups for several years may have similar lifetime reproductive success as a male whose

36   reproduction is limited to one short period of residency, especially in a small group. Our

37   findings suggest that one should not assume a resident reproductive advantage for males

38   in one-male groups in all circumstances.

39   INTRODUCTION

40   In species with strong male-male competition for females, individual males often

41   adopt alternative reproductive tactics to maximize reproductive output within the

42   constraints of social, demographic, and ecological conditions (Gross 1996; Neff &

43   Svensson 2013). In male mammals, alternative reproductive tactics usually have unequal

44   fitness payoffs; the most competitive males use the tactic with the highest payoff, while

45   less competitive males use surreptitious behavior to gain access to females, resulting in

46   lower reproductive success (Wolff 2008; Taborsky & Brockmann 2010). Individuals

47   may, however, switch tactics over the course of a lifetime or even during a single

48   breeding season, in response to factors like their relative competitive ability and the

49   proportion of males pursuing each tactic (Repka & Gross 1995; Taborsky & Brockmann

50   2010).

51   Many mammals live in one-male/multi-female groups, a type of social

52   organization in which one resident male is consistently associated with a group of

53   females while bachelor males live alone or form bachelor groups. Males compete for the

54   resident position (e.g., Le Boeuf 1974; Clutton-Brock 1982), suggesting that the resident

55   tactic of defending access to a group of females results in higher fitness than the bachelor

56   tactic of stealing matings. Paternity studies from several mammals living in one-male

57   groups strongly support this prediction, in that residents sired all offspring born in their

58   groups (Schwartz & Armitage 1980; Pope 1990; Launhardt et al. 2001), which suggests

59   that lifelong bachelors do not sire any offspring. In other mammals, however, residents

60   lost some paternity to outsiders, including bachelors and residents of adjacent groups

61   (Pemberton et al. 1992; Asa 1999; Hoelzel et al. 1999; Storz, Bhat & Kunz 2001; Heckel

62   & Von Helversen 2003; Fabiani et al. 2004; Feh & Munkhtuya 2008; Hirsch &

63   Maldonado 2011; Roberts, Nikitopoulos & Cords 2014). While an alternative

64   reproductive tactic may exist in these species, the success of individual bachelors and the

65   factors affecting whether they sire offspring are not well understood. Furthermore, few

66   studies have directly compared the success of bachelor and resident tactics in long-lived

67   mammals (but see: Sommer & Rajpurohit 1989; MacLeod, Ross & Lawes 2002) because

68   it is difficult to follow males over their entire reproductive lives. Quantifying the success

69   of alternative tactics and identifying the conditions under which each does best allows us

70   to better understand the role of male-male competition in determining the evolution of

71   social organization.

72   We studied male reproductive tactics in blue monkeys (*Cercopithecus mitis*), a

73   guenon that lives typically in one-male groups. Even as a long-term resident, male blue

74   monkeys regularly face competition from extra-group males, who may be bachelors,

75   unattached to any group, or residents in adjacent groups (n.b., there are no all-male

76   groups). These extra-group males compete with a resident by spending time in his group

77   during the mating season, and copulating with his females (Cords 2000). Neighboring

78   residents are especially likely to steal copulations during aggressive intergroup

79   encounters (which involve primarily the females; Cords 2007). In addition, about 25% of

80   mating seasons in our study population are characterized by particularly strong male-

81   male competition when multiple extra-group males temporarily join the group for various

82   periods (from days to months), leaving when the mating season ends (Cords 2002). These

83   multi-male influxes are especially likely when multiple females are simultaneously

84   sexually active (Cords 2002; Mugatha et al. 2007) and they reduce the probability that a

85   resident male sires offspring conceived in his group (Roberts, Nikitopoulos & Cords

86   2014). These findings suggest that stealing matings may be a profitable bachelor tactic

87   (Rowell & Chism 1986).

88   Individual bachelors in the study population typically sire fewer offspring than

89   residents within a single group-year (Roberts et al. 2014), but there is variation in

90   bachelor success, and its causes are as yet unexplored. In addition, little is known about

91   how resident or bachelor tactics translate into lifetime reproductive success. Comparing

92   resident and bachelor reproductive success would help determine if the high costs

93   associated with residency allow bachelors to make up some of the difference in

94   reproduction by pursuing the lower-cost, lower-gain tactic for an extended period

95   (Widemo 1998; MacLeod, Ross & Lawes 2002). In this study, we used molecular,

96   demographic, and behavioral data collected from 8 social groups of wild blue monkeys

97   over 10 years to assess the absolute and relative success of the bachelor tactic. We

98   present our methods and results in two parts to increase clarity: Part I focuses on the

99   factors that drive differential siring success among extra-group males, while Part II

100   compares the lifetime reproductive success of bachelors vs. residents.

101   **PART I: FACTORS AFFECTING EXTRA-GROUP MALE SIRING SUCCESS**

102   PART I METHODS

103   *Ethical Note*

104   This research adhered to the ABS guidelines for the treatment of animals in

105   behavioral research. Methods were approved by the Columbia University IACUC (# AC-

106   AAAD9003), the National Council for Science and Technology, the Kenya Wildlife

107   Service and National Environmental Management Authority.

108   *Study Site and Population*

109   The study population of blue monkeys in the Kakamega Forest, Kenya (Mitchell,

110   Schaab & Wagele 2009) has been monitored since 1979 (Cords 2012). Our study focused

111   on the period between 2002 and 2011, during which 3 group fissions increased the

112   number of simultaneously existing study groups from 3 to 6. We used data from a total of

113   8 unique groups, each present for 1-10 years during the study period. Authors and field

114   assistants observed groups on a near daily basis to record demographic information

115   including infant birthdates, presence of sexually active females and of extra-group males

116   (both neighboring residents and bachelors) in or on the edge of the group, and dates of

117   resident male turnover. They also recorded all observed agonistic interactions among

118   males, noting participant identity and outcome.

119   *Genetic Data*

120   We used fecal samples from 126 infants, 64 mothers, and 60 adult males,

121   including 11 resident males in our study groups, for genetic analysis. We collected

122   samples shortly after defecation, storing them in sterile tubes mixed with RNALater™

123   (Ambion) to preserve the DNA.

124   Extraction and genotyping methods are described in Roberts et al. (2014). Briefly,

125   we extracted DNA from fecal samples using the QIAamp® DNA Stool Mini Kit

126   (Qiagen) and amplified it at 13 human MapPairs® microsatellite markers (Invitrogen).

127   We used the ABI 3730 Automated DNA Analysis system and *GeneMapper 3.7* (Applied

128   Biosystems) for genotyping.

129   We conducted likelihood-based paternity analysis with Cervus *3.0* (Kalinowski,

130   Taper & Marshall 2007), using simulation parameters noted in Roberts et al. (2014).

131   CERVUS assigned paternity to 108 offspring with 80% or 95% confidence (for details, see

132   Roberts et al. 2014). We further verified assignments by examining the number of

133   mismatches between the offspring and assigned sire, excluding mismatches for which

134   both individuals were homozygous because they may have resulted from allelic dropout.

135   Mother-offspring pairs mismatched rarely and never at more than 1 locus. Similarly, 104

136   of the 108 offspring-assigned sire pairs mismatched at 0 or 1 locus and we considered

137   these assignments to be robust. The remaining 4 offspring mismatched their assigned sire

138   at 2 loci, so we omitted them from the final analysis.

139   *Behavioral Data*

140   We used demographic data to identify factors affecting the siring success of extra-

141   group males. We were interested in how extra-group males compete among themselves

142   for reproductive opportunities so considered only the offspring sired by bachelors or

143   residents of adjacent groups (i.e., neighboring residents). Specifically, we tested how

144   male presence and dominance rank affected the probability of siring an offspring.

145   Blue monkey females do not signal fertile periods with morphological changes

146   such as sexual swellings, so we identified the period in which an infant's conception

147   occurred (conceptive period) using a combination of demographic records and behavioral

148   observations. First we identified a 29-day conception window for each offspring by

149   subtracting the length of one gestation (176±14 days, the 95% confidence interval, Pazol,

150   Carlson & Ziegler 2002) from offspring birthdates, which were accurate to 1-3 days.

151   Within this window, we then identified the conceptive period based on female sexual

152   behavior (copulations and proceptive behavior), following Pazol (2003) and Roberts et al.

153   (2014). We identified conceptive periods for the mothers of 28 of the 36 offspring sired

154 by extra-group males. The mean length of these periods was 5.4±5.1 days (range=1-22

155 days, N=28).

156   We summarized our data as offspring-male pairs, each corresponding to one male

157 observed in or near the group during the conceptive period of the mother of each

158 offspring. We included offspring-male pairs only if the male was individually identified

159 and genotyped because we were unable to predict siring success for males who we could

160 not readily identify or for whom we lacked genetic data. Individually-identified and

161 genotyped males comprised most of the males observed in the groups during conceptive

162 periods (mean±sd = 83±18%, range=44-100%, N=28 offspring). Our data sets did not

163 include the resident of the group in which the offspring was conceived because we

164 focused on competition among extra-group males. The average number of males present

165 in a group per month varied by group and time of year, with peaks typically occurring

166 during mating seasons (Figure 1; Cords 2000). The mean ± SD number of extra-group

167 males present per conceptive period was 2.5±2.4, which included 2.2±2.1 bachelor males.

168 *Factors Determining Siring Success of Extra-Group Males*

169   Our first predictor, male presence, was the proportion of days in the mother's

170 conceptive period in which we observed the male in or on the edge of her group. Our

171 second predictor was male dominance rank. Although male blue monkeys do not

172 regularly live in groups together, they do interact agonistically, thus establishing

173 dominance relationships that may order them into a queue for reproduction (Alberts,

174 Watts & Altmann 2003). We assigned ranks using the Elo-rating method (Albers & de

175 Vries 2001; Neumann et al. 2011) implemented with the EloRating package in R (version

176 0.98.1102). In this method, each individual is assigned an initial Elo-rating, which is

177   recalculated after each dyadic contest, with the winner gaining and the loser losing

178   points. The number of points gained or lost is based on the expected probability of each

179   participant winning the interaction. For example, if a higher-ranking male wins a contest

180   against a lower-ranking male, his Elo-rating increases (and the lower-ranking male's Elo-

181   rating decreases) only slightly. If, however, a lower-ranking male wins an interaction

182   against a higher-ranking male, each male gains or loses more points. This method is

183   particularly appropriate for our study system because it accommodates a varying number

184   and identity of individuals over time, and allows an assessment of rank at any specific

185   timepoint (Neumann et al. 2011). Additionally, the Elo-method can use interactions

186   between all males (including residents) to assign ratings, so bachelors can be ranked

187   relative to each other even if they have not directly interacted.

188   We compiled the 2002-2011 records of dyadic agonistic behavior (chase, attack,

189   lunge, bite, hit, avoid, flee, nasal scream) in which there was a clear winner and loser. All

190   males had a starting rank of 1000 and interacted for 6 months before we assessed their

191   Elo-rating for our data analyses. For our analyses, we used a male's Elo-rating on the day

192   representing the midpoint of the conceptive period for each offspring.

193   *Statistical Analysis*

194   We used conditional logistic regression (in Stata 13.1) stratified by infant to

195   evaluate how male presence and rank affected the log odds of siring an offspring. We

196   assessed the significance of entire models and individual predictors using likelihood ratio

197   tests to compare models with the predictor(s) present versus absent. Conditional logistic

198   regression requires variation in the dependent variable within each stratum, so for each

199   offspring sired by an extra-group male, we had to observe both the sire and at least one

200   non-sire (also an extra-group male) at conception. We therefore excluded any offspring

201   for which we observed only one extra-group male at conception. Our first analysis

202   included both neighboring residents and bachelors (both as sires and non-sires). We also

203   assessed how rank and male presence affected the relative success of bachelor males only

204   by generating a second data set that included only bachelor males (both as sires and non-

205   sires).

206   PART I RESULTS

207   Of the 104 offspring with verified paternity assignments, 68 were assigned to

208   residents. The remaining 36 were assigned to extra-group males, 12 to residents of

209   adjacent groups and 24 to bachelors.

210   *Factors Determining Siring Success of Extra-Group Males*

211   When we considered offspring sired by any extra-group male, a conditional

212   logistic model including both male presence and rank was better than a null model at

213   predicting which male sired an offspring (likelihood ratio test: χ^2=13.81, P=0.001, N=11

214   offspring with one sire and 1-7 non-sires each). However, the effect of male presence was

215   not significant (Wald P=0.943 for rank model), and likelihood ratio tests showed that a

216   model including this predictor did not differ from one that excluded it (rank: χ^2=0.01,

217   P=0.9433). We concluded that male presence was not a useful predictor of siring

218   probability among extra-group males, while rank had significant effects. A final

219   univariate model showed that an extra-group male increased his odds of siring an

220   offspring by a factor of 1.01 with a one-step increase in Elo rating (odds ratio=1.007,

221   Wald P=0.008; likelihood ratio test, χ^2=13.809, P=0.0002). The average number of Elo-

222   steps between two adjacently ranked males was 154, so the odds of siring an offspring

223 would increase by a factor of approximately 156 for a one-step increase in ordinal rank.

224 This large rank advantage occurred because the highest-ranked male sired eight of the

225 eleven offspring in our data set and in only one case did a male more than 79 Elo-steps

226 below the highest-ranked male sire the offspring. Overall, the average Elo rating of sires

227 was 1181 (N=11), while for non-sires it was 902 (N=35).

228   We analyzed the effect of male rank and male presence on the log odds of siring

229 an offspring for a subset of the above cases in which bachelors were the sires, and here

230 included only other bachelors as non-sires (N=6 offspring, with one sire and 1-4 non-

231 sires each). For bachelors competing amongst themselves, neither male presence (Wald

232 P=0.645) nor rank (Wald P=0.180) predicted siring an offspring, and a model including

233 these predictors was not significantly different from a null model (likelihood ratio test,

234 χ^2=3.031, P=0.220).

235   Because conditional logistic regression requires both positive and negative

236 outcomes (sires and non-sires for each offspring), our analyses could not use data from (i)

237 7 infants who were known *not* to be the offspring of their group's resident male, even

238 though they were not assigned to any other male that was present in their group at

239 conception, or (ii) 3 infants whose paternity was assigned to the single extra-group male

240 that visited the group at the time of their conception. These cases can provide information

241 about both non-sires and sires, but one cannot stratify the comparison by offspring. When

242 we considered both neighboring residents and bachelors as sires and non-sires for all 21

243 offspring, we again found that sires had significantly higher Elo-ratings (median for sire:

244 1222 vs. non-sires: 912; Mann Whitney U Test, U=649.5, Z=-3.77, 2-tailed P=0.0002,

245 N=14 sires, 56 non-sires) but there was no difference for male presence (U=357.5,

246   Z=0.50, P=0.6171). When we considered only those offspring sired by bachelors (N=8),

247   we found no significant difference in rank or male presence between bachelor sires and

248   non-sires (rank: U=68, P>0.05; time in group: U=63, P>0.05, N=8 sires, 14 non-sires for

249   both tests). Thus these results incorporating additional offspring corroborated those from

250   the conditional logistic regression.

251   **PART II: COMPARING RESIDENT AND BACHELOR SUCCESS**

252   PART II METHODS

253   *Comparing Resident and Bachelor Tactics*

254   Comparing the long-term success of resident and bachelor tactics required

255   estimating reproduction across multiple groups and years. While our paternity data

256   spanned multiple groups and years, some parameters were not directly measured and

257   were inferred based on known patterns of reproduction in study groups. As such, our

258   calculations were exploratory and served to determine if there are any conditions under

259   which bachelorhood and residency may be comparably successful reproductive tactics.

260   Our calculations were based on MacLeod et al. (2002) who aimed to discover if,

261   over an entire reproductive lifetime, a bachelor samango monkey could steal enough

262   matings to be as successful as a resident male siring at the average rate for one average

263   period of tenure. These authors concluded that a bachelor would have to pursue the steal

264   strategy for 15.1 years to obtain the same number of matings as a resident in one average

265   period of tenure. They judged 15 years to exceed the length of the male reproductive

266   lifespan and concluded that a resident male with just one period of tenure would always

267   obtain more matings than a bachelor. Importantly for our purposes, however, this

268   calculation made four assumptions: (1) the resident confines his reproduction to his

269   group, (2) the resident loses reproduction to only one bachelor, (3) the bachelor confines

270   his reproduction to one group and (4) that matings map directly onto reproduction. Our

271   paternity results indicated that our study population violated all four assumptions, so we

272   developed a new calculation for comparing bachelor and resident siring success to

273   account for siring success in multiple groups and by multiple bachelors within one group.

274   Specifically, we identified components of bachelor and resident reproduction and used

275   summary statistics to determine how long the average bachelor would have to pursue the

276   bachelor tactic to match the siring success of the average resident.

277   As acknowledged earlier, blue monkey males may switch among tactics during

278   their lives, so some males may sire offspring as bachelors before or after attaining

279   residency. Genetic and behavioral evidence suggest, however, that a resident's siring

280   success is concentrated during residency. In the study population, males who became

281   residents appeared to gain this status around the time they attained full adult body size.

282   As we almost never observed young adult males (i.e., those that are not full grown)

283   copulating, the window in which males that become residents are old enough to copulate

284   but not yet resident in a group is very short, thereby limiting pre-residency siring success.

285   Supporting this inference, only 1 of 8 males sired offspring in a study group before

286   attaining residency and all these offspring were in the group with an infertile resident. We

287   know less about post-residency siring success because many deposed residents (e.g. 7 of

288   18 during the study period) disappear. However, demographic records indicate that 5 of

289   the 11 (45%) residents with known fate died and genetic data indicate the other six did

290   not sire offspring as a post-resident bachelor. We therefore computed a resident's siring

291   success based only on his period of residency.

292   Additionally, 4 of the 11 resident males in our study groups were known to have

293   two periods of residency (in different groups). We therefore computed a resident's siring

294   success based on one or two periods of residency.

295   *Resident parameters*

296   Resident siring success during his tenure is expressed as follows (Equation 1):

$$R = \sum_{t=1}^{T} (R_i + R_o N_r)_t$$

297   R_i is the annual siring rate (number of offspring) in the resident's own group, R_o is his

298   annual siring rate per outside group, N_r is the number of outside groups, and T is tenure

299   length, measured as the number of mating seasons (one per year in blue monkeys). The

300   product of R_o and N_r equals "outside-group" siring success, so the value in parentheses is

301   equal to the resident's total annual siring success, which is summed over his entire tenure.

302   We estimated within-group siring success (R_i) by summing the number of

303   offspring sired in a resident's group during his entire tenure and dividing by the number

304   of years he was resident. One resident, Ro, did not sire any of the 19 offspring conceived

305   in his group despite mating during most conceptive windows, which suggests that he was

306   infertile. We therefore calculated summary statistics for siring success excluding Ro.

307   There are likely more reproductive opportunities in larger groups, so we

308   calculated R_i for small and large groups separately. Small groups contained ≤15 females

309   over age 5 (the age at which females begin to exhibit proceptive behavior) and large

310   groups contained >15 females over age 5. Group fissions during the study period resulted

311   in two study group residents (Sa and Pu) being represented twice, once as resident of the

312   parent group and once as resident of one of the daughter groups.

313   Tenure length (T) equaled the number of mating seasons a resident male was in

314   his group, using observations of 23 residents for which we observed complete periods of

315   tenure since 1994. Most conceptions occur during the 5-month mating season from June-

316   October (Cords & Chowdhury 2010) and we considered a resident to be present for a

317   mating season if he was in the group for more than half of this 5-month period.

318   We estimated the number of outside groups in which a resident may sire offspring

319   (N_r) as the number of adjacent groups, because a resident has never been observed more

320   than one home range away from his own group. Group members collaborate to defend

321   territories against adjacent groups (Cords 2007) and we used observations of intergroup

322   encounters from 2002-2012 to assess the number of adjacent groups for each study group.

323   Group fissions and home range shifts may cause the number of adjacent groups to change

324   over time, so we assessed this number annually. In a few cases, the identity of an adjacent

325   group was ambiguous because it was a non-study group without readily identifiable

326   individuals in an area where multiple group home ranges overlapped. In those cases, we

327   calculated the minimum and maximum number of adjacent groups and used the average

328   of those values. Minimum values reflected the number of identified adjacent groups and

329   maximum values included the unidentified adjacent groups, although it may have been a

330   known group that was unrecognized at the time.

331   We estimated outside-group siring success (R_o) from resident paternity success in

332   other study groups. We calculated this parameter for 20 residents with a total of 22

333   periods of residency by dividing the total number of offspring sired in adjacent study

334   groups by the number of adjacent study groups and by tenure length.

335   *Bachelor parameters*

336   Bachelor siring success is expressed as follows (Equation 2):

$$B = \sum_{l=1}^{L} (R_b N_b)_l$$

337   R_b is the annual siring rate per group, N_b is the number of groups encountered, and L is a

338   bachelor's reproductive lifespan. The value in parentheses equals the number of offspring

339   a bachelor produces annually, which is summed over his entire lifetime.

340   We genotyped 47 males who were bachelors for part or all of the time they were

341   observed in the study population and used long-term records to identify the years of

342   bachelorhood and study groups each male visited. To calculate annual siring rate per

343   study group (R_b), we divided the total number of offspring a bachelor sired in the study

344   groups by the total number of study groups and years that he was observed.

345   We later omitted some of these males from the calculations to ensure that the

346   summary statistics were good estimates of bachelor parameters. First, we omitted 19

347   bachelors observed for only 1 year, as most were either subadults who had recently

348   emigrated from their natal groups but had not yet left the local population or males that

349   were passing through (i.e., seen only few times and could not be consistently identified).

350   We omitted 3 bachelors who were not observed in any of the study groups because we

351   were unable to assess their siring success. These 22 bachelors were particularly unlikely

352   to sire offspring in the study groups (only one sired one offspring) and removing them

353   increased bachelor siring rate. Of the remaining 25 bachelors, 10 eventually became

354   residents in the study groups or adjacent non-study groups. To control for differences

355   between "committed" bachelors and bachelors who later became residents, we limited

356   our calculations to the 15 bachelors who were bachelors for the entire time we knew

357   them, although we acknowledge that they may have been residents before or after they

358   were observed.

359   We estimated the number of groups a bachelor encountered as the number of

360   group home ranges that his home range overlapped. From June-September 2011, SJR

361   walked transects following pre-existing linear footpaths spanning the study group home

362   ranges. When she encountered a bachelor, she followed him and recorded his location

363   every 30 minutes with a handheld GPS unit (Garmin GPSMAP® 60 CSx) until she lost

364   him. We have location data for 11 bachelor males, but used data from the 5 that were

365   tracked for $\geq$15 hours each (mean±sd=24.3±9.4, range=16-38 hours over 5-11 days).

366   During the same period, we collected location data to map the home ranges of the

367   6 study groups. The field team contacted each group daily and recorded the location of

368   the group center every 60 minutes with a handheld GPS unit. We recorded 414±167

369   (mean±sd) hours of location data per study group (range=139-579) distributed over 81-

370   123 days. SJR and one field assistant also tracked the location of 4 adjacent non-study

371   groups, recording the location of the group center every 30 minutes for a mean of 74±30

372   hours of location data per group (range=37-110) distributed over 14-19 days. We plotted

373   all points on a 50x50m grid. When a point fell within a grid cell, that cell was considered

374   to be part of the group home range (Figure 2).

375   We overlaid bachelor points on group home ranges and counted the number of

376   group home ranges in which each bachelor was observed (i.e., the minimum number of

377   groups encountered). Four of the 5 bachelors were observed outside the mapped group

378   home ranges. Based on home range sizes of known groups and opportunistic observation

379   of unidentified groups, we estimated the total number of group home ranges that

380   bachelors may have overlapped (i.e., the maximum number of groups encountered). We

381   used the midpoint of minimum and maximum values for each bachelor as the total

382   number of groups encountered.

383   *Comparing tactics*

384   We used mean values for each parameter to calculate the number of years a

385   bachelor siring offspring at the average rate in the average number of groups (i.e., the

386   average bachelor) would have to pursue the bachelor tactic to sire as many offspring as a

387   resident siring at the average rate in his own group and at the average rate in the average

388   number of outside groups (i.e., the average resident) for one period of tenure. The way

389   we calculated all variables accounted for variation across years, so we set Equations 1

390   and 2 equal to each other and solved for the length of a bachelor's reproductive lifespan,

391   L (Equation 3):

$$L = \frac{T(R_i + R_o N_r)}{R_b N_b}$$

392   The length of male reproductive lifespans varies widely among cercopithecines

393   (4.3 years in Japanese macaques to 12.7 years in mandrills, Clutton-Brock & Isvaran

394   2007). We do not know the length of male reproductive lifespans in blue monkeys, so we

395   used estimates of female lifespan to identify plausible values. The oldest female in the

396   study population was 33.5 years old (Cords & Chowdhury 2010) and males attain full

397   body size around 9 years old, so we estimated the maximum male reproductive lifespan

398   to be the difference between these two values, 24.5 years. We considered it to be

399   impossible for a bachelor to sire as many offspring as a resident if Equation 3 yielded an

400   estimate of L that exceeded 24.5 years.

401   Given the large range in tenure length in our population (1-8 years) and the

402   importance of tenure in the above equation, we repeated the calculations using the same

403   parameters but replacing average tenure length with minimum or maximum tenure

404   length. We also doubled all values of L to compare the average bachelor to the average

405   resident with 2 periods of tenure. These repetitions allowed us to compare bachelor and

406   resident success in a total of 12 unique circumstances.

407   PART II RESULTS

408   *Resident parameters*

409   The mean annual siring success in a resident's own group was 1.4±0.9 offspring

410   per year in small groups (N=5 residents in 4 study groups) and 2.9±1.7 offspring per year

411   in large groups (N=6 residents in 4 study groups; Table 2). Four residents sired offspring

412   in adjacent groups: 3 residents sired 1 offspring and 1 sired 9 offspring over his 8-year

413   tenure. Despite high outside-group siring success by some males, the average rate across

414   residents was low (mean±sd=0.1±0.3 offspring per adjacent group per year, N=22 periods

415   of residency; Table 1). The number of adjacent groups varied across group-years, but

416   given low rates of outside-group siring success, reproduction in adjacent groups

417   contributed much less to the total number of offspring sired during resident tenure than

418   within-group siring success.

419   Tenure length varied greatly across residents (mean±sd=2.8±2.1, range=1-8

420   mating seasons, N=23 periods of residency; Table 1), with observed values skewed

421   towards shorter tenure lengths. Three males maintained residency for 6 years each, but

422   only 1 was resident for the maximum 8 years.

423   Plugging mean values for resident within-group and outside-group siring success

424   and the number of outside groups into Equation 1 indicated that the average resident in a

425   small group produces 1.4 offspring in his own group and 0.4 offspring in adjacent groups

426   each year, for a total of 1.8 offspring annually. Maintaining this rate would yield 5.0

427   offspring during a period of tenure of average length and 14.7 offspring during a period

428   of tenure of maximum length (Figure 3). In contrast, the average resident in a large group

429   produces 3.3 offspring annually, 9.2 offspring during a period of tenure of average

430   length, and 26.8 offspring during a period of tenure of maximum length (Figure 3). Many

431   of the 10 residents in our study (excluding Ro, who seemed to be infertile; Roberts,

432   Nikitopoulos & Cords 2014) matched the siring profile of the hypothetical "average

433   resident," siring approximately as many offspring as predicted by the calculations (Figure

434   3).

435   *Bachelor parameters*

436   An average bachelor sired 0.1 offspring per study group per year (Table 2). We

437   found little variation in the number of group home ranges that a bachelor used

438   (mean±sd=3.2±0.4, range=2.5-3.5 groups, Table 2). Using mean values for R_b and N_b, the

439   average bachelor would sire 0.3 offspring per year. There was some variation in siring

440   success among 15 bachelors present in our study population for multiple years (Figure 4).

441   While some had no offspring in our study groups, others sired multiple offspring and

442   several matched the siring profile of the hypothetical "average bachelor," predicted by

443   the calculations (Figure 4).

444   *Bachelorhood versus residency*

445   Our calculations indicate that the average bachelor may eventually sire as many

446   offspring as the average resident who is present for one period of tenure of minimum

447   length in either a small or large group (Table 3). It will always take less time for the

448   average bachelor to match the siring success of a resident in a small group than a resident

449   in a large group, so there are more circumstances that allow the average bachelor to sire

450   as many offspring as the average resident in a small group. For example, the average

451   bachelor may catch up to the average resident who is present for one period of tenure of

452   average length if that resident is in a small group, but not if he is in a large group. The

453   average bachelor would never be able to sire as many offspring as a resident if that

454   resident remains in his group for the maximum tenure length, regardless of group size

455   (Table 3).

456   Doubling all values of L indicates that there are fewer circumstances in which the

457   average bachelor can catch up with the average resident with two periods of residency.

458   Specifically, a bachelor may be as successful as a resident with two periods of residency

459   only if both periods of tenure are short (Table 3). If the average resident has one period of

460   tenure in a small group that lasts the minimum tenure length and a second period of

461   tenure in another small group that lasts that mean length, a bachelor may match the

462   resident's siring success in 21.9 years, which is less than our estimate of the maximum

463   male reproductive lifespan.

464   DISCUSSION

465   *Factors Affecting Extra-Group Male Siring Success*

466   The relationship between rank and male mating and siring success has been a

467   topic of investigation for decades (e.g., Cowlishaw & Dunbar 1991; Ellis 1995; Majolo et

468   al. 2012). Studies have focused on species living in multi-male groups where males

469   interact regularly and competitors are in close proximity. To our knowledge, our study is

470   the first to rank extra-group males and use those ranks to predict siring success in a one-

471   male species. Although the resident male of a group dominates within-group reproduction

472   in blue monkeys (Roberts, Nikitopoulos & Cords 2014), other males also participate, and

473   do so differentially. Our results suggest that higher-ranking extra-group males have a

474   substantial siring advantage; the odds of siring an infant by increased roughly by a factor

475   of 156 with a one-step increase in ordinal rank. High-ranking males include the residents

476   of neighboring groups, which were represented disproportionately among the extra-group

477   sires. Neighboring residents were present during the conceptive period of nine infants and

478   sired six of these infants.

479   Among bachelors, rank was not a significant predictor of siring success, which

480   suggests that bachelors do not engage in contests with other bachelors for access to

481   reproductive opportunities. Indeed, the majority of observed male-male contests involve

482   at least one resident (pers. obs.). Bachelor blue monkeys probably use a highly

483   opportunistic tactic to reproduce, mating when they encounter a sexually active female

484   rather than queuing for reproduction as seen in wild savannah baboons (Alberts, Watts &

485   Altmann 2003). Opportunistic matings may be more likely to occur in forest-dwelling

486   taxa than in those inhabiting open habitats, because limited visibility decreases the

487   chance that a higher-ranking competitor would interfere (Rowell 1988). We have seen

488   bachelors copulate with females in our study population near to but on the other side of

489   vine tangles from a resident, suggesting that limited visibility does allow bachelors to

490   steal copulations. The dense forest habitat may similarly negate any effect of dominance

491   rank on siring success among bachelors, allowing low-ranking bachelors to mate and

492   reproduce opportunistically, despite the presence of other higher-ranking bachelors

493   nearby.

494   It is perhaps more surprising that the time an extra-group male visited the group

495   during a mother's conceptive period did not significantly predict siring success. Even in

496   the absence of contests, one might expect extra-group males that are more consistently

497   present to sire more offspring. Perhaps, however, rare opportunities to mate with

498   conceptive females (copulations and mounts during conceptive periods occurred at a rate

499   of 0.21 events/hour; unpublished data from 86 hours of focal samples of 48 adult females

500   in their conceptive period) combined with the difficulty of monitoring their sexual

501   activity in large and widely dispersed groups (group spread: mean±sd=81±46m,

502   range=15-282m, unpublished data from 198 measurements of 6 groups with 8-49

503   individuals) in a visually opaque environment introduces a large element of serendipity

504   into relative mating (and ultimately reproductive) success of bachelor males.

505   *Comparing Male Reproductive Tactics*

506   If bachelor male blue monkeys are pursuing an alternative reproductive tactic

507   instead of simply making the best of a bad job, we would expect the lifetime reproductive

508   success of a lifelong bachelor to resemble that of a male who incorporated a period of

509   residency into his reproductive lifespan. Although resident males have a verified

510   reproductive advantage in the short term and on a small scale (Roberts et al. 2014), a

511   bachelor may be able to make up for this reproductive disadvantage by reproducing for a

512   longer period or in more groups (MacLeod, Ross & Lawes 2002). Our calculations,

513   however, indicate that it will usually take many years for a bachelor to sire as many

514   offspring as a resident during one period of tenure, and in most circumstances, the

515   resident tactic probably results in higher lifetime reproductive success than the bachelor

516   tactic.

517   Although residency usually confers a reproductive advantage, we identified some

518   circumstances in which an average bachelor's reproductive success would match an

519   average resident with one or two periods of tenure. Specifically, an average bachelor

520   would take 5.8 years to match the siring success of an average resident in a small group

521   with a period of tenure of minimum length. This estimate increases to 10.4 years when

522   one compares an average bachelor to an average resident with minimal tenure in a large

523   group and to 16.1 years in comparison to the average resident in a small group with

524   period of tenure of average length. There were fewer circumstances in which the average

525   bachelor could sire as many offspring as the average resident with two periods of tenure,

526   but it was not impossible.

527   When calculating resident and bachelor parameters, we made several decisions

528   that affected the comparison. We limited resident siring success to the period of residency

529   because the available genetic and behavioral evidence suggests that resident males rarely

530   sire offspring before or after becoming resident. Our data indicate that reproduction by

531   males with at least one period of residency occurred almost entirely during their

532   residency, but it remains possible that this restriction caused us to underestimate resident

533   lifetime reproductive success. Specifically, if residents do sire offspring before and after

534   residency *and* they both sire offspring at the same rate and live as long as life-long

535   bachelors, the lifetime reproductive success of a resident will always be greater than the

536   lifetime reproductive success of a bachelor.

537   When calculating annual siring success for bachelors, we eliminated young

538   bachelors who had recently left their natal groups and temporary visitors that were unable

539   to be recognized. These bachelors had very low siring success, so omitting them from our

540   calculation increased the average bachelor siring success and gave the average bachelor a

541   better chance of catching up with a resident. If we included these males, the rate of

542   bachelor siring success was half of the estimated values (0.05 offspring per group per

543   year instead of 0.1 offspring per group per year), which would double the number of

544   years required for the average bachelor to sire as many offspring as a resident. The

545   average bachelor would be unable to catch up with the average resident with one period

546   of tenure unless the resident had a very short tenure. The average bachelor would be able

547   to catch up with the resident with two periods of tenure only if the resident had two very

548   short periods of tenure in a small group.

549   We judged the estimates of bachelor reproductive lifespan to be plausible if they

550   were less than 24.5 years, based on the difference between maximum female lifespan and

551   the age at which males attain full adult body size. This male reproductive lifespan

552   represents a maximum, as it is unlikely that male blue monkeys live as long as females.

553   In long-lived species that live in one-male or multi-male groups, males typically show

554   higher annual mortality rates and a more rapid decline in survival with age (Clutton-

555   Brock & Isvaran 2007; Bronikowski et al. 2011). If we estimated male reproductive

556   lifespan more conservatively by assuming that the oldest reproductive male was as old as

557   the oldest *reproductive* female (26.5 years), the male reproductive lifespan would be 17.5

558   years instead of 24.5. This change means there would be fewer circumstances in which a

559   bachelor male could sire as many offspring as a resident during one period of tenure, but

560   there would still be some (Table 3).

561   *Conclusion*

562   Although resident male blue monkeys sire most offspring born in their groups,

563   they lose about 40% of paternity to outside males (Roberts et al. 2014). When a resident

564   male did not monopolize reproduction in his group, the rank of extra-group males

565   influenced their relative success, with high-ranking males (who were often neighboring

566   residents) having a special advantage. Neither bachelor rank nor male presence affected

567   siring success relative to other bachelors, however, suggesting that bachelors do not use

568   contest competition to allocate reproductive opportunities and that opportunistic matings

569   play an important role in bachelor siring success.

570   Bachelor males sire offspring at a much lower rate than do residents, but a

571   bachelor may be able to make up for this reproductive disadvantage by reproducing for a

572   longer period of time or in multiple groups. Our comparison of average bachelor and

573   resident siring success indicated that in most circumstances, a lifelong bachelor would be

574   unlikely to sire as many offspring during his lifetime as a resident during one or two

575   periods of residency. However, a bachelor who sires offspring at the average rate in

576   multiple groups for several years may have similar lifetime reproductive success as a

577   male whose reproduction is limited to one average period of residency, especially in a

578   small group. Our findings thus suggest that one should not assume a resident reproductive

579   advantage for males in one-male groups in all circumstances.

580   ACKNOWLEDGEMENTS

581   We thank the Government of Kenya for permission to conduct the research, and

582   the Centre for Kakamega Tropical Forest Studies at Masinde Muliro University of

583   Science and Technology for local sponsorship. Genetic resources utilized in this study

584   were provided by the government and people of Kenya. We are grateful to the local forest

585   station personnel, and many field and lab assistants. We especially thank T. Disotell for

586   hosting the genetic analysis and D. Rabinowitz for statistical advice.

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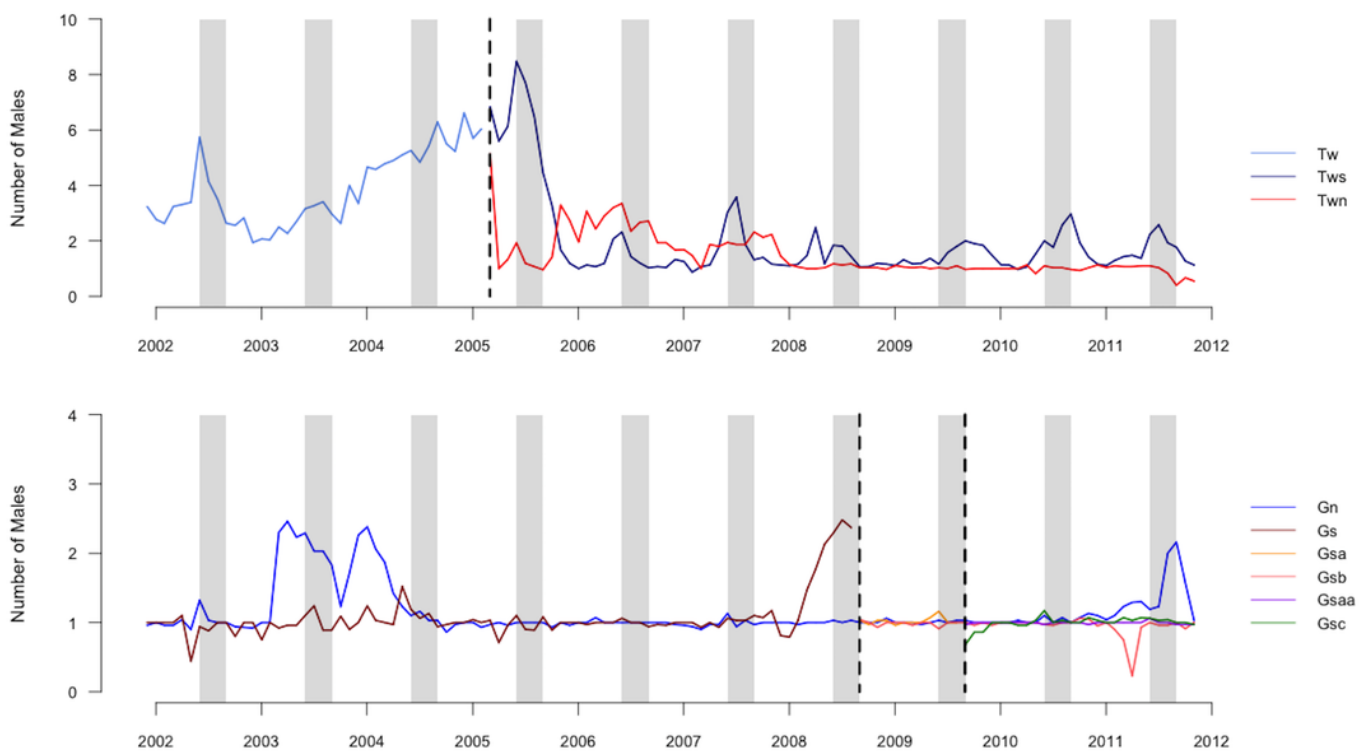
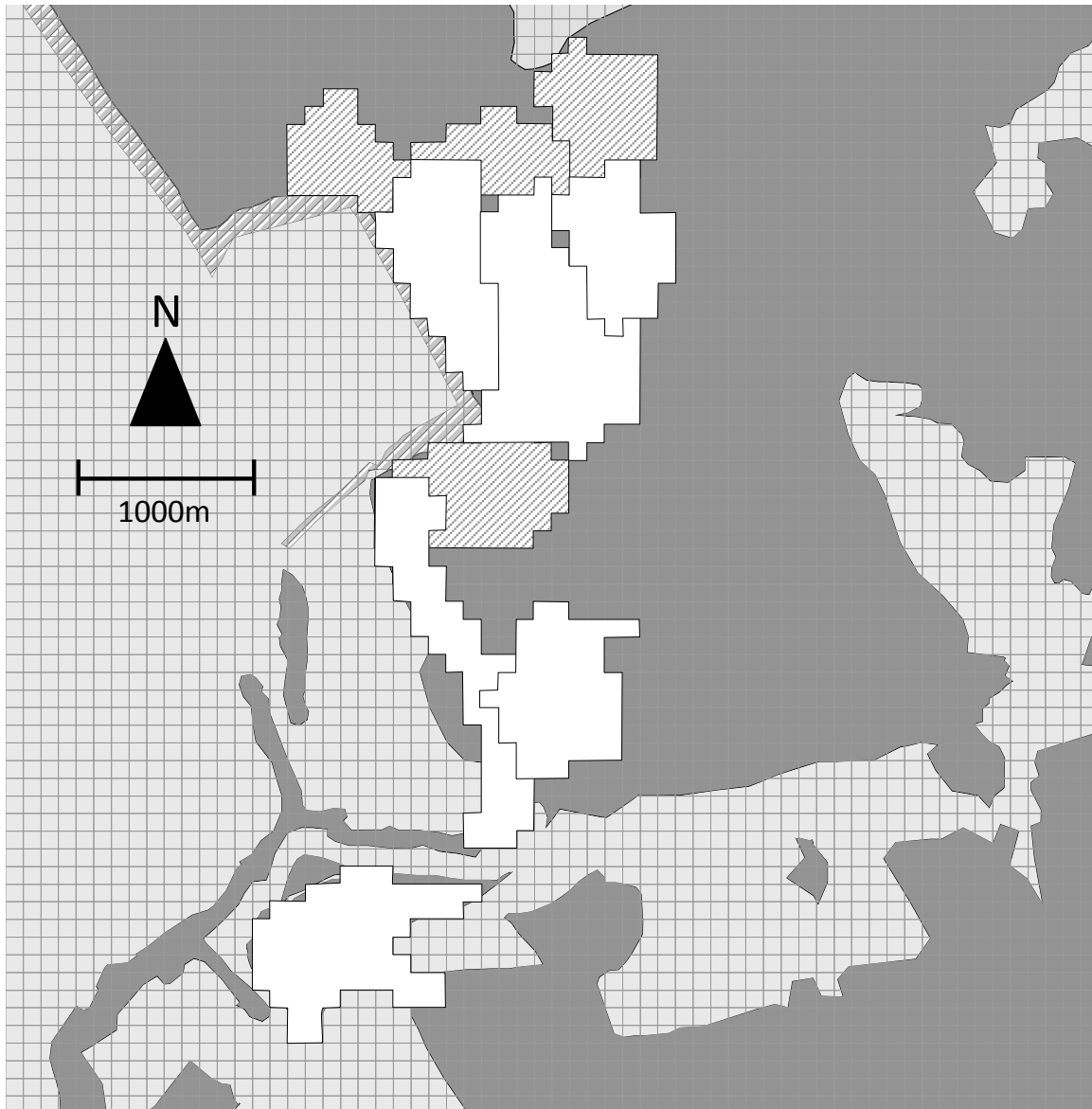
697

1

Graph of number of males in groups

Average number of males (including the resident male) present in each group averaged by month during the study period. Vertical dashed lines indicate dates of group fission events. Gray columns indicate the population peak in conceptions, which occurs from July until September.

Map of group home ranges

Home ranges of 6 study groups (white) and 4 adjacent non-study groups (hatched). Dark grey indicates forested areas, light grey non-forested areas.

Resident parameters

Resident parameters

Statistic	Annual within-group siring rate in small groups (R_i)	Annual within-group siring rate in large groups (R_i)	Annual siring rate per neighboring group (R_o)	Number of neighboring groups (N_r)	Tenure length in years (T)
Mean ± SD	1.4 ± 0.9	2.9 ± 1.7	0.1 ± 0.3	4.4 ± 1.5	2.8 ± 2.1
Median	1.3	3.1	0	4	2
Range	0.5-3	0-5	0-1	1-7	1-8
N	5 residents in 4 study groups	6 residents in 4 study groups	20 residents in the study pop, 22 periods of residency	45 group-years	21 residents in the study pop, 23 periods of residency

Bachelor parameters

Bachelor parameters

2 **Table 2** Bachelor parameters

Statistic	Annual siring rate per group (R_b)	Number of groups (N_b)
Mean ± sd	0.1±0.1	3.2 ±0.4
Median	0	3.5
Range	0-0.3	2.5-3.5
N	29 bachelors	5 bachelors

Comparison of resident and bachelor success

The number of years (L) an average bachelor would need to pursue the bachelor tactic to sire as many offspring as an average resident with one (A) or two (B) periods of tenure of various lengths. Gray cells correspond to values that exceed a male's maximum reproductive lifespan (24.5 years) and therefore circumstances in which a bachelor could not sire as many offspring in his lifetime as a resident sires during his tenure.

A. Average Resident with One Period of Tenure

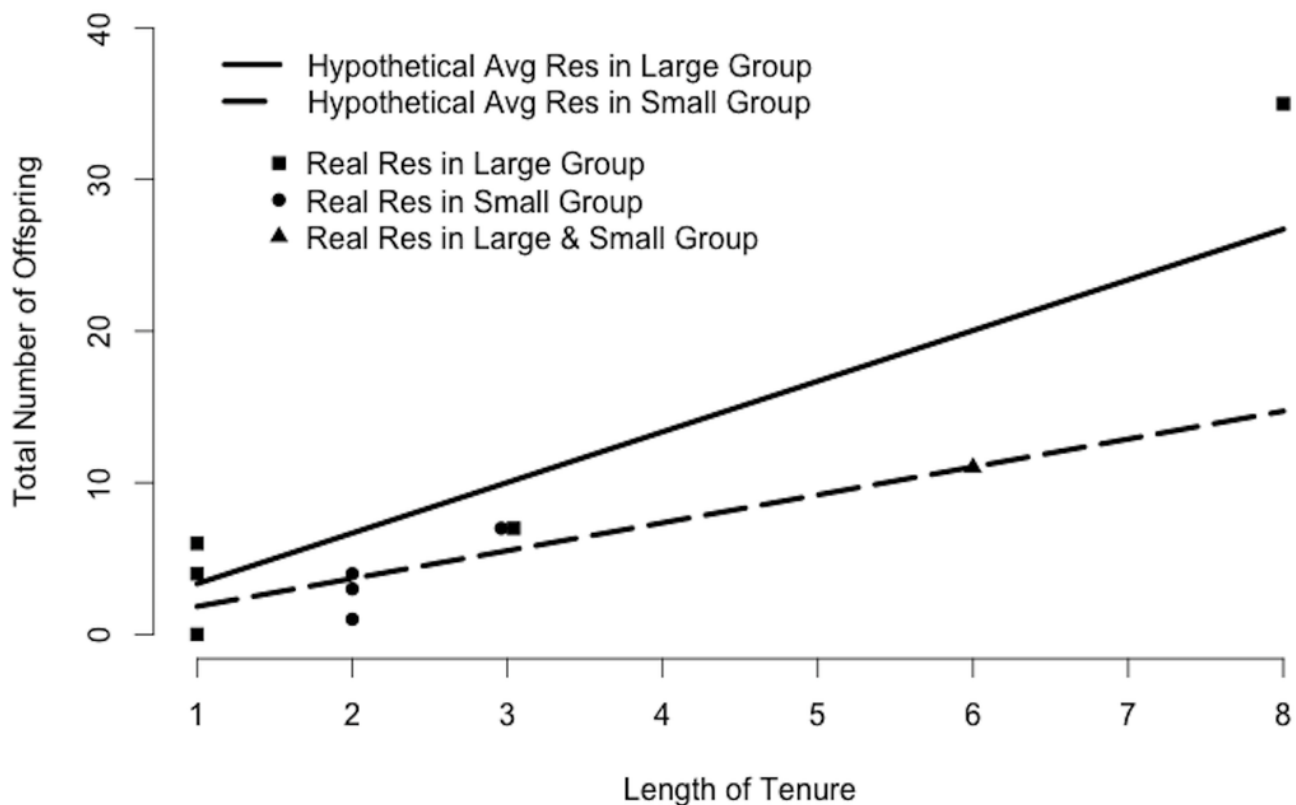
	Min Tenure (1 year)		Mean Tenure (2.8 years)		Max Tenure (8 years)	
	Small Group	Large Group	Small Group	Large Group	Small Group	Large Group
L for the Average Bachelor	5.8	10.4	16.1	29.3	46.0	83.5

B. Average Resident with Two Periods of Tenure

	Min Tenure (1 year)		Mean Tenure (2.8 years)		Max Tenure (8 years)	
	Small Group	Large Group	Small Group	Large Group	Small Group	Large Group
L for the Average Bachelor	11.6	20.8	32.2	58.6	92.0	167.0

3

Resident siring success

Predicted siring success of hypothetical average residents as calculated by substituting mean values for R_i, R_o, and N_r into Equation 1. Points correspond to 10 real residents in our study population and indicate the total number of offspring sired in the study groups during one period of tenure. One male was resident in both a large and a small group.

Bachelor siring success

Predicted siring success of a hypothetical average bachelor as calculated by substituting mean values for R_b and N_b into Equation 2. Points correspond to 15 real bachelors and indicate the total number of offspring sired in the study groups during the years the bachelor was observed in our study population.