

4 **Male takeover, infanticide, and female countertactics**
5 **in white-headed leaf monkeys (*Trachypithecus leucocephalus*)**

6 **Qing Zhao · Carola Borries · Wenshi Pan**

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9 **Abstract** Infanticide by males is common in mammalian
10 species such as primates in which lactation lasts much
11 longer than gestation. It frequently occurs in one-male
12 groups following male takeovers and is likely a male
13 reproductive strategy. Reported female countertactics
14 include abrupt weaning of infants, dispersal, or paternity
15 confusion. Here, we estimated costs of female counter-
16 tactics in terms of weaning ages and interbirth intervals.
17 We observed a population of white-headed leaf monkeys
18 (*Trachypithecus leucocephalus*) in Nongguan Nature Re-
19 serve, China (1995–2006) mainly composed of one-male
20 groups. Takeovers ($N=11$) coincided with the peak concep-
21 tion period. Detailed data are presented for five takeovers
22 (34 females, 29 infants, and 47 group-years) leading to six
23 infant disappearances (42.9% of infant mortality). All
24 presumed infanticides were in accordance with the sexual
25 selection hypothesis. Following a takeover, females without
26 infants or with old infants stayed with the new males,
27 incurring no or low costs (via abrupt weaning). Females with
28 young infants dispersing with the old males also experienced
29 low costs. High costs (due to infant loss) were incurred by
30 pregnant females and those with young infants who stayed
31 with the new males indicating that paternity was not
32

confused. Costs in terms of long interbirth intervals were 33
also high for females leaving with the old males to later join 34
the new males, despite infant survival. Female countertactics 35
reflected female philopatry mediated by infant age. 36
Presumably due to the seasonal timing of takeovers, 37
most countertactics seemed successful given that 32.3% 38
of females apparently incurred no costs and 41.2% 39
incurred only low costs. 40

Keywords Female philopatry · Infant loss · Interbirth 41
interval · Seasonal breeding · Weaning age 42

Introduction 43

In the animal kingdom, infanticide by males seems to be 44
a widespread phenomenon occurring in very diverse taxa 45
(Alcock 2001; Ebensperger 1998). It has for example 46
been reported in birds (overview in Veiga 2000), fish 47
(*Pelvicachromis pulcher*, Nelson and Elwood 1997), 48
beetles (*Nicrophorus orbicollis*, Trumbo 2006), and 49
spiders (*Stegodyphus lineatus*, Schneider and Lubin 50
1996) but is perhaps most frequently documented in the 51
different social systems of mammals (overview, e.g., 52
Ebensperger 1998). It occurs in solitary, seasonally 53
breeding brown bears (*Ursus arctos*, Bellemain et al. 54
2006), gregarious equids (*Equus caballus*, Cameron et al. 55
2003; *Equus burchelli*, Pluhacek et al. 2006), and 56
dolphins (*Tursiops truncatus*, Patterson et al. 1998). In 57
all these examples, infanticide was found to be in 58
accordance with the sexual selection hypothesis. This 59
hypothesis postulates that infanticide by males will 60
increase male reproductive success as long as males do 61
not kill their own offspring, the next conception of the 62
infants' mothers is accelerated, and males increase their 63

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64 chances of siring the next infants (Hrdy 1974, 1979). The
65 longer the lactation period in relation to gestation, the
66 more time a male can potentially gain for his own
67 reproduction, which is why infanticide in mammals seems
68 to be most frequent in primates and particularly frequent
69 in Old World monkeys (van Schaik and Janson 2000; van
70 Schaik et al. 1999).

71 On a proximate level, losing an offspring prematurely
72 leads to early resumption of cycling and females conceiving
73 sooner (van Schaik and Janson 2000). This makes a time
74 gain and with it improved reproductive performance for
75 infanticidal males all the more likely. Seasonal breeding
76 does not annul these effects as long as interbirth intervals
77 after surviving infants span more than 1 year (e.g.,
78 Bellemain et al. 2006; Borries 1997; Lewison 1998). Even
79 in annual breeders where the interbirth interval cannot be
80 abbreviated, increased chances of conception or improved
81 infant survival are reported or suspected (Enstam et al.
82 2002; Pereira and Weiss 1991; Wright 1995). These effects
83 can improve the reproductive output of infanticidal males.

84 In primates, infanticide is common in one-male groups
85 following male takeovers (van Schaik and Janson 2000),
86 when incoming males are almost certainly unrelated to any
87 infants in the groups. But infanticide has also been
88 documented in primate multimale groups, both by newly
89 immigrant and maturing natal males (e.g., Hanuman
90 langurs, Borries 1997; red howler monkeys, Crockett and
91 Janson 2000; sooty mangabeys, Fruteau et al. 2010; chacma
92 baboons, Palombit et al. 2000; and Japanese macaques,
93 Soltis et al. 2000). The past mating history with the infants'
94 mothers is the most likely proximate mechanism for males
95 in assessing paternity probability for infants present or born
96 in the groups (Borries et al. 1999b; Hrdy 1979; van Schaik
97 2000).

98 In contrast to unrelated males, females do not gain when
99 their infants are killed. They lose offspring for which the
100 replacement requires extra time and energy which makes
101 the evolution of countertactics very likely (Agrell et al.
102 1998; Clarke et al. 2009). For example mothers, and also
103 other females and older resident males, could defend the
104 infants (Borries et al. 1999b; Fruteau et al. 2010; Gray
105 2009; Soltis et al. 2000). Females could preferentially stay
106 in the vicinity of potential defenders, as reported for ursine
107 colobus monkeys (Teichroeb and Sicotte 2008), and
108 reliance on male protection might explain male–female
109 friendships in chacma baboons (Palombit et al. 2000).
110 Alternatively, females could leave the group together with
111 their infants following a takeover (African lions, Packer and
112 Pusey 1983 and purple-faced leaf monkeys, Rudran 1973).
113 However, this option is rare in primates and in most cases
114 in which females emigrated following takeovers, they did
115 so without infants (Sterck and Korstjens 2000). More
116 generally, phylogeny and ecology constrain female dispersal

options (Isbell 2004), and it might not be possible to live
117 solitarily or without an adult male. Group splitting might
118 then be an option, as in the case of Hanuman langurs. In this
119 female philopatric species, a group may split after male
120 immigration so that females without infants stay with the
121 immigrant male and females with infants leave with the
122 former resident male (Sugiyama 1965; Winkler et al. 1984).
123

124 Female countertactics also depend on infant age (Sterck
125 et al. 2005). If the infant is old enough to survive on its
126 own, it could be left behind (Thomas' langurs, Sterck
127 1997). A less drastic option is to wean the infant abruptly,
128 even prematurely, without necessarily abandoning it (as in
129 ursine colobus monkeys, Teichroeb and Sicotte 2008). This
130 might lead to suboptimal nutritional conditions early in life
131 that translate into low weaning weight, low resistance to
132 diseases, and increased mortality (Molbak et al. 1994). It
133 might even result in significant differences in life spans,
134 reproductive rates, and lifetime reproductive success
135 (baboons, Altmann 1998). Infants too young to be weaned
136 will put additional constraints on their mothers. To avoid
137 exposing their infants to unrelated adult males, these
138 females should leave with their infants. They could remain
139 with the presumed fathers because these males might
140 protect the infants (Hrdy 1974); but this seems to be rare
141 (Sterck and Korstjens 2000). Pregnant females may resume
142 proceptivity and mate with immigrant males to conceal
143 paternity (van Schaik et al. 1999). Evidence for the success
144 of this tactic is mixed: in Hanuman langurs, the mating
145 pattern of pregnant females does not depend on the identity
146 of the males (Sommer 1994). Once born, infants may be
147 attacked by non-fathers even if they had mated with the
148 mothers during pregnancy (Borries et al. 1999b).

149 Occasionally, an increased rate of abortions or miscar-
150 riages is reported following male takeovers (Hanuman
151 langurs, Agoramorthy et al. 1988; Sommer 1994; geladas,
152 Beehner and Bergman 2008; Fashing et al. 2009; and
153 Hamadryas baboons, Colmenares and Gomendio 1988).
154 However, due to the relatively high reproductive costs to
155 the female, this response is assumed to be rare in primates
156 (van Schaik et al. 1999) and reports center on only a few
157 species. In sum, theoretical considerations and available
158 evidence suggest that infant age and female reproductive
159 state at the time of a takeover (mediated by constraints on
160 dispersal) are likely to determine female countertactics.

161 Concerning infanticide in primates, the subfamily Colo-
162 binae, particularly the Asian group, has played a prominent
163 role: one of the first published cases of witnessed
164 infanticide in primates (Hanuman langurs, Mohnot 1971;
165 Sugiyama 1965) and one of the first evolutionary
166 approaches to explain the phenomenon (the sexual selection
167 hypothesis, Hrdy 1974) refer to this taxon. Colobines are
168 typically folivorous, and infanticide may be especially
169 frequent in folivorous primates, in which small one-male

170 groups are much more common than in more frugivorous
 171 species (Janson and van Schaik 2000). Paternity probability
 172 in these small one-male groups can be very high (100% in
 173 Hanuman langurs, Launhardt et al. 2001) so that new
 174 immigrant males can be rather certain that the infants
 175 present in the groups are not their offspring (Borries et al.
 176 1999a). Infanticidal males sired the next offspring of the
 177 victims' mothers in a Hanuman langur population studied
 178 by Borries et al. (1999a). Indeed, infanticide by males
 179 seems to be a regularly occurring phenomenon in Asian
 180 colobines. The actual killing of an infant has been observed
 181 in black-and-white snub-nosed monkeys (Xiang and
 182 Grueter 2007), golden snub-nosed monkeys (Zhang et al.
 183 1999), Hanuman langurs (Newton 1988; Sommer 1994),
 184 and Proboscis monkeys (Agoramoorthy and Hsu 2005).
 185 Witnessed cases for African colobines stem from red
 186 colobus monkeys (Struhsaker and Leland 1985), black-
 187 and-white colobus monkeys (Onderdonk 2000), and ursine
 188 colobus monkeys (Teichroeb and Sicotte 2008). Further-
 189 more, suspected cases for which only parts of the sequence
 190 were witnessed are reported for silvered leaf monkeys
 191 (Wolf and Fleagle 1977), purple-faced leaf monkeys
 192 (Rudran 1973), and Thomas' langurs (Sterck 1997). In
 193 most cases, males were observed to attack infants or infants
 194 disappeared shortly after new males immigrated into the
 195 groups. Infanticide by males accounts for 30% to 70% of
 196 the infant mortality in these populations and is assumed to
 197 be a major influence on reproductive tactics and reproduc-
 198 tive success for both males and females.

199 Here we investigated the circumstances of infant
 200 disappearances in connection with male takeovers in female
 201 philopatric white-headed leaf monkeys (*Trachypithecus*
 202 *leucocephalus*) predominantly living in one-male groups.
 203 We estimated potential costs to females by comparing
 204 weaning ages and length of interbirth intervals following
 205 male takeovers to values for these variables during periods
 206 of stable male tenure, proceeding from the assumption that
 207 the conditions during stable periods are optimal. We
 208 examined if the presence of an infant and its age had an
 209 influence on female countertactics, predicting that
 210 females (1) without infants stayed with the new males;
 211 (2) those with old infants weaned the infants abruptly,
 212 the infants survived, and the mothers stayed with the new
 213 males; (3) and those with young infants remained with
 214 the old male, at least until their infants were weaned.
 215 Predictions for pregnant females could not be examined
 216 because those largely depend on mating behavior, which
 217 was not documented systematically. It therefore is
 218 unclear whether paternity could be confused and thus
 219 whether pregnant females are expected to stay with the
 220 new males or the old males. Finally, we investigated if in
 221 the study population the conditions of the sexual
 222 selection hypothesis were met.

Materials and methods

223

Study site

224

225 A population of white-headed leaf monkeys was studied at
 226 the Nongguan site within the Nongguan Nature Reserve
 227 (22°15–17' N, 107°29–32' E, 150–430 m a.s.l.), Chongzuo
 228 county, Guangxi Zhuang Autonomous Region, China. The
 229 climate is mild but seasonal. The mean annual temperature
 230 is 22.8°C, and the mean annual precipitation is 1,152 mm
 231 (details in Jin et al. 2009a, b). The site consists of about
 232 22 km² karstland dominated by limestone hills. Much of the
 233 original subtropical, deciduous, broadleaf forest growing on
 234 the limestone hills has been replaced by secondary shrub
 235 vegetation (up to 5 m in height). Lowland areas and valleys
 236 are farmland. There are no villages in the study area. People
 237 use the hills to collect firewood and to catch small animals
 238 (e.g., snakes or squirrels). The leaf monkeys were rarely
 239 seen close to people, the farmland or villages. Crop raiding
 240 was never observed. Hunting of monkeys and other animals
 241 had been common in the past but has been prohibited since
 242 1998 (Jin et al. 2009b). Extant predators include leopard
 243 cats (*Felis bengalensis*), Asiatic golden cats (*Felis*
 244 *temmincki*), yellow-throated martens (*Martes flavigula*),
 245 and golden eagles (*Aquila chrysaetos*). Locally extinct are
 246 tigers (*Panthera tigris*), leopards (*Panthera pardus*), and
 247 clouded leopards (*Neofelis nebulosa*). Predator densities
 248 are assumed to be low based on the rarity of sightings but
 249 no systematic data are available. The species mentioned
 250 here would all be capable of preying at least on juvenile
 251 leaf monkeys even though we never witnessed such an
 252 event and predator pressure is assumed to be low.

Study population

253

254 The leaf monkeys inhabit several of the limestone hills
 255 in the northern part of the reserve (see Fig. 1 in Jin et al.
 256 2009b: 207). Each group occupied one or several hills
 257 with very little overlap between home ranges of adjacent
 258 bisexual groups. On occasion, individuals use ridges to
 259 cross the farmland between hills. With 88.3% of the mean
 260 annual feeding time spent on leaves, the degree of
 261 folivory is comparatively high (Yin et al., unpublished
 262 data).

263 The majority of the bisexual groups (96.3%) were one-
 264 male multifemale while multimale groups were rare (3.7%,
 265 calculated from Jin et al. 2009b). Similar proportions are
 266 reported for another population of the same species (Li and
 267 Rogers 2004). Furthermore, 21.9% of all adult males in the
 268 population lived in so called non-reproductive groups
 269 mainly composed of males of different ages (except infants)
 270 and a few immature (but no adult) females (Jin et al.
 271 2009b).

272	Although infants have been born during all months of	321
273	the year, births were distributed unevenly throughout the	322
274	year and 82.0% of all births occurred from December	323
275	through March (Jin et al. 2009a). Thus, most conceptions	324
276	must have occurred between June and September based on	325
277	an estimated gestation length of 6 months. This value was	326
278	determined for captive Francoise leaf monkeys (<i>Trachypithecus</i>	327
279	<i>francoisi</i>), a closely related species (184 days; $N=16$, Mei	328
280	1991). If gestation would, however, be closer to 200 days (i.e.,	329
281	almost 7 months) as reported for other wild Asian colobines	330
282	(Borries et al. 2011), then the conception peak would last	331
283	from May to August instead.	332
284	Study periods, data collection, and sample sizes	333
285	A total of 28 groups have been studied by several observers	334
286	(see acknowledgements) from 1995 through 2006 for	335
287	varying durations (Jin et al. 2009b). Takeover frequency	336
288	and its annual distribution, the percentage of partial take-	337
289	overs, and the duration of male tenure (definitions below)	338
290	were calculated based on this largest possible dataset. All	339
291	other results are based on a subsample of 11 groups, which	340
292	have been studied for 3 to 11 years (47 group-years total)	341
293	and group members were individually distinguished. Each	342
294	month these groups were followed for at least 10 days	343
295	(mean=18.4±5.8SD; range=10–28) and births, deaths,	344
296	disappearances, and nipple contact were recorded for all	345
297	contact days.	346
298	In the course of the study 11 takeovers by adult males	347
299	(definition below) could be documented. Detailed data were	348
300	available for five of these takeovers, which occurred in four	349
301	groups. These concerned 34 individual adult females and	350
302	their 29 infants. For 17 females, the following births could	351
303	also be documented. Three females with old infants were	352
304	pregnant at the time of the takeover and thus enter the	353
305	analysis twice (in relation to the old and the new infant).	354
306	For comparison, we also present data (weaning age and	355
307	interbirth interval) during stable tenures for the same	356
308	groups.	357
309	Definitions	358
310	<i>Age class</i> definitions follow Rajpurohit et al. (1995) and Jin	359
311	et al. (2009b) although, the present analysis only deals with	360
312	infants and adults (fates of juveniles will be presented	361
313	elsewhere). Leaf monkeys were classified as infants as	362
314	long as they had nipple contact (mean 19.2 months, Zhao	363
315	et al. 2008). At the time of takeovers we furthermore	364
316	distinguished <i>young</i> infants (4–14 months) from <i>old</i>	365
317	infants (16+ months) based on the bimodal distribution	366
318	of infant age due to seasonal breeding. From age 5 years	367
319	onward females were considered adult (mean age at first	368
320	reproduction 5.4 years, Jin et al. 2009a). Larger males who	369
	had not reached the full head–body length or the shoulder	370
	width of an adult male were classified as sub-adults. Adult	371
	males had the maximum head–body length and shoulder	
	width.	
	Following Sterck (1998), a <i>takeover</i> occurred when the	
	former resident adult male of a bisexual group was ousted	
	by another male. Unsuccessful takeovers not resulting in	
	permanent group membership changes were rare (assumed	
	twice based on aggressive interactions between males) and	
	were not considered here. We distinguished the <i>old male</i>	
	(residing with the females prior to the takeover) from the	
	<i>new male</i> (challenging the old male and finally taking	
	over). Note that in all cases the new males appeared to be	
	noticeably younger than the old males even though the “old	
	males” were not necessarily past their prime.	
	A takeover was considered <i>complete</i> if all adult females	
	stayed with the new male once the old male was ousted. In	
	<i>partial</i> takeovers, most females stayed with the new male,	
	but at least one female left together with the old male. <i>Male</i>	
	<i>tenure length</i> encompassed the time period during which an	
	adult male lived with at least one adult female who was not	
	born during his tenure (Sterck et al. 2005). It was calculated	
	to the month.	
	The <i>weaning age</i> was calculated from the month of birth	
	to the month when nipple contact was last observed	
	(inclusively). The <i>interbirth interval</i> lasted from the month	
	of parturition until the month of the next birth. To	
	approximate female reproductive costs, we calculated the	
	interbirth interval back to the female’s last infant that	
	survived its first year of life. Consequently, if an infant was	
	lost prematurely (i.e., during its first year) its birth was not	
	considered resulting in a comparatively long interval. To	
	avoid confusion we introduce the abbreviation <i>IBI-S</i> for this	
	measure (with <i>S</i> for surviving infants). The longer the <i>IBI-S</i>	
	the higher female reproductive costs. Due to the intermit-	
	tent nature of our observations, weaning age and <i>IBI-S</i>	
	were calculated to the month.	
	Data analyses	
	Weaning ages and <i>IBI-S</i> following takeovers were tested	
	against the control condition during stable male tenures	
	with a Kruskal–Wallis test and a post hoc test based on the	
	α -level reached by the Kruskal–Wallis test (Siegel and	
	Castellan 1988). Infant survival in relation to maternal	
	tactics as well as the sex ratio of presumed infanticide	
	victims compared with the birth sex ratio was tested with a	
	Fisher’s exact test. Annual distributions of infant dis-	
	appearances and takeover events were tested with	
	circular statistics (Batschelet 1981). Tests were performed	
	in STATISTICA 6.1 (© StatSoft Inc. 1984–2003), and R	
	2.12.0 using CircStats 0.2–4, and the post hoc test was	
	calculated by hand.	

372 **Results**

373 Male takeovers

374 Of the 11 male takeovers, ten occurred in one-male groups
 375 and one in a non-reproductive group (see below). Take-
 376 overs were not evenly distributed throughout the year and
 377 the majority (ten of 11; 90.9%) took place from May
 378 through August (Fig. 1; $r=0.761$, $P<0.001$, Rayleigh test of
 379 uniformity, Batschelet 1981). Thus, most new males took
 380 over at the beginning of the conception period. Note that
 381 the match of takeovers with the peak conception period is
 382 improved if the latter is calculated based on 7 months of
 383 gestation instead of six. Perhaps as a consequence of this
 384 general timing only three (i.e., 12.0%) of the females likely
 385 to conceive in the given season (those with no infants or old
 386 infants, $N=25$), or 8.8% of all 34 females, were already
 387 pregnant at the time of the takeover.

388 A takeover occurred every 50.1 group-months on
 389 average (range, 29–63; $N=9$). When a new male entered
 390 the home range of a bisexual group, the old and the new
 391 males chased and fought each other, often with high
 392 intensity and frequent physical contact. Injuries were
 393 common, but we did not witness male deaths during these
 394 interactions. In all cases the old male was ousted within less
 395 than 2 months. Females were not involved in agonistic
 396 interactions between the males and it did not seem as if
 397 either of the males aggressively targeted them or their
 398 infants. Ousted males withdrew from their groups' home
 399 ranges while the new males stayed.

400 One takeover occurred in a non-reproductive group
 401 composed of an older adult male and his presumed
 402 offspring: a young adult male, five subadult males, and
 403 three young, nulliparous females. These ten individuals had
 404 previously split off together from a bisexual group after a
 405 takeover (Jin et al. 2009b; Zhao and Pan 2006). When a

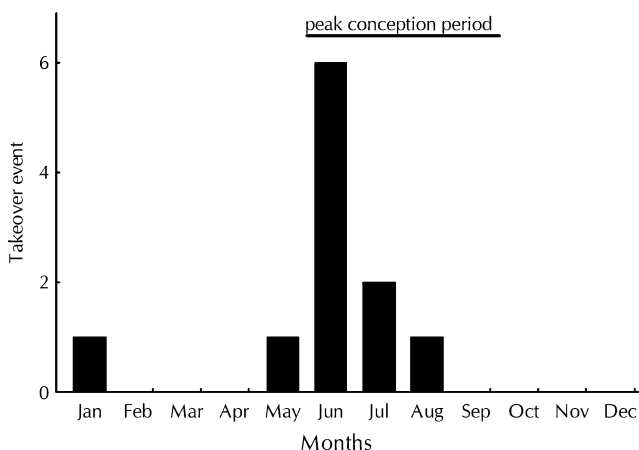


Fig. 1 Annual distribution of male takeovers; plotted are months when takeovers began

new adult male invaded, the old male and his presumed
 oldest adult son often fought him cooperatively. Once
 defeated, they both disappeared while the subadult males
 began to move about independently as all-male band. The
 three nulliparous females stayed with the new male.

Although the exact origin of the new males was
 unknown, they were neither residents in neighboring
 groups nor maturing natal males. In most cases ($N=10$)
 the new males came alone. Only once (in group SHY) did
 an all-male band of four adult males jointly attack the old
 male. After the old male was ousted, the group was
 multimale for 12 months. Thereafter only one adult male
 remained with the group (Jin et al. 2009b).

Five of the takeovers (i.e., 45.5%) were “complete”; the
 other six were “partial”. Male tenureship length in one-male
 groups averaged 54.5 months (range, 34–73; $N=8$) and was
 thus longer than the interval between takeovers (see above)
 because six old males continued to stay with females
 (partial takeovers).

Female tactics

Following a takeover, most females stayed with the new
 males (82.4%, Fig. 2); the rest left the area with the old
 males. Half of the females who initially left later rejoined
 their groups and the new males (Fig. 2). In the following,
 we describe how female reproductive status and infant age

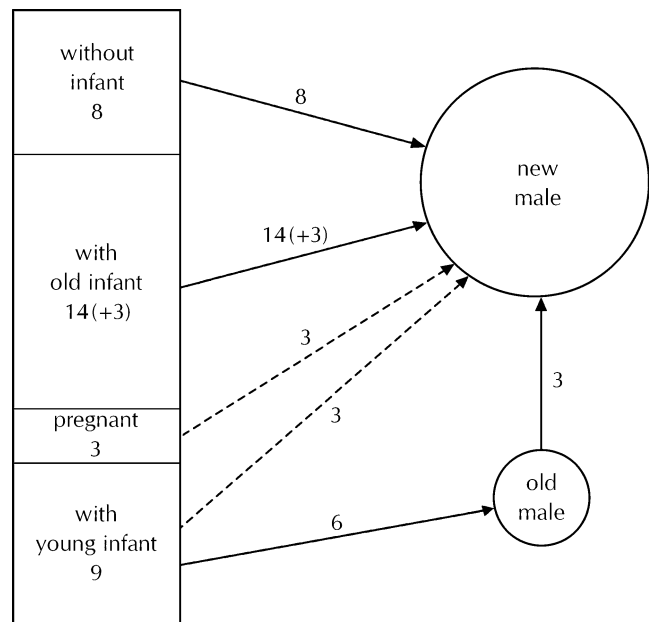


Fig. 2 Females staying with the new or the ousted, old male following takeover (in relation to female reproductive state). The new males stayed in the groups' home range while the old males left the area; numbers represent N adult females; we use 14 (+3) to indicate that three of the 17 females with an old infant were again pregnant and are also represented as pregnant females; *solid arrow*, infant survived or no infant; *hatched arrow*, infant loss

431 might have shaped these female tactics and assess the
432 potential costs in terms of weaning ages and IBI-S.

433 Weaning age and IBI-S following takeovers

434 There were 17 females with old infants present during
435 takeovers (Fig. 2). All weaned their infants (rather abruptly)
436 before the takeover was completed at a mean age of
437 17.7 months. These infants were thus 2.6 months or 12.8%
438 younger than infants weaned during stable tenures (average,
439 20.3 months; Table 1; Fig. 3). All these old infants survived
440 for at least another year. In addition, nine females with
441 young infants experienced a takeover, of which 66.7%
442 ($N=6$) left the groups with their infants and the old males
443 and the infants survived. Three of these six females
444 remained and continued to breed with the old males
445 (Fig. 2). They weaned their infants at a younger age
446 compared with stable tenures (mean=17.7 months; i.e.,
447 2.6 months or 12.8% younger; Table 1; Fig. 3). The other
448 three females later joined the new males (Fig. 2) after they
449 had weaned their infants. With a mean age of 18.3 months,
450 these infants were weaned 2.0 months or 9.9% younger
451 than those weaned during stable tenures (Table 1; Fig. 3).
452 All weaning ages following takeovers differed significantly
453 from those during stable tenures (Kruskal–Wallis test
454 $H_{(3, N=32)}=18.64, P=0.0003$; post hoc test $\alpha<0.001$;
455 significant conditions marked in Fig. 3).

456 Females with old infants had a mean IBI-S of
457 24.9 months, which was very similar to the mean interval
458 during stable tenures (24.5 months, Table 1; Fig. 4).
459 Likewise, females with young infants who continued to

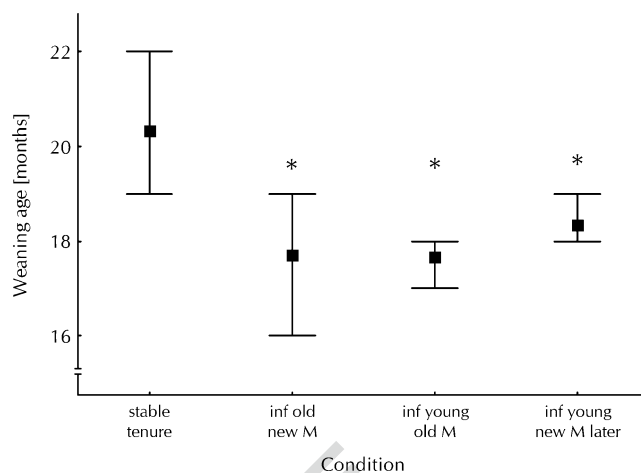


Fig. 3 Mean weaning age under the different conditions; whiskers, range; Asterisk, significantly different from stable tenure (Kruskal–Wallis post hoc test, $\alpha=0.001$); *inf* infant, *M* male

stay and breed with the old males had similar IBI-S (mean, 24.7; Table 1; Fig. 4). However, females with young infants who later rejoined the new males had longer IBI-S (mean=31.0 months, i.e., 6.5 months or 26.5% longer) compared with IBI-S during stable tenures (Table 1; Fig. 4). Of the females with young infants who stayed with the new males, one gave birth with an IBI-S of 32.0 months. This was 7.5 months or 30.6% longer than during stable tenures (Table 1; Fig. 4). Finally, three pregnant females stayed with the new males after takeovers. All lost their infants (details below), resulting in a mean IBI-S of 33.7 months, 9.2 months (or 37.6%) longer than intervals during stable tenures (Table 1; Fig. 4). The lengths of the IBI-S following

t1.1 **Table 1** Female countertactics after male takeover and their potential costs in terms of weaning age (current infant) and interbirth interval (to the last infant surviving 1 year)

Condition	N	Infant age ^a at takeover	Weaning age			IBI-S (to last infant surviving 1 year)			
			Mean (months)	Median (months)	Range (months)	mean (months)	Median (months)	Range (months)	N
With new male	17	Old	17.7	18.0	16–19	24.9	25.0	24–27	7
	3	Young	Infant disappeared			32.0			1
	(3)	(Pregnant)	Infant disappeared			33.7	33.0	33–35	3
	8 ^b	No infant							
With new male (later only) ^c	3	Young	18.3	18.0	18–19	31.0	32.0	27–34	3
With old male ^c	3	Young	17.7	18.0	17–18	24.7	25.0	24–25	3
Stable tenure	9		20.3	20.0	19–22	24.5	24.5	24–25	4

Pregnant females in parentheses because they had an unweaned old infant at the time of the takeover too and are thus mentioned twice. For test results see text

^a Infant age: old=16–19 months; young=4–14 months; pregnant=1–3 months after conception based on the subsequent birth observed

^b For these eight females, future reproduction could not be documented (three were nulliparous, adults, and for the other five pluriparous females the takeover took place close to the end of the study period)

^c Initially stayed with the old male

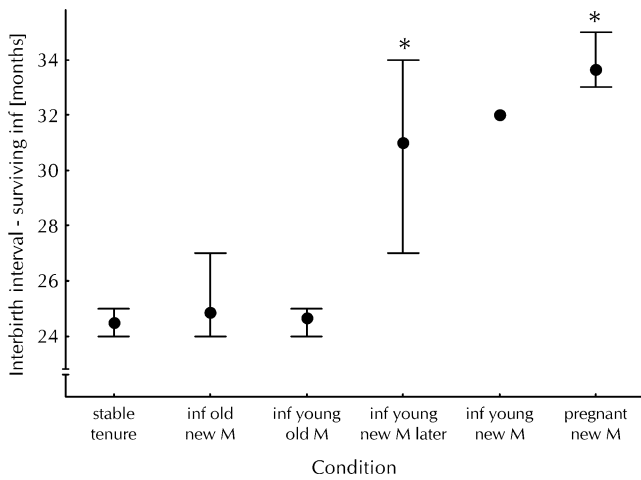


Fig. 4 Mean interbirth interval after a surviving infant under the different conditions; *whiskers* range; *Asterisk*, significantly different from stable tenure (Kruskal–Wallis post hoc test, $\alpha=0.02$); *inf* infant, *M* male

473 takeovers differed significantly from those during stable
474 tenures (Kruskal–Wallis test $H_{(4, N=20)}=12.86$; $P=0.012$;
475 post hoc test $\alpha<0.02$; significant conditions marked in
476 Fig. 4; the condition resulting in a single IBI-S was
477 excluded from the test).

478 **Infant loss and presumed infanticides**

479 Of the 17 old infants weaned abruptly after takeovers, three
480 remained with their mothers and the new males and
481 survived. The other 14 dispersed without their mothers
482 and survived. All six young infants who stayed with their
483 mothers and the old males survived, whereas the three
484 young infants who stayed with their mothers and the new
485 males disappeared within 2 weeks after the old males had
486 been ousted, at a mean age of 7.0 months (cases 4, 7, and 8,
487 Table 2). Survival of young infants thus significantly
488 depended on the females' dispersal decision (Fisher's exact

test, one-tailed; $P=0.012$). One of these infants (NY) was
twice exposed to new males within a few weeks. Initially,
when the new male (ZHI) immigrated, the mother and
infant left with the old male. When the old male was again
ousted by yet another male (CID), the mother and infant
rejoined the infant's natal group, where new male ZHI
resided. He attacked the infant, but it survived (case 3 in
Table 2; see also Wang 2004). Next, the mother and infant
rejoined the male who had ousted the old male the second
time (CID). He was once observed stalking the infant (case
4), which disappeared the following day.

Three infants were born into groups with new males
within 3–5 months after takeovers. Based on a 6-month
gestation period, the females must have been pregnant at
the time of the takeovers (cases 1, 2, and 6, Table 2). All
three infants disappeared within 1–3 months after birth
(mean=1.7 months). Another young infant (NP, case 5
Table 2), whose mother was not pregnant, was attacked at
the age of 9 months and survived (Wang 2004).

The eight cases described in Table 2 took place in three
different one-male groups after the old males had been
ousted. Four different males were suspected of infanticide.
In the two cases for which we had observations, the infants'
mothers defended or rescued the infants either by fleeing
the approaching males (thus carrying the infants away) or
by attacking them. Other females joined in the defense.
Whether female defense delayed infanticide cannot be
decided. In three cases, males were observed to stalk and/
or attack infants; this includes the one case when the male
was observed to bite and injure the infant at the neck (case
3; Wang 2004). It survived the attack but disappeared later
(as described above, cases 3 and 4, Table 2). In five of the
eight cases, the timing of infant disappearance in relation to
a recent male takeover was the main reason we inferred
infanticide by males.

Infants were between 1 and 8 months of age (mean=
4.3 months; $N=6$) when they disappeared. At least five of

t2.1 **Table 2** Circumstances under which infants were attacked or stalked by new males and infant disappearances following a takeover (cases in chronological order per infant)

t2.2	Case	Infant name	Infant sex	Infant age at takeover (months)	Date of event/ observation	Infant age at death/ disappearance (months)	Male name	Male observed to	Females defend/rescue	Infant seen with injuries	Infant fate
t2.3	1	K1	?	Unborn	Feb 2001	1	ZLP		?	No	Disappeared
t2.4	2	K2	M	Unborn	Apr 2001	3	ZLP		?	No	Disappeared
t2.5	3	NY	M	7	Sep 24, 2002	Survived	ZHI	Attack and stalk	Yes	Yes	Survived
t2.6	4	–	–	–	Oct 01, 2002	7	CID	Stalk	Yes	No	Disappeared
t2.7	5	NP	M	9	Sep 26, 2002	Survived	ZHI	Attack and stalk	?	No	Survived
t2.8	6	NQ	?	Unborn	Feb 2003	1	CID		?	No	Disappeared
t2.9	7	NA	M	8	Sep 2006	8	XS		?	No	Disappeared
t2.10	8	NE	M	6	Sep 2006	6	XS		?	No	Disappeared

526 the seven suspected targets were males (71.4%), a ratio that
 527 did not differ significantly from the significantly biased
 528 birth sex ratio of 59.8% male in the study population (Zhao
 529 et al. 2009) ($N=122$, Fisher's exact test, one tailed; $P=$
 530 0.427). During our study period, 14 infants disappeared
 531 prior to weaning. If the six cases of presumed infanticide
 532 were indeed infanticides, infanticide would account for
 533 42.9% of infant mortality. Unfortunately, no further
 534 comparisons were possible because causes of death were
 535 not known for the study population. Population wide,
 536 15.0% of the infants did not survive their first year of life
 537 (Jin et al. 2009a). If these data were analyzed separately for
 538 stable tenures and takeovers, infant mortality during stable
 539 tenures was 7.2% (8 out of 111 infants) and thus
 540 significantly lower than the 54.5% after takeovers (six of
 541 11 infants; one young infant already older than 12 months
 542 of age excluded here; Fisher's exact test, one tailed; $P<0.003$).
 543 Despite the fact that takeovers occurred mainly during the
 544 peak conception season, infant disappearances were
 545 distributed evenly throughout the year ($r=0.118$; $P<0.831$,
 546 Rayleigh test of uniformity, Batschelet 1981, data not
 547 shown). This refers to all infant disappearances (the number
 548 of losses following takeover was too small to be tested
 549 independently).

550 **Discussion**

551 Due to the small sample size (six infants disappeared after a
 552 takeover) and the fact that infanticides were only presumed,
 553 the results need to be treated with caution, although
 554 additional supporting evidence such as attacks and stalking
 555 of infants by males were also observed (Table 2). If all
 556 presumed infanticides were indeed infanticides, the impact
 557 exceeded 40% of the infant mortality in the study
 558 population and more than 50% of infants experiencing
 559 takeovers in their first year of life did not survive. A similar
 560 or even higher impact of infanticide on infant mortality has
 561 been reported for other primate species, including both
 562 folivores (Hanuman langurs: 31–44%, Borries and Koenig
 563 2000; red howler monkeys: 44–85%, Crockett and Janson
 564 2000; red colobus monkeys: 30.0%, Struhsaker and Leland
 565 1985; ursine colobus monkeys: 71.4%, Teichroeb and
 566 Sicotte 2008) and non-folivores (geladas: 57.2%, Beehner
 567 and Bergman 2008; white-handed gibbons: 83.3%, Borries
 568 et al. 2010; white-faced capuchins: 60.9%, calculated from
 569 Fedigan 2003; see also compilation in Janson and van
 570 Schaik 2000). These high proportions can be stable if
 571 overall infant mortality is low (e.g., red colobus monkeys
 572 and our study) or reproductive rates are high (e.g., some
 573 *Semnopithecus* populations) but may threaten the survival
 574 of small populations (cetaceans: Patterson et al. 1998). The
 575 high proportion of infanticides on infant mortality further-

576 more emphasize the evolutionary importance and the 576
 577 potential impact of infanticide on male and female 577
 578 reproductive success (Agrell et al. 1998; Ebensperger 578
 579 1998; Hrdy 1979). 579

580 Infanticide in white-headed leaf monkeys 580

581 The circumstances under which presumed infanticides 581
 582 occurred at our site fit the conditions proposed under the 582
 583 sexual selection hypothesis (e.g., Hrdy 1979). Firstly, new 583
 584 males were probably not related to the victims because they 584
 585 were neither former residents in neighboring groups nor 585
 586 natal males. Furthermore, extra-group copulations have 586
 587 never been observed and are at most rare, perhaps because 587
 588 of the small home range overlap, excellent visibility, and 588
 589 low intruder pressure (low number of extra-group males, 589
 590 Jin et al. 2009b). This will result in high paternity 590
 591 probability for resident males and very low probability for 591
 592 new immigrant males. Unfortunately, however, no paternity 592
 593 data are available for the study population or a closely 593
 594 related species. But in one-male groups of Hanuman 594
 595 langurs at Ramnagar, the old males sired all infants while 595
 596 new males were unrelated to the infants in the groups 596
 597 (Borries et al. 1999a; Launhardt et al. 2001). Second, 597
 598 premature loss of an infant significantly accelerated the 598
 599 subsequent birth generally (Jin et al. 2009a); this holds 599
 600 specifically for infants lost due to presumed infanticide 600
 601 (mean interval till next birth: 10.5 months; range, 8–16; $N=4$). 601
 602 Infanticidal males can thus gain time by reproducing sooner 602
 603 with the mothers. Lastly, the new males' chances of siring 603
 604 the subsequent infants of the victims' mothers must be rated 604
 605 as very high due to the long male tenure (average, 605
 606 54.5 months) with even the shortest tenure lasting 34 months. 606
 607 Given the presumed high paternity certainty, the new male is 607
 608 likely to father most if not all infants in a group and thus to 608
 609 benefit by infanticide, as in Hanuman langurs at Ramnagar 609
 610 (Borries et al. 1999a). 610

611 Seasonal breeding did not prevent infanticide, which is 611
 612 in accordance with data on some other seasonally breeding 612
 613 primates (Borries 1997; Lewison 1998; Pereira and Weiss 613
 614 1991; Soltis et al. 2000). This is likely because premature 614
 615 infant loss almost always provides a reproductive advantage 615
 616 to males either in terms of subsequently improved infant 616
 617 survival or faster breeding with the infants' mothers. In this 617
 618 connection the timing of male takeovers in the study 618
 619 population seems important: takeovers mainly occurred 619
 620 early in the mating season (Fig. 1), when chances were high 620
 621 that most if not all females would still be cycling. In other 621
 622 seasonally breeding primates, a similar concentration of 622
 623 male dispersal events occurred prior to the mating season 623
 624 (sifakas, Morelli et al. 2009) or during the mating season 624
 625 (Hanuman langurs, Borries 2000; guenons, Cords 2000; 625
 626 Japanese macaques, Sugiyama and Ohsawa 1974). 626

627 Estimating costs of female countertactics

628 A younger weaning age may indicate suboptimal postnatal
 629 maternal investment and thus be costly. Nutritional con-
 630 ditions early in life can be strong predictors for lifetime
 631 reproductive success, as has been shown for baboons
 632 (Altmann 1998). Furthermore, prolonged breast feeding in
 633 humans improved the infants' resistance to intestinal
 634 problems and significantly lowered infant mortality
 635 (Molbak et al. 1994).

636 As a composite measure of infant survival and speed of
 637 reproduction, the IBI-S provides information about any
 638 costs in terms of time and energy lost due to failed
 639 reproduction. Costs associated with increased IBI-S should
 640 typically be more severe than any due to early weaning,
 641 especially given seasonal breeding.

642 *Females without infants* Following male takeovers, all
 643 females without infants stayed with the new males.
 644 Unfortunately, however, costs could not be determined as
 645 the IBI-S were not known: three females were nulliparous
 646 and the other five experienced the takeover at the end of the
 647 study period. Conception delays were unlikely, however,
 648 because females in a comparable physiological state (those
 649 with old infants) had average-length IBI-S following a
 650 takeover (Fig. 4). Breeding delays with a new male are also
 651 absent in mountain gorillas (Robbins et al. 2009) but
 652 significant in Thomas langurs (Sterck et al. 2005) and lions
 653 (Packer and Pusey 1983).

654 *Females with old infants* Staying with the new male and
 655 weaning a current infant abruptly was the tactics employed
 656 by all 17 females with old infants (Figs. 2 and 3); all these
 657 infants survived. To our knowledge, this is one of the first
 658 times that significantly younger weaning ages after take-
 659 overs have been documented. Most studies of mating
 660 behavior following male takeovers in primates have not
 661 included information on the cessation of nipple contact (e.g.,
 662 Colmenares and Gomendio 1988; van Schaik et al. 1999).
 663 One case is reported for wild ursine colobus monkeys and
 664 the infant survived despite being weaned at 7 months of age
 665 (Teichroeb and Sicotte 2008).

666 The youngest of the abruptly weaned old infants was
 667 16 months old (Table 1). This is apparently an age at
 668 which white-headed leaf monkeys can survive without
 669 nipple contact even if they are still significantly younger
 670 than infants weaned during stable tenures (Fig. 3).
 671 However, we could not detect any adverse effects
 672 following this shorter postnatal maternal investment and
 673 costs for females were rated as low (Table 3). We note,
 674 however, that no data on the infants' performances later in
 675 life (such as age at first reproduction, reproductive rate or
 676 survival) are available.

677 At 16 to 19 months of age, these old infants were 677
 678 considerably older than most monkey targets of infanticide 678
 679 (van Schaik 2000). Older targets are also reported for the 679
 680 seasonally breeding Hanuman langurs at Ramnagar (up to 680
 681 21 months, Borries 1997), where the IBI following a 681
 682 surviving infant was also comparatively long (32 months, 682
 683 Borries and Koenig 2000), so that even the death of an 683
 684 older infant would shorten the time till next conception. 684
 685 However, the oldest infant attacked in our study was only 685
 686 9 months old (infant NP, Table 2; details below), much 686
 687 younger than the infants weaned abruptly. Rather than 687
 688 providing protection from infanticide, the termination of 688
 689 nipple contact in old infants might mainly signal resump- 689
 690 tion of cycling to the new male. Comparison of a new 690
 691 male's behavior towards receptive females with or without 691
 692 nursing infant would clarify this issue. 692

693 The mean IBI-S value for females with old infants was 693
 694 similar to that for intervals during stable periods (Table 1; 694
 695 Fig. 3); in combination with the younger weaning age, the 695
 696 total costs of takeovers for these females were thus low 696
 697 (Table 3). The ursine colobus female who weaned her 697
 698 infant at 7 months had an IBI-S of 17 months compared 698
 699 with the average of 22 months (Teichroeb and Sicotte 699
 700 2008). However, this population breeds year round, so the 700
 701 resumption of cycling should be much less restricted than 701
 702 in our study population. 702

703 *Females with young infants and pregnant females* Most 703
 704 females with young infants at the time of takeovers left 704
 705 with the old males, the presumed fathers of the infants. 705
 706 The infants survived but were weaned at a significantly 706
 707 younger age than infants weaned during stable tenures. 707
 708 Early weaning presumably imposes low costs on the 708
 709 mothers who did not face extra costs in terms of IBI-S if 709
 710 they stayed and reproduced with the old males. However, 710
 711 if they joined the new males later, costs were high 711
 712 despite infant survival. In fact, these were the only 712
 713 females experiencing costs in weaning age as well as 713
 714 IBI-S. They joined the new male 7–8 months prior to the 714
 715 next parturition. Based on a 6–7 months gestation period, 715
 716 the new male is likely to have sired the next infant with 716
 717 very little delay. The long IBI-S mainly resulted from the 717
 718 time spent with the old males. Perhaps, as assumed for 718
 719 Thomas' langurs (Sterck 1997), females remaining with a 719
 720 defeated male delay the next conception until after 720
 721 dispersal. Alternatively, only females who did not con- 721
 722 ceive again left the old males while those who conceived 722
 723 stayed on. Data on female reproductive hormone levels 723
 724 and mating behavior could address these alternative 724
 725 explanations. What remains unclear is why females 725
 726 leaving with the old males still weaned their infants 726
 727 sooner than during stable tenures (at the same age as the 727
 728 abruptly weaned old infants), particularly because subse- 728

Table 3 Rating of estimated costs for the different female countertactics (relative to stable tenures)

	Infant present/infant age	Female	Costs weaning		Costs IBI-S		Overall rating of costs	Infant loss
			Months	Rating	Months	Rating		
t3.4	Pregnant ^a	With new male			+9.2	H	H	Yes
t3.5	Yes/old	With new male	-2.6*	L	+0.4	0	L	No
t3.6	Yes/young	With new male			+7.5	H	H	Yes
t3.7	Yes/young	Disperse With old male	-2.6*	L	+0.2	0	L	No
t3.8	Yes/young	Disperse with old male and with new male later	-2.0*	L	+6.5	H	L+H	No

0 average, L low, H high

^a At the time of the takeover, these three pregnant females had an old infant which they weaned abruptly; both their infants, i.e., the old one and the still unborn were included in the analysis

729 quent conceptions did not occur sooner. Early weaning
730 could have been a precaution in case the old males who
731 had already been ousted once were overthrown again by
732 another new male.

733 In contrast to the predictions, three females with
734 young infants remained with the new males after take-
735 overs, as did the three pregnant females. All lost their
736 infants and had longer IBI-S than those during stable
737 tenures, and thus experienced high costs. While it is
738 generally true that chances for surviving a takeover are
739 low for young infants (van Schaik 2000), the loss of all
740 these infants suggests high paternity certainty. Overall,
741 more than half of the infants experiencing a takeover
742 during their first year of life were lost, a 7.6-fold increase
743 in infant mortality compared with stable tenures (54.5%
744 versus 7.2%). High infant mortality following takeovers is
745 also reported for other primate populations (32 times
746 higher in geladas: Beehner and Bergman 2008; 100% in
747 white-handed gibbons: Borries et al. 2010) and African
748 lions (89.5%, Packer and Pusey 1984). Researchers
749 studying other primates have also reported that infants
750 born soon after takeovers were attacked by males and were
751 either seen dead or disappeared (Tana River red colobus
752 monkeys, Marsh 1979; red colobus monkeys, Struhsaker
753 and Leland 1985; ursine colobus monkeys, Teichroeb and
754 Sicotte 2008). Only rarely have all infants survived
755 takeovers (e.g., Yoshida 1968, Hanuman langurs). Overall,
756 pregnant females very rarely disperse (Pusey and Packer
757 1994) even in female dispersal species (Sterck and
758 Korstjens 2000). Still, why do new males behave as if
759 they knew that those infants were unrelated? Similarly, as
760 deduced from sexual interactions, male Hanuman langurs
761 seem to distinguish between female reproductive states
762 (Borries et al. 1999b; Ostner et al. 2006), as do males of
763 other primate species (e.g., chimpanzees, Deschner et al.
764 2004; long-tailed macaques, Engelhardt et al. 2004) and
765 other mammals (brown bears, Bellemain et al. 2006; feral
766 horses, Cameron et al. 2003). In our study population,

767 these questions can be addressed by a detailed study of
768 sexual behavior in connection with hormonal assessments
769 of female reproductive states.
770

Female countertactics and their constraints 771

772 Most adult females stayed with new males immediately
773 following takeovers. The other three initially stayed with the
774 old males, but then joined the new males, which suggests that
775 philopatry is the preferred female option. Philopatry offers
776 advantages in finding food and can provide the chance for kin
777 support in within and between group competition (Isbell
778 2004), but it can also be the result of high dispersal costs
779 (Isbell and van Vuren 1996; Sterck 1998). Possible
780 advantages of kin support within groups have yet to be
781 explored for the study population. However, female-female
782 support is probably not important in between group contests
783 in our study population because females rarely participate in
784 between group encounters (Zhao et al., unpublished data).

785 Females only dispersed when they had young infants
786 and faced threats of infanticide; these attempts to avoid
787 infanticide succeeded. This contrasts with the general
788 dispersal pattern in primate species in which females
789 typically disperse without their infants (Sterck and
790 Korstjens 2000). More recently, however, a few more
791 cases of dispersal to avoid infanticide have been reported
792 (Jack and Fedigan 2009; Morelli et al. 2009; Teichroeb et
793 al. 2009) and previous work has documented other cases
794 of females with infants leaving with an ousted male in
795 Asian colobines (maroon leaf monkeys, Davies 1987;
796 purple-faced leaf monkeys, Rudran 1973; Hanuman
797 langurs, Winkler et al. 1984).

798 Abrupt weaning was the most common, and most
799 successful, low-cost countertactic for infants which were
800 16 months or older at the time of takeovers. Overall, male
801 takeovers led to significant costs in 26.5% cases, while
802 41.2% of females had low costs due to early weaning and

803 32.3% had no costs. That most tactics were associated with
 804 low costs or none could be due to the timing of takeovers in
 805 relation to the breeding season.

806
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823 **References**

825 Agoramoorthy G, Hsu MJ (2005) Occurrence of infanticide among
 826 wild proboscis monkeys (*Nasalis larvatus*) in Sabah, Northern
 827 Borneo. *Folia Primatol* 76:177–179. doi:10.1159/000084380
 828 Agoramoorthy G, Mohnot SM, Sommer V, Srivastava A (1988)
 829 Abortions in free ranging Hanuman langurs (*Presbytis entellus*)
 830 —a male induced strategy? *Hum Evol* 3:297–308. doi:10.1007/
 831 BF02435859
 832 Agrell J, Wolff JO, Yloenen H (1998) Counter-strategies to infanticide
 833 in mammals: costs and consequences. *Oikos* 83:507–517
 834 Alcock J (2001) Animal behavior—an evolutionary approach, 7th
 835 edn. Sinauer Associates, Sunderland
 836 Altmann SA (1998) Foraging for survival: yearling baboons in Africa.
 837 University of Chicago Press, Chicago
 838 Batschelet E (1981) Circular statistics in biology, 1st edn. Academic,
 839 London
 840 Beehner JC, Bergman TJ (2008) Infant mortality following male
 841 takeovers in wild geladas. *Am J Primatol* 70:1152–1159.
 842 doi:10.1002/ajp.20614
 843 Bellemain E, Swenson JE, Taberlet P (2006) Mating strategies in
 844 relation to sexually selected infanticide in a non-social carnivore:
 845 the brown bear. *Ethology* 112:238–246. doi:10.1111/j.1439-
 846 0310.2006.01152.x
 847 Borries C (1997) Infanticide in seasonally breeding multimale groups
 848 of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South
 849 Nepal). *Behav Ecol Sociobiol* 41:139–150. doi:10.1007/
 850 s002650050373
 851 Borries C (2000) Male dispersal and mating season influxes in
 852 Hanuman langurs living in multi-male groups. In: Kappeler PM
 853 (ed) Primate males: causes and consequences of variation in
 854 group composition. Cambridge University Press, Cambridge, pp
 855 146–158
 856 Borries C, Koenig A (2000) Infanticide in Hanuman langurs: social
 857 organization, male migration, and weaning age. In: van Schaik
 858 CP, Janson CH (eds) Infanticide by males and its implications.
 859 Cambridge University Press, Cambridge, pp 99–122
 860 Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999a)
 861 DNA analyses support the hypothesis that infanticide is adaptive
 862 in langur monkeys. *Proc R Soc Lond B* 266:901–904.
 863 doi:10.1098/rspb.1999.0721

Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999b) 864
 Males as infant protectors in Hanuman langurs (*Presbytis* 865
entellus) living in multimale groups—defence pattern, paternity 866
 and sexual behaviour. *Behav Ecol Sociobiol* 46:350–356. 867
 doi:10.1007/s002650050629 868
 Borries C, Savini T, Koenig A (2010) Social monogamy and the threat 869
 of infanticide in larger mammals. *Behav Ecol Sociobiol*. 870
 doi:10.1007/s00265-010-1070-5 871
 Borries C, Lu A, Ossi-Lupo K, Larney E, Koenig A (2011) Primate 872
 life histories and dietary adaptations: a comparison of Asian 873
 colobines and macaques. *Am J Phys Anthropol* 144:286–299. 874
 doi:10.1002/ajpa.21403 875
 Cameron EZ, Linklater WL, Stafford KJ, Minot EO (2003) Social 876
 grouping and maternal behaviour in feral horses (*Equus caballus*): 877
 the influence of males on maternal protectiveness. *Behav Ecol* 878
Sociobiol 53:92–101. doi:10.1007/s00265-002-0556-1 879
 Clarke PMR, Pradhan GR, van Schaik CP (2009) Intersexual conflict 880
 in primates: infanticide, paternity allocation, and the role of 881
 coercion. In: Muller MN, Wrangham RW (eds) Sexual coercion 882
 in primates and humans: an evolutionary perspective on male 883
 aggression against females. Harvard University Press, Cam- 884
 bridge, pp 42–77 885
 Colmenares F, Gomendio M (1988) Changes in female reproductive 886
 condition following male take-overs in a colony of hamadryas 887
 and hybrid baboons. *Folia Primatol* 50:157–174. doi:10.1159/
 000156343 888
 Cords M (2000) The number of males in guenon groups. In: Kappeler 890
 PM (ed) Primate males: causes and consequences of variation in 891
 group composition. Cambridge University Press, Cambridge, pp 892
 84–96 893
 Crockett CM, Janson CH (2000) Infanticide in red howlers: female 894
 group size, male membership, and a possible link to folivory. In: 895
 van Schaik CP, Janson CH (eds) Infanticide by males and its 896
 implications. Cambridge University Press, Cambridge, pp 75–98 897
 Davies AG (1987) Adult male replacement and group formation in 898
Presbytis rubicunda. *Folia Primatol* 49:111–114. doi:10.1159/
 000156313 899
 Deschner T, Heistermann M, Hodges JK, Boesch C (2004) Female 900
 sexual swelling size, timing of ovulation, and male behavior in 901
 wild African chimpanzees. *Horm Behav* 46:204–215. 902
 doi:10.1016/j.yhbeh.2004.03.013 903
 Ebensperger LA (1998) Strategies and counterstrategies to infanticide 904
 in mammals. *Biol Rev* 73:321–346. doi:10.1111/j.1469-
 185X.1998.tb00034.x 905
 Engelhardt A, Pfeifer J-B, Heistermann M, Niemitz C, van Hooff 906
 JARAM, Hodges JK (2004) Assessment of female reproductive 907
 status by male longtailed macaques, *Macaca fascicularis*, under 908
 natural conditions. *Anim Behav* 67:915–924. doi:10.1016/j.
 anbehav.2003.09.006 909
 Enstam KL, Isbell LA, de Maar T (2002) Male demography, 910
 female mating behavior, and infanticide in wild patas monkeys 911
 (*Erythrocebus patas*). *Int J Primatol* 23:85–104. doi:10.1023/
 A:1013249808137 912
 Fashing PJ, Nguyen N, Kerby JT, Lee LM, Nurmi N, Venkataraman 913
 VV (2009) Two group takeovers, infanticide and pregnancy 914
 terminations in *Theropithecus gelada* at Guassa, Ethiopia. *Am J* 915
Phys Anthropol 138:127 916
 Fedigan LM (2003) Impact of male takeovers on infant deaths, births 917
 and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. 918
Int J Primatol 24:723–741. doi:10.1023/A:1024620620454 919
 Fruteau C, Range F, Noe R (2010) Infanticide risk and infant defence 920
 in multi-male free-ranging sooty mangabeys, *Cercocebus atys*. 921
Behav Process 83:113–118. doi:10.1016/j.beproc.2009.11.004 922
 Gray ME (2009) An infanticide attempt by a free-roaming feral 923
 stallion (*Equus caballus*). *Biol Lett* 5:23–25. doi:10.1098/
 rsbl.2008.0571 924
 925
 926
 927
 928
 929

930 Hrdy SB (1974) Male-male competition and infanticide among the
 931 langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol*
 932 22:19–58. doi:10.1159/000155616

933 Hrdy SB (1979) Infanticide among animals: a review, classification,
 934 and examination of the implications for the reproductive
 935 strategies of females. *Ethol Sociobiol* 1:13–40. doi:10.1016/
 936 0162-3095(79)90004-9

937 Isbell LA (2004) Is there no place like home? Ecological bases of
 938 female dispersal and philopatry and their consequences for the
 939 formation of kin groups. In: Chapais B, Berman CM (eds)
 940 Kinship and behavior in primates. Oxford University Press, New
 941 York, pp 71–108

942 Isbell LA, van Vuren D (1996) Differential costs of locational and
 943 social dispersal and their consequences for female group-living
 944 primates. *Behaviour* 133:1–36. doi:10.1163/156853996X00017

945 Jack KM, Fedigan LM (2009) Female dispersal in a female-philopatric
 946 species, *Cebus capucinus*. *Behaviour* 146:471–497. doi:10.1163/
 947 156853909X404420

948 Janson CH, van Schaik CP (2000) The behavioral ecology of
 949 infanticide by males. In: van Schaik CP, Janson CH (eds)
 950 Infanticide by males and its implications. Cambridge University
 951 Press, Cambridge, pp 469–494

952 Jin T, Wang DZ, Zhao Q, Yin L, Qin D, Ran W, Pan W (2009a)
 953 Reproductive parameters of wild *Trachypithecus leucocephalus*:
 954 seasonality, infant mortality and interbirth interval. *Am J*
 955 *Primatol* 71:558–566. doi:10.1002/ajp.20688

956 Jin T, Wang DZ, Zhao Q, Yin L, Qin D, Ran W, Pan W (2009b) Social
 957 organization of white-headed langurs (*Trachypithecus leucocephalus*)
 958 in the Nongguan karst hills, Guangxi, China. *Am J Primatol* 71:206–
 959 213. doi:10.1002/ajp.20637

960 Launhardt K, Borries C, Hardt C, Epplen JT, Winkler P (2001)
 961 Paternity analysis of alternative male reproductive routes among
 962 the langurs (*Semnopithecus entellus*) of Ramnagar. *Anim Behav*
 963 61:53–64. doi:10.1006/anbe.2000.1590

964 Lewison R (1998) Infanticide in the hippopotamus: evidence for
 965 polygynous ungulates. *Ethol Ecol Evol* 10:277–286

966 Li Z, Rogers ME (2004) Social organization of white-headed langurs
 967 *Trachypithecus leucocephalus* in Fusui, China. *Folia Primatol*
 968 75:97–100. doi:10.1159/000076268

969 Marsh CW (1979) Female transference and mate choice among Tana
 970 River red colobus. *Nature* 281:568–569

971 Mei Q (1991) Reproductive cycle of captive black crested langurs
 972 (*Presbytis francoisi*) and the growth and development of their
 973 offspring. *J Beij Teach Coll* 12:74–79

974 Mohnot SM (1971) Some aspects of social change and infant-killing
 975 in the Hanuman langur *Presbytis entellus* (Primates: Cercopithe-
 976 cidae) in western India. *Mammalia* 35:175–198

977 Molbak K, Gottschau A, Aaby P, Hojlung N, Ongholt L, da Silva APJ
 978 (1994) Prolonged breast feeding, diarrhoeal disease, and survival
 979 of children in Guinea-Bissau. *BMJ* 308:1403–1406

980 Morelli TL, King SJ, Pochron ST, Wright PC (2009) The rules of
 981 disengagement: takeovers, infanticide, and dispersal in a rain-
 982 forest lemur, *Propithecus edwardsi*. *Behaviour* 146:499–523.
 983 doi:10.1163/15683908X399554

984 Nelson CTJ, Elwood RW (1997) Paternal state and offspring
 985 recognition in the biparental cichlid fish *Pelvicachromis pulcher*.
 986 *Anim Behav* 54:803–809. doi:10.1006/anbe.1996.0507

987 Newton PN (1988) The variable social organization of Hanuman
 988 langurs (*Presbytis entellus*), infanticide, and the monopoliza-
 989 tion of females. *Int J Primatol* 9:59–77. doi:10.1007/
 990 BF02740198

991 Onderdonk DA (2000) Infanticide of a newborn black-and-white
 992 colobus monkey (*Colobus guereza*) in Kibale National Park,
 993 Uganda. *Primates* 41:209–212. doi:10.1007/BF02557802

994 Ostner J, Chalise MK, Koenig A, Launhardt K, Nikolei J, Podzuweit
 995 D, Borries C (2006) What Hanuman langur males know about
 female reproductive status. *Am J Primatol* 68:701–712. 996
 doi:10.1002/ajp.20260 997

Packer C, Pusey AE (1983) Adaptations of female lions to infanticide
 998 by incoming males. *Am Nat* 121:716–728. doi:10.1086/284097 999

Packer C, Pusey AE (1984) Infanticide in carnivores. In: Hausfater G,
 1000 Hrdy SB (eds) Infanticide: comparative and evolutionary per-
 1001 spectives. Aldine, New York, pp 31–42 1002

Palombit RA, Cheney DL, Fischer J, Johnson SE, Rendall D, Seyfarth
 1003 RM, Silk JB (2000) Male infanticide and defense of infants in
 1004 chacma baboons. In: van Schaik CP, Janson CH (eds) Infanticide
 1005 by males and its implications. Cambridge University Press,
 1006 Cambridge, pp 123–152 1007

Patterson IAP, Reid RJ, Wilson B, Grelhier K, Ross HM, Thompson
 1008 PM (1998) Evidence for infanticide in bottlenose dolphins: an
 1009 explanation for violent interactions with harbour porpoises? *Proc*
 1010 *R Soc Lond B* 265:1167–1170. doi:10.1098/rspb.1998.0414 1011

Pereira ME, Weiss ML (1991) Female mate choice, male migration,
 1012 and the threat of infanticide in ringtailed lemurs. *Behav Ecol*
 1013 *Sociobiol* 28:141–152. doi:10.1007/BF00180991 1014

Pluhacek J, Bartos L, Vichova J (2006) Variation in incidence of male
 1015 infanticide within subspecies of plains zebra (*Equus burchelli*). *J*
 1016 *Mammal* 87:35–40 1017

Pusey AE, Packer C (1994) Infanticide in lions: consequences and
 1018 counterstrategies. In: Parmigiani S, vom Saal FS (eds) Infanticide
 1019 and parental care. Harwood Academic Publishers, Chur, pp 277–
 1020 299 1021

Rajpurohit LS, Sommer V, Mohnot SM (1995) Wanderers between
 1022 harems and bachelor bands: male Hanuman langurs (*Presbytis*
 1023 *entellus*) at Jodhpur in Rajasthan. *Behaviour* 132:255–299.
 1024 doi:10.1163/156853995X00739 1025

Robbins AM, Stoinski TS, Fawcett KA, Robbins MM (2009) Does
 1026 dispersal cause reproductive delays in female mountain gorillas?
 1027 *Behaviour* 146:525–549. doi:10.1163/156853909X426354 1028

Rudran R (1973) Adult male replacement in one-male troops of
 1029 purple-faced langurs (*Presbytis senex senex*) and its effect on
 1030 population structure. *Folia Primatol* 19:166–192. doi:10.1159/
 1031 000155537 1032

Schneider JM, Lubin Y (1996) Infanticidal male eresid spiders. *Nature*
 1033 381:655–656. doi:10.1038/381655a0 1034

Siegel S, Castellan NJJ (1988) Nonparametric statistics for the
 1035 behavioral sciences. McGraw-Hill, New York 1036

Soltis J, Thomsen R, Matsubayashi K, Takenaka O (2000) Infanticide
 1037 by resident males and female counter-strategies in wild Japanese
 1038 macaques (*Macaca fuscata*). *Behav Ecol Sociobiol* 48:195–202.
 1039 doi:10.1007/s002650000224 1040

Sommer V (1994) Infanticide among the langurs of Jodhpur: testing
 1041 the sexual selection hypothesis with a long-term record. In:
 1042 Parmigiani S, vom Saal FS (eds) Infanticide and parental care.
 1043 Harwood Academic Publishers, Chur, pp 155–198 1044

Sterck EHM (1997) Determinants of female dispersal in Thomas
 1045 langurs. *Am J Primatol* 42:179–198. doi:10.1002/(SICI)1098-
 1046 2345(1997)42:3<179::AID-AJP2>3.0.CO;2-U 1047

Sterck EHM (1998) Female dispersal, social organization, and
 1048 infanticide in langurs: are they linked to human disturbance?
 1049 *Am J Primatol* 44:235–254. doi:10.1002/(SICI)1098-2345(1998)
 1050 44:4<235::AID-AJP1>3.0.CO;2-X 1051

Sterck EHM, Korstjens AH (2000) Female dispersal and infanticide
 1052 avoidance in primates. In: van Schaik CP, Janson CH (eds)
 1053 Infanticide by males and its implications. Cambridge University
 1054 Press, Cambridge, pp 293–321 1055

Sterck EHM, Willems EP, van Hooff JARAM, Wich SA (2005)
 1056 Female dispersal, inbreeding avoidance and mate choice in
 1057 Thomas langurs (*Presbytis thomasi*). *Behaviour* 142:845–868.
 1058 doi:10.1163/1568539055010093 1059

Struhsaker TT, Leland L (1985) Infanticide in a patrilineal society of
 1060 red colobus monkeys. *Z Tierpsychol* 69:89–132 1061

1062 Sugiyama Y (1965) On the social change of Hanuman langurs
 1063 (*Presbytis entellus*) in their natural condition. *Primates* 6:381–
 1064 418. doi:10.1007/BF01730356

1065 Sugiyama Y, Ohsawa H (1974) Life history of male Japanese
 1066 macaques at Ryozenyama. In: Kondo S, Kawai M, Ehara A
 1067 (eds) Contemporary primatology: proceedings of the fifth
 1068 international congress of primatology. Karger, Basel, pp 407–410

1069 Teichroeb JA, Sicotte P (2008) Infanticide in ursine colobus monkeys
 1070 (*Colobus vellerosus*) in Ghana: new cases and a test of the
 1071 existing hypotheses. *Behaviour* 145:727–755. doi:10.1163/
 1072 156853908783929160

1073 Teichroeb JA, Wikberg EC, Sicotte P (2009) Female dispersal patterns
 1074 in six groups of ursine colobus (*Colobus vellerosus*): infanticide
 1075 avoidance is important. *Behaviour* 146:551–582. doi:10.1163/
 1076 156853909X426363

1077 Trumbo ST (2006) Infanticide, sexual selection and task specialization
 1078 in a biparental burying beetle. *Anim Behav* 72:1159–1167.
 1079 doi:10.1016/j.anbehav.2006.05.004

1080 van Schaik CP (2000) Infanticide by male primates: the sexual
 1081 selection hypothesis revisited. In: van Schaik CP, Janson CH
 1082 (eds) Infanticide by males and its implications. Cambridge
 1083 University Press, Cambridge, pp 27–60

1084 van Schaik CP, Janson CH (2000) Infanticide by males and its
 1085 implications. Cambridge University Press, Cambridge

1086 van Schaik CP, van Noordwijk MA, Nunn CL (1999) Sex and social
 1087 evolution in primates. In: Lee PC (ed) Comparative primate
 1088 socioecology. Cambridge University Press, Cambridge, pp 204–
 1089 240

1090 Veiga JP (2000) Infanticide by male birds. In: van Schaik CP, Janson
 1091 CH (eds) Infanticide by males and its implications. Cambridge
 1092 University Press, Cambridge, pp 198–220

1093 Wang DZ (2004) Social structure of wild white-headed langurs
 1094 (*Trachypithecus leucocephalus*): a case study at the Nongguan
 1128 karst hills, Guangxi, China. In: Department of Environmental
 1095 Biology and Ecology. Beijing University, Beijing 1096

Winkler P, Loch H, Vogel C (1984) Life history of Hanuman langurs
 1097 (*Presbytis entellus*)—reproductive parameters, infant mortality,
 1098 and troop development. *Folia Primatol* 43:1–23. doi:10.1159/
 1099 000156167 1100

Wolf KE, Fleagle JG (1977) Adult male replacement in a group of
 1101 silvered leaf-monkeys (*Presbytis cristata*) at Kuala Selangor,
 1102 Malaysia. *Primates* 18:949–955. doi:10.1007/BF02382945 1103

Wright PC (1995) Demography and life history of free-ranging
 1104 *Propithecus diadema edwardsi* in Ranomafana National Park,
 1105 Madagascar. *Int J Primatol* 16:835–854. doi:10.1007/BF02735722 1106

Xiang Z-F, Grueter CC (2007) First direct evidence of infanticide and
 1107 cannibalism in wild snub-nosed monkeys (*Rhinopithecus bieti*).
 1108 *Am J Primatol* 69:249–254. doi:10.1002/ajp.20333 1109

Yoshihara K (1968) Local and intertroop variability in ecology and
 1110 social behavior of common Indian langurs. In: Jay PC (ed)
 1111 *Primates: studies in adaptation and variability*. Holt, Rinehart and
 1112 Winston, New York, pp 217–242 1113

Zhang S, Liang B, Wang L (1999) Infanticide within captive groups of
 1114 Sichuan golden snub-nosed monkeys (*Rhinopithecus roxellana*).
 1115 *Folia Primatol* 70:274–276. doi:10.1159/000021707 1116

Zhao Q, Pan W (2006) Male-immature interactions seem to depend on
 1117 group composition in white-headed langur (*Trachypithecus*
 1118 *leucocephalus*). *Acta Ethol* 9:91–94. doi:10.1007/s10211-006-
 1119 0019-1 1120

Zhao Q, Tan CL, Pan W (2008) Weaning age, infant care, and
 1121 behavioral development in *Trachypithecus leucocephalus*. *Int J*
 1122 *Primatol* 29:583–591. doi:10.1007/s10764-008-9255-8 1123

Zhao Q, Jin T, Wang DZ, Qin D, Ran W, Pan W (2009) Lack of sex-
 1124 biased maternal investment in spite of a skewed birth sex ratio in
 1125 white-headed langurs (*Trachypithecus leucocephalus*). *Ethology*
 1126 115:280–286. doi:10.1111/j.1439-0310.2008.01609.x 1127

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