Infanticide and reproductive restraint in a polygynous social mammal

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Alpha male chacma baboons experience uncontested access to individual estrus females. Consequently, alpha male paternity certainty is high and underpins significant levels of infanticide by immigrant males that, in turn, has selected for male defense of infants. There is also, however, a high probability that alpha males will be absent during the period when their own offspring are vulnerable, suggesting selection for additional countermeasures. We use data from a long-term study to test the prediction that alpha male chacma baboons cede reproductive opportunities to subordinate males and that this leads to the presence of other fathers that can serve as a buffer against infanticidal attack. We found that subordinate males obtained significantly more conceptive opportunities than predicted by priority of access alone, and that this occurred because alpha males did not consort all receptive periods. There was no evidence that this was due to energetic constraint, large male cohorts, alpha male inexperience, or the competitive strength of queuing subordinates. The number of males who benefited from concession and the length of time that they were resident relative to those who did not benefit in this way greatly reduced the probability that infants of alpha males would face immigrant males without a surrogate father whose own offspring were vulnerable. The absence of such males was associated with observed infanticide as well as, unexpectedly, an increased likelihood of takeover when alpha males with vulnerable infants were present.

chacma baboons | paternity certainty | reproductive concession | sexual conflict

In despotic systems the reproductive success of dominant individuals may be a function of pressures that either constrain their ability to secure mating monopolies or encourage them to cede conceptions to subordinates (1, 2). As a rule, reproductive skew among male mammals is generally considered a product of the former; the often intense intermale competition combined with the brevity of alpha tenure means that although males are assumed to favor complete monopolies, they are prevented from doing so by the costs of mate guarding and/or the reproductive demography of females (3–5). By virtue of their greater reproductive output, however, dominant males may suffer disproportionately from pressures that have a negative effect on infant survival. In the case of mammals, the most notable of these is infanticide (6–8). Given this, if the presence or behavior of subordinates can mitigate this pressure and is mediated by reproductive success, skew theory predicts that the pursuit of a total reproductive monopoly may not, in fact, be adaptive (9–11).

Male chacma baboons (*Papio hamadryas ursinus*) consistently form strong rank-based queues for reproductive access to females (12, 13). This rank-based priority of access also structures the nature of the consortships that are formed around the time of increased ovulation probability; specifically, consortships involve very few males, male succession is nonviolent with no harassment of consort pairs, and the length of the ultimate period of mate guarding matches or exceeds the accepted window of ovulation for the species (5-7 days) (14). This gives rise to a high general level of paternity assurance and suggests that alpha males may have the potential to father all infants except when the conceptive cycles of more than one female overlap (15).

An inevitable consequence of this skew in paternity certainty is that chacma infants are at a high risk of infanticide, primarily from young recently immigrated males. These males represent the primary contenders for alpha status and, as such, are most likely to benefit from infanticidal behavior (16, 17). This threat from nonresident males has apparently selected for a female strategy aimed at predisposing resident males to protect their infants both by elevating their paternity estimates and cultivating affiliative associations (or "friendships") with them following conception. Accordingly, likely sires, when present, are seen to protect their putative infants from attack and improve their survivorship as a consequence (18, 19). It is often the case, however, that previous alpha males are absent from the group following their usurpation by an immigrant. Consequently, alpha males are not in a position to protect some of their infants during the period when the infants are most vulnerable (20). As such, in the absence of countermeasures, a proportion of alpha male reproductive output may consistently be lost following alpha male turnover, as is often the case in single-male mating systems (7).

This postusurpation absence of former alpha males has imposed strong selection on females, who exhibit behavioral and physiological traits aimed at increasing the pool of putative fathers that can provide additional, or backup, protection (20). The fact that despite the absence of the former alpha male all vulnerable infants are almost invariably associated with a protector male suggests the strategy is effective and highlights the potential value of subordinate males both to females and alpha males alike (16, 18). This being so, it is possible that rather than the female strategy being a source of sexual conflict, selection may actually favor dominant males who facilitate it to some degree. Specifically, we suggest that dominant males may do well to cede conceptions if this augments the female strategy and increases the chances that subordinates will be available to protect the alpha's infants throughout their period of vulnerability. This suggestion is based on the observation that intertroop movement by subordinates is sensitive to stochastic fluctuations in operational sex ratio and, therefore, frequent and unpredictable (21). Consequently, in the absence of any incentive to remain, the chances that subordinate males will be resident throughout an infant's period of vulnerability may be relatively low.

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It has long been known that baboon alpha males do not always consort receptive females (22–25) and that these decisions, though linked to the likelihood of female conception, are nevertheless prone to error (i.e., alpha males do not consort on a cycle during which the female conceives) (12, 15). The fact that alpha males do not always press their mating advantage suggests a plausible mechanism by which conceptions may accrue to subordinates and on which selection can act. To test the hypothesis that alpha males show reproductive restraint with respect to mating (as opposed to facing constraints on their ability to monopolize matings), we use data from a long-term study population of chacma baboons. Specifically, we consider (*i*) whether alpha males forfeit conception opportunities in the absence of any obvious constraints on their ability to guard females and (*ii*) whether this influences subordinate male residency decisions in ways that might benefit infant survival. The alternative hypothesis is that there are constraints on alpha male mating monopolization that presents subordinate males with a window of mating opportunity that lies beyond alpha male control. Consequently, we assess the following predictions that arise from these competing hypotheses:

i. If alpha males are able to monopolize females but lack complete control as a consequence of an overlap in female fertile periods, a priority-of-access model (PoA) should provide the best fit to the conception data. Alternatively, if alpha males are showing reproductive restraint (RR), then subordinate males will obtain more conceptions than predicted by PoA.

ii. If there is RR, then alpha males should not consort all female cycles, and subordinate males should obtain conceptions from consortships that go completely uncontested by alpha males. This may, however, merely reflect incomplete control driven by the energetic costs of consortship. Accordingly, we predict that if energy deficits are constraining, then there should be (*i*) a reduction in foraging during consortship (26), (*ii*) an associated reduction in guarding activity, and (*iii*) an associated rise in the probability of conceptive access by subordinate males.

iii. As alpha male detection of conceptive cycles is not perfect, we expect the baseline distribution of subordinate male conceptions against alpha male tenure length to follow a Poisson distribution. We know too, however, that alpha male accuracy improves with increasing tenure length (15). If alpha males show incomplete control, we predict that subordinate male conceptions will accrue disproportionately early in an alpha males tenure. Alternatively, we predict that subordinate conceptions will simply conform to the Poisson distribution or be clustered toward the end of alpha male tenure because it should pay alpha males to concede conceptions as their ability to sustain alpha status declines (27).

iv. Data from yellow baboons (*P.h.cynocephalus*) and chimpanzees (*Pan troglodytes*), as well as for species that do not form consortships (5), indicate that PoA breaks down with increasing male cohort size (28, 29). This is due to an increase in the number of challenges faced by the alpha male. If alpha male chacma baboons show incomplete control, then subordinate male mating success should be positively related to male cohort size. Alternatively, if alpha males show RR, subordinate conceptions should occur in the smallest as well as the largest male cohorts, so that cohort size has no explanatory power.

v. If alpha male RR has positive effects on the survival of alpha male offspring because of the presence of subordinate fathers, then subordinate males that become fathers should have longer residence times in the troop than nonfather subordinates. If conception success mediates the length of time that subordinate males remain in the troop, we also predict that subordinates will acquire their first conceptions early in their period of residency. It is also possible, however, that the attainment of conceptions early in a subordinate's residency reflects high competitive ability and the potential to attain alpha status. If conceptions are more likely to accrue to those subordinates that are "queuing" for alpha status, then we can predict that these males should have some nontrivial probability of acquiring alpha status.

vi. If the extended stay by subordinate male fathers has benefits for the infants of alpha males, we expect these to derive from a reduced possibility that the infants are left without a father or a surrogate (i.e., a male that has an equally vulnerable infant present in the troop) when they are vulnerable to attack. By the same token, an alpha male's infants should face a higher probability of successful attack when neither the alpha male nor any subordinate surrogate males are present.

vii. Finally, we use a simple probabilistic model to assess the prediction that paternity certainty and infanticide risk combine to align the reproductive strategies of alpha males and females on the need for additional protectors.

Results

Fit to the PoA Model. Under strict priority of access, conceptions should accrue to subordinate males only when female conceptive cycles overlap (30). We used a model based on a 7-day conceptive window to predict the expected distribution of conceptions between alphas and subordinates (19). The predicted number of subordinate conceptions (10.8/72) did not differ significantly from that observed to be due to overlap alone (8/72; $\chi^2 = 0.86$; 1 df, NS). With these eight conceptions accounted for, we expected subordinate males to obtain no further conceptions. We found, however, that they were responsible for an additional 23. This observed allocation to alpha and subordinate males respectively of 41:23 conceptions differed significantly from the expected ratio of 64:0 ($\chi^2 = 57.3$; 1 df; $P < 0.001$). Seven of the 10 alpha males ceded conceptions, and two of the three males who did not held alpha status for very short periods. Of the seven who did, all ceded to more than one other male (mean = 2.57; range: 2–4).

Costs of Consortship. Following others (15, 28), we use the extent to which consorting disrupts male activity budgets as a proxy for its potential energetic costs and compare the proportion of the activity budget males allocated to foraging, moving, and resting in and out of consortships. Although there is already evidence that consorting does not affect male activity at De Hoop Nature Reserve (South Africa) (15), this analysis used relatively coarse scan sample data and did not account for seasonality. Here, we use continuous focal data on male activity collected across multiple seasons. Our rationale is that if consorting is costly and seasonal variation in day length affects the time that can be directed at energy acquisition and conservation (31), its impact is likely to be seasonal. With this mind, we can then determine whether the mating monopolies of alpha males are mediated by the costs of consortship by quantifying any corresponding seasonal variance in the duration of male guarding.

Consort status [guarding vs. not guarding: generalized linear mixed model (GLMM): $F_{1,1669} = 6.7$; $P = 0.01$) and season (short winter vs. long summer days: GLMM: $F_{1,1669} = 56.4$; $P < 0.001$) both affected male foraging effort. The effect of consort status, however, was only significant during the austral summer when consorting males foraged less (winter: $\beta \pm$ SE: -0.137 ± 0.168, NS; summer: $\beta \pm$ SE: -0.339 ± 0.128, $P = 0.008$). Season also affected the amount of time males spent resting and moving (short winter vs. long summer days: resting: GLMM: $F_{1,1617} = 88.016$; $P < 0.001$;

moving: GLMM: $F_{1,1617} = 18.270$; $P < 0.001$). The effect of consort status was, however, only significant in interaction with season (guarding vs. not guarding: resting: GLMM: $F_{2,1617} = 3.293$; $P = 0.037$; moving: GLMM: $F_{2,1618} = 3.719$; $P = 0.025$). Consorting males rested significantly less and moved significantly more during winter (resting: winter: $\beta \pm$ SE: -0.610 ± 0.168, $P = 0.001$; summer: $\beta \pm$ SE: -0.123 ± 0.128, NS; moving: winter: $\beta \pm$ SE: 0.462 ± 0.183, $P = 0.011$; summer: $\beta \pm$ SE: -0.189 ± 0.188, NS). These seasonal constraints on time budgets did not, however, affect male guarding strategy. We found no difference across seasons in the duration of guarding bouts sustained by a female's ultimate mating partner (winter: 7.8 ± 0.64 days; summer: 7.6 ± 0.59 days: GLMM: $F_{1,35} = 0.055$, NS), nor in the acquisition of conceptions by subordinate males despite the greater number of consort days accruing to alpha males overall (15) (summer: $N_{Alpha} = 21$; $N_{Subordinate} = 15$; winter: $N_{Alpha} = 20$; $N_{Subordinate} = 8$. $\chi^2 = 1.16$; 1 df, NS).

Alpha Male Consort Contestation and Subordinate Success. Of the 23 subordinate conceptions, 21 were from conceptive cycles that were not contested in any way by the alpha males, and two were from cycles during which the alpha male consorted briefly on D-0. We base subsequent analyses on the 41:23 ratio (excluding overlap conceptions from consideration), although a 43:21 division of conceptions does not alter the findings. Subordinate fathers comprised males who did not achieve alpha status ($n = 8$), former alpha males ($n = 7$), and one natal, subadult male.

Alpha Male Tenure Length and Subordinate Success. Deviations from the expected Poisson distribution, though significant (Kolmogorov's D = 0.44; $n = 23$; $P < 0.001$), were associated with both new and experienced alpha males (Fig. 1). That is, subordinate male access falls outside the 95% confidence limits of the Poisson distribution at both short and long alpha-male tenure lengths. Identification of the conceptions of primiparous females rule out the possibility that RR late in alpha male tenure was simply a consequence of some stochastic overrepresentation of females with which they had had little previous sexual contact.

Cohort Size and Subordinate Male Success. Because the number of males in our study troops varied considerably (21), we used logistic regression to test the prediction that the probability of conceptions accruing to alpha males would be a negative function of male number, with male number log-transformed to improve linearity (32). We found, instead, that alpha male conception success was positively associated with cohort size ($\beta = 1.4 \pm 0.7$ SE $\chi^2 = 3.98$, $P = 0.046$; odds ratio = 4.05).

Duration of Residence by Fathers and Nonfathers. We have data on the total duration of residence of 16 subordinate males that did not achieve conceptive matings (mean = 5.1 months) and seven that did (mean = 22.6 months), and nine alpha males (mean total duration = 37.6 months; mean post-alpha duration = 24 months). Survival analysis reveals significant differences between the three groups, with subordinate fathers staying longer than nonfathers (Wilcoxon $\chi^2 = 18.36$; 2 df; $P < 0.001$). Data on the first conceptive opportunities presented to subordinates suggested that this generally occurred early in their residency and, though not definitive, that this may prompt their continued presence (Fig. 2). Alpha status was achieved, on average, within 1.8 months of immigration ($n = 10$; range: 0–4 months), and subordinates who benefited from concession never rose in rank subsequently.

Immigration, Infanticide, and Prospects for Concession. The long-term study troop (VT) experienced 26 separate periods of male influx, each of which involved a mean of 1.4 males (range: 1–3). Of these, eight resulted in the defeat of the alpha male by an immigrant. Infants of alpha males consequently experienced, on average, 2.75 periods of influx and 0.84 alpha male turnovers during their first year, which is when they are vulnerable to infanticide (16). Whereas an alpha male's infant had a 0.36 probability of being without a father at this time, it had only a 0.19 probability of being without a surrogate father (i.e., one with an infant that was also vulnerable). The probability, then, of it being without either was only 0.07.

For those influxes when the current alpha male had vulnerable infants, surrogates were present during all seven influxes that did not result in turnover, whereas they were absent during four of the five that did (Fisher's exact test, $P = 0.01$). Although the sample size is small, turnovers in the absence of surrogates ($n = 4$) were not associated with (*i*) larger immigrant cohorts than influxes when surrogates were present (Mann–Whitney $U = 15$, z = −0.18, NS), (*ii*) smaller resident male cohorts (Mann–Whitney $U = 9$, z = −0.12, NS) or larger ratios of immigrants to residents (Mann–Whitney $U = 10.5$, z = −0.94, NS).

We observed five successful infanticides in the wake of male immigration, and these were associated with both successful and unsuccessful attempts at turnover. One infant was killed while both its father and surrogates were present, but it was without its mother, who had died. Two infants were killed while neither their fathers nor surrogates were in the troop. Finally, two infants that had no resident surrogate fathers were killed while their fathers were present but actively resisting turnover. Taken together, this suggests that in the presence of their mothers, the alpha male's infants are at increased risk if either he or surrogate fathers are absent.

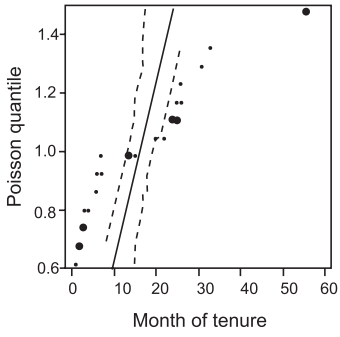

Fig. 1. Access to conceptive cycles by subordinate males ($n = 23$) in relation to the length of alpha male tenure. The solid line indicates the expected distribution (dashed lines: 95% CI) and the circles indicate the observed pattern of subordinate male conceptions. Large circles indicate conceptions by primiparous females ($n = 6$).

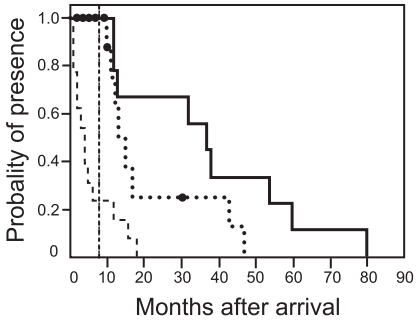

Fig. 2. Survival curves for the three classes of male: nonfathers (–), subordinate fathers (···), and alpha fathers (—). The curves indicate the likelihood of male presence as a function of the time that has passed since their arrival. Circles indicate the month at which each immigrant, subordinate father first achieved a conceptive mating (median: dashed vertical line).

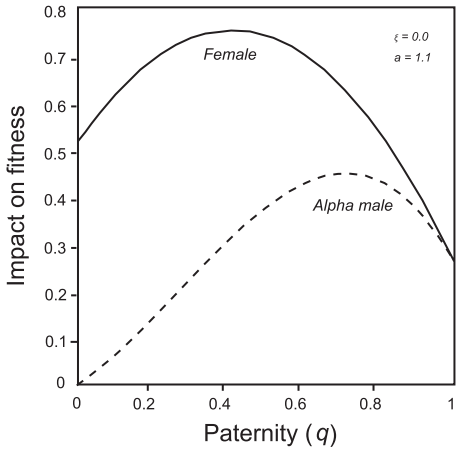

Fig. 3. The impact on fitness for both the male and the female as a function of the dominant male's paternity probability. The parameter values for chacma baboons are as follows: l = maternal impact on infant survival = 0.25; c = 0.924 and a = 1.1, giving c/a = takeover probability = 0.84; d = 0.5; $1 - \varepsilon$, i.e., probability of takeover from outside is set at 1.0 because the takeovers are always from outside; k = 0.75, A = 1.0 (45).

Convergence in the Sexes' Reproductive Strategies. The impact on fitness for both the alpha male and the female as a function of the alpha male's paternity probability is plotted in Fig. 3, using the study population parameters. Male fitness is maximized when paternity probability = 0.72 ($P_{\text{observed paternity}} = 0.64$), whereas the value for females = 0.4.

Discussion

Our data suggest that alpha male chacma baboons did not contest all of the conceptive cycles available to them and that this had significant reproductive consequences for resident subordinate males. Though it is intrinsically difficult to eliminate the possibility entirely, our analyses do not support the limited control model of reproductive skew, which assumes that the potential for complete monopoly is circumscribed. The ability of alpha males in our study to monopolize mating access—as measured by the duration of their guarding bouts and the number of consorted conceptive cycles—was not diminished by larger male cohorts, detectable energetic constraints, the naïvety of new alphas, or the competitive strength of potentially queuing males. In addition, the model outcome closely predicted the observed skew. This consilience of evidence leads us to conclude that the distribution of reproductive success in this polygynous social mammal derives from concession by powerful alpha males.

The success of subordinate males in smaller male cohorts—also reported in mandrills, *Mandrillus sphinx* (4)—is intriguing and may shed light on the proximate mechanism underpinning restraint in chacma baboons. Given the general relationship between operational sex ratio and aggressive competition (33), shifts in the number of coexisting competitors should affect male tension levels. The reduced size of a male olive baboon cohort (*P.h. anubis*), for example, has been linked both to conflict reduction and an increase in social grooming among males (34). There is also evidence from chacma baboons that males in small cohorts are less likely to maintain close consortships and are more relaxed about the consortships of others (35, 36). Reduced tension of alpha males in smaller cohorts may therefore result in less concerted efforts by such males to exclude others from mating, thus giving rise to the observed distribution of subordinate male conceptive opportunities. If, in addition, alpha males are increasingly relaxed as their tenure lengthens, then subordinates will continue to obtain conceptive opportunities despite the improved ability of alphas to detect conceptive cycles (15). This fits theoretical expectations of male response under high infanticide risk (27), and is supported by our data.

The high probability of alpha male absence, in conjunction with elevated infanticide risk, led us to propose that reproductive concession counters future infanticide by involving other males in the improved survival of alpha infants. The unanticipated finding that surrogate absence—but not reduced cohort size—was linked to alpha turnover suggests two things. First, the presence of subordinate fathers has a direct influence on alpha males' tenure length in a way that nonfathers do not; thus, the value of subordinate fathers lies precisely in the fact that they are fathers. Second, although the role of surrogates is linked directly to infant protection, its derivative effect of extending alpha male tenure length allows alphas to augment their lifetime reproductive success. Though the ramifications of this await exploration, it underscores the value of concession, which, if it is to work, must increase the probability that at least one surrogate father will be available to alpha infants. This can be achieved in two ways: concession by an alpha benefits several males and/or it increases the likelihood that successful subordinates are more likely to remain. Our data provide evidence for both of these possibilities, though we acknowledge that the direction of causality between success and subsequent

Fig. 4. This photograph, taken during a fight between an immigrant and the alpha male, show six mothers with vulnerable infants clustered around a subordinate male, who is the father of only two of them.

residence is ambiguous. It is possible that some males, of lower competitive ability, choose to remain and consequently acquire conceptive consortships. Even so, such males remain the beneficiaries of concession, and the survival prospects of the alpha males' infants are, consequently, improved. It may also be the case that current residence patterns reflect past selection, with the low-risk accumulation of offspring as subordinate residents traded off against the high-risk pursuit of alpha status elsewhere (21).

Regardless of the proximate cause of prolonged residence, the data indicate that alpha infants are rarely without either a father or a surrogate and that observed instances of infanticide occurred in the absence of surrogates. Given the degree of paternity certainty in this taxon, the critical question concerns the nature of the help provided by subordinates. Though their continued residence alone may reduce the rate of immigration (21), no consideration of their role in the presence of an infanticidal immigrant can exclude the influence of mothers' behavior. More specifically, the consequences of surrogate absence during attempted takeovers offer an indication of the way in which alpha male and female responses to acute infanticide risk intersect. We presume that when surrogates are absent, alpha males are hampered in attack, either by an immediate need to defend infants or by the close presence of mothers with vulnerable infants seeking protection. At a minimum, then, another male with vulnerable infants, and therefore sensitive to risk, can cast an "attack shadow" (37) in which mothers may shelter (Fig. 4).

The effectiveness of such passive help is, nevertheless, circumscribed. If several females are in need simultaneously, it is likely that some will be precluded from attaining sufficiently close proximity. Also, if attacked, infants will be considerably more vulnerable if not actively assisted. Friendships between males and females are found in all baboon populations, and a lack of paternity in chacma is demonstrably no barrier to the formation of protective relationships (38). Clearly, female behavior in the context of friendship formation is effective at securing active male support. The challenge for future work is to determine exactly how females achieve this, and why there has been no counterselection on males to resist active, and potentially costly, protection of nonoffspring.

Methods

Study Site and Data Collection. The data come from our main study troop (VT; N_{mean} = 39; range: 31–50) at the De Hoop Nature Reserve in the Western Cape Province of South Africa (21) and were collected over an 11-year period (March 1997 through February 2008). An additional datum on one alpha male's reproductive success comes from a second, more recently habituated, study troop (BT; N ≈ 50). As part of a daily troop census, we recorded the reproductive condition of females and the identity, if any, of their consort partners. We used the cessation of monthly sexual swelling as evidence of conception, and identified as the father the male who had been the consort partner over the 7-day period (D-7 to D-1) preceding the deflation of the sexual skin (D-0) on the female's last reproductive cycle. Given that mating behavior predicts paternity even in those baboon taxa where consort turnover is high (39, 40), the 10-day duration of ultimate consortships in conceptive cycles (19, 20), together with the absence of consort disruption and surreptitious copulation, lend added confidence to this behavioral determination of paternity. Males were assigned rank on the basis of ad libitum observations of aggression and spatial displacement.

Data on male activity budgets come from both troops, sampled over an 18-month period (March 2002 through October 2004). Data were collected using 20-min continuous focal sampling (41) that yielded 1,692 focal samples (564 h). We used these to calculate the amount of time(s) a male allocated to each of the three key activities (resting, moving, and foraging). These data, expressed as proportions of the total budget, were analyzed using general linear mixed models (GLMM), assuming binomial errors. Statistical analyses were conducted using either R statistical software (42) or JMP 7.1 (43).

Model. In addition to our empirical data, we use a model that describes the conflict between female primates and alpha males over the extent of polyandrous mating (44). The basic assumptions of this are as follows. The primate group is multimale, containing a dominant male, subordinate males, and only one female in estrous at a time. We further assume that infanticide by males is an adaptive strategy so that protection from possible sires against infanticide is crucial for infant survival. For simplicity, the effect of all subordinate males has been combined into a single strongest subordinate male. We also assume that there is one outsider male interested in taking over the group, who is just as strong as the strongest subordinate male in the group.

Pradhan and van Schaik (44) proposed that female fitness can be maximized by maximizing infant survival to weaning, whereas male fitness is maximized only when the male's paternity probability (q) × infant survival is maximized. Based on this idea, and using the parameters described below, we can write equations for impact on female and male fitness as:

$$F_F(q) = l + g(q)(1-(c/a)) + (c/a)(\xi(g(1-q) + g(q)d) + (1-\xi)(g(q=0) + g(q)d + (g(1-q))) \quad [1]$$

$$M_F(q) = qF_F(q), \quad [2]$$

where g(q) = impact on infant survival as a function of male paternity probability (q); l = impact on infant survival due to maternal efforts; a = relative strength of the alpha male; *c*/a = probability of takeover in which c is a constant; ξ = probability of takeover from inside; and d = probability that the defeated alpha male is available to defend infants.

Note that Eq. **1** differs slightly from the master Eq. **2** in Pradhan and van Schaik (44). This takes account of the fact that the probability with which the alpha male is available to protect unweaned infants, generally constant and high, is unusually low for chacma baboons, and so needs to be factored into the model. We have also assumed that the probability of takeover and death, and the percentage of takeovers from the outside, are both external parameters (i.e., not under the control of the alpha male) or are at values that are optimal for him for other reasons.

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