

# Ecological and social determinants of birth intervals in baboons

R. A. Hill, J. E. Lycett, and R. I. M. Dunbar

Centre for Economic Learning and Social Evolution, School of Biological Sciences, Nicholson Building, University of Liverpool, Liverpool L69 3BX, UK

Birth rates in primates have long been proposed to result from an interaction between ecological and social factors. We analyzed a variety of social and environmental variables to determine which ones best explain the observed variation in interbirth intervals across 14 baboon populations. Both the number of females in the group and mean annual temperature were found to be important, and a multivariate equation containing the quadratic components of both these variables accounts for almost all the observed variance in interbirth intervals. The quadratic relationship with temperature is explained in terms of the energetic costs of maintaining a stable body temperature at both low and high temperatures. The quadratic relationship with number of females results from relationships with both food availability and the costs of increasing intragroup competition as group size increases. Although females may be able to exert a certain degree of choice in their reproductive scheduling decisions, they are ultimately constrained by limits imposed upon them by the complex interactions between their ecological and demographic environment. *Key words*: baboons, birth rate, interbirth interval, intragroup competition, *Papio*, thermoregulation. [*Behav Ecol* 11:560–564 (2000)]

For mammals, birth rate is one of four key factors that underlie a female's lifetime reproductive output (Dunbar, 1988) and is affected by both ecological and social elements. In terms of ecological correlates, a number of studies have reported an association between food availability and birth rate (California vole, *Microtus californicus*: Ford and Pitelka, 1984; African rodents, *Arvicanthis noticus*, *Mastomys natalensis*: Taylor and Green, 1976; Japanese macaques, *Macaca fuscata*: Mori, 1979; long-tailed macaques, *Macaca fascicularis*: van Schaik and van Noordwijk, 1985; baboons, *Papio cynocephalus*: Hall, 1963), in which birth rate declines during periods of reduced food availability. Among klipspringer antelope (*Oreotragus oreotragus*), ambient temperature has been identified as the key factor influencing interpopulation variability in birth rate (Dunbar, 1990). Similar trends have also been observed for gelada baboons (*Theropithecus gelada*), in which altitude, which is highly correlated with ambient temperature, was found to correlate negatively with birth rate (Dunbar, 1980; Ohsawa and Dunbar, 1984). Furthermore, litter sizes have been reported to decline with altitude in the golden-mantled ground squirrels (*Spermophilus lateralis*: Bronson, 1979), providing further evidence of a thermal constraint on reproductive options. It has also been suggested that environmental seasonality influences birth rate through its effect on reproductive synchrony, which often results in oscillations in birth rate from year to year (Dunbar, 1988). Goldizen et al. (1988) demonstrated that rainfall (probably acting via fruit production) correlates with the monthly distribution of births in saddle-back tamarins (*Saguinus fuscicollis*), and Lycett et al. (1999) and Wasser and Norton (1993) found similar trends for baboons. Similarly, Srivastava and Dunbar (1995) reported that birth rates and rainfall seasonality are negatively related for Hanuman langurs (*Presbytis entellus*), while Dunbar (1995) found that interbirth intervals increase with latitude

(and hence environmental seasonality) in South American callitrichids.

Social factors are thought to influence birth rate through the demographic structure of a group. Van Schaik (1983) reported a negative correlation between the number of offspring per female and the number of females in a group for the majority of Old and New World monkey species reviewed. Kumar (1995) found a similar relationship for Japanese macaques, with birth rate linearly decreasing with group size. These data were taken to support van Schaik's (1983) assertion that birth rates should decrease as group size increases due to intragroup competition. However, Wrangham (1980) predicted that birth rate should exhibit a humped curve against group size due to the interaction between intragroup and intergroup competition. In a recent paper, Takahata et al. (1998) found general support for this idea with data from Japanese macaques.

Other demographic factors have also been implicated. Dunbar and Sharman (1983) found that, for baboons, the more females per male in a group, the lower was the mean birth rate. They explained this relationship in terms of female–female competition for access to male coalition partners as a means of reducing harassment from other group members. Srivastava and Dunbar (1996) found that birth rates increased with the proportion of groups containing a single male in hanuman langurs, possibly because overt competition between males in multimale groups adversely influences female fertility. Dunbar (1987) reported a similar relationship for African colobines. In the langurs, birth rates were also negatively associated with female group size confirming the adverse effects of stress due to between-female competition (Srivastava and Dunbar, 1996). Wasser and Starling (1988) provide evidence from baboons to support this, since attacks from female coalitions led to reproductive suppression in the attacked individuals.

More recently, Lycett et al. (1998) examined the influence of predation risk and the relationship between care-dependent and care-independent sources of mortality on female reproductive scheduling. They found that for mothers with surviving infants, the range of interbirth intervals across nine baboon populations could be partly accounted for by the level

Address correspondence to R. A. Hill. E-mail: r.a.hill@liverpool.ac.uk.

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**Table 1**  
**Climatic, demographic, and interbirth interval data**

Species/site	Interbirth interval (months)	Mean annual temperature (°C)	Mean annual rainfall (mm)	Altitude (m)	Group size	No. of males	No. of females	References <sup>a</sup>
<i>Papio cynocephalus anubis</i>								
Chololo, Kenya	23.5	22.9	476	1661	43.3	5.3	10.7	1
Gilgil, Kenya	26.5	18.1	691	1768	65	5.2	22.1	2
Shai Hills, Ghana	30.3	25.9	1229	100	30.3	3.2	7.1	3
<i>Papio cynocephalus cynocephalus</i>								
Amboseli, Kenya	24	23.4	335	1127	42	10	17	4
Gombe, Tanzania	25	24.5	1380	680	38.3	8.8	9.5	5
Mikumi, Tanzania	21	25.3	851	550	51.7	7.7	16	6
Ruaha, Tanzania	26.3	21.7 <sup>b</sup>	298	1230	72	7	19	7
Tana River, Kenya	27.9	28.1 <sup>b</sup>	494	55	78.8	4.6	21.8	8
<i>Papio cynocephalus hamadryas</i>								
Erer Gota, Ethiopia	24	24.2	665	1200	83	12	22.5	9
<i>Papio cynocephalus ursinus</i>								
Cape of Good Hope, S. Africa	27.7	17.9	631	10	85	12	26	10
De Hoop, S. Africa	25	17.0	428	10	44	2	12	11
Drakensberg, S. Africa	38	14.6	1149	1800	19.2	3.4	6.6	12
Mkuzi, S. Africa	20	22.4	630	480	47.3	6.0	11.3	13
Moremi, Botswana	24.6	23.6 <sup>b</sup>	457	300	69.7	14.3	19.7	14

<sup>a</sup> References: 1, Kenyatta, 1995; 2, Nicholson, 1982, Harding, 1976; 3, Depew, 1983; 4, Altmann, 1980, Bronikowski and Altmann, 1996; 5, Collins et al., 1984, Ransom, 1981; 6, Rhine RJ, personal communication, Wasser and Wasser, 1995, Hawkins D, personal communication; 7, Lee PC, personal communication, Oliver JI, personal communication; 8, Bently-Condit and Smith, 1997, Marsh, 1978; 9, Sigg et al., 1982; 10, Davidge, 1978; 11, Barrett et al., 1999, Hill, unpublished data; 12 Lycett et al., 1998, 1999; 13, Henzi SP, personal communication, Gaynor, 1994; 14, Bulger and Hamilton, 1987.

<sup>b</sup> Temperature estimated based on Dunbar (1992a).

of predation risk at that site. Females living under conditions of low predation risk are able to care for infants for longer periods; longer interbirth intervals are consequently a feature of these habitats. Where the risk of care-independent mortality to offspring is high, the emphasis shifts to producing offspring at a faster rate, and thus interbirth intervals are reduced. However, the degree to which females are able to exhibit this behavioral plasticity will ultimately depend on their ecological and demographic situation.

In this study we considered a number of demographic and environmental variables that might influence interbirth intervals across baboon populations. We used data from the original baboon data set analyzed by Lycett et al. (1998), as well as data from additional *Papio* baboon studies that were not available at that time.

## METHODS

*Papio* baboons are widespread throughout sub-Saharan Africa and inhabit a wide variety of habitats including forest, swampy woodland, savannah, desert, coastal scrub, and high montane slopes. Their ecological flexibility is paralleled by variation in demography and social organization, with baboons forming social groups ranging from small one-male units to large cohesive multimale groups and females generally remaining in their natal group throughout their lives.

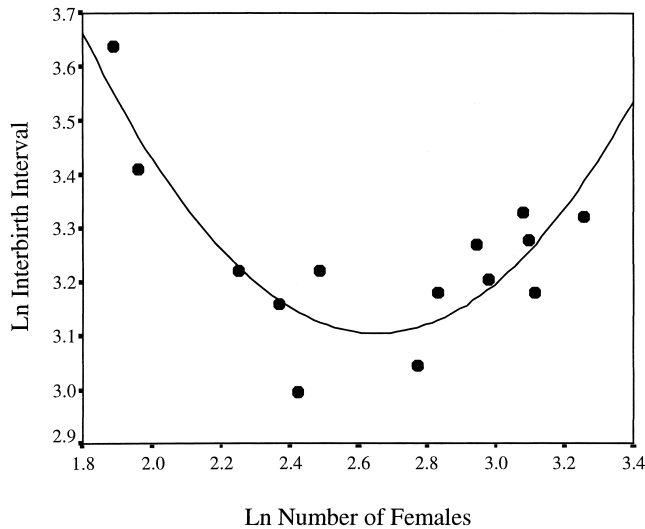
Data on interbirth intervals are available for 14 populations of *Papio* baboons (see Table 1). Data were extracted from the literature, with populations only included for which data had been collected from unprovisioned troops for a minimum observation period of 12 months. Where data on actual interbirth intervals were not available, alternative estimates of

mean birth rates were obtained by summing the total number of adult female-months studied and dividing by the number of infants born in those troops over that time (sensu Dittus, 1975; Dunbar and Dunbar, 1975). Although these estimates may not equate precisely to observed interbirth intervals, they are unlikely to be significantly biased. Where possible, we also took climatic and demographic data from the sources from which the interbirth interval data were obtained. Where the original sources did not contain these data, we took values from literature relating to the same study period. Where climatic data were not available from these sources, the data were taken from Dunbar (1992b).

All data were log<sub>e</sub> transformed to ensure normality for parametric analysis. We used regression analysis to determine the relationships between interbirth intervals and the independent variables. However, many of the relationships with interbirth intervals were quadratic, and thus stepwise procedures could not be used because the linear and quadratic components did not always have significant independent effects. As a consequence, a combination of enter and backward regression was used to determine the best fit equations where necessary. All tests are two tailed. This paper follows convention in considering the five *Papio* species as subspecies of a single superspecies, *Papio cynocephalus* (e.g., Dunbar, 1992b; Jolly, 1993), and thus no distinctions are made on the basis of phylogeny during analysis.

## RESULTS

With respect to the demographic variables, there were significant quadratic regressions between interbirth intervals and both number of females ( $r^2 = .753$ ,  $F_{2,11} = 16.774$ ,  $p < .001$ )



**Figure 1**  
The relationship between interbirth interval and the number of females in the troop.

and group size ( $r^2 = .741$ ,  $F_{2,11} = 15.769$ ,  $p = .001$ ), although there were no significant relationships with number of males ( $r^2 = .148$ ,  $F_{2,11} = .955$ ,  $p > 0.40$ ) or the adult sex ratio ( $r^2 = .025$ ,  $F_{1,12} = .308$ ,  $p > .55$ ).

It is possible that the highly significant correlations with number of females and group size may result from a strong linear interrelationship between these two variables ( $r^2 = .876$ ,  $F_{1,12} = 84.579$ ,  $p < .001$ ). Incorporating the quadratic components of both of these independent variables into a backward regression reveals that number of females is the principal factor because only this quadratic relationship remains significant (see Figure 1). The best-fit equation is:

$$\ln(\text{IBI}) = 8.533 - 4.096[\ln(F)] + 0.772[\ln(F)]^2 \quad (1)$$

where IBI is the interbirth interval (in months), and  $F$  is the number of females in the group.

Of the climatic variables, only temperature shows a significant relationship with interbirth interval, and again the best-fit equation was quadratic (Figure 2;  $r^2 = .633$ ,  $F_{2,11} = 9.482$ ,  $p = .004$ ). This relationship is independent of the number of females because there is no correlation between temperature and the number of females ( $r^2 = .026$ ,  $F_{1,12} = 0.318$ ,  $p > .55$ ). The best-fit equation with respect to temperature is:

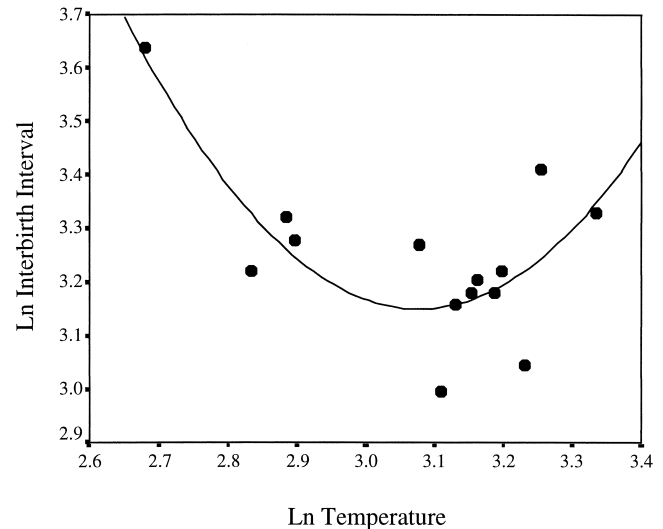
$$\ln(\text{IBI}) = 31.480 - 18.413[\ln(T)] + 2.992[\ln(T)]^2 \quad (2)$$

where  $T$  is the mean annual temperature ( $^{\circ}\text{C}$ ). No significant linear or quadratic relationships were found with respect to either rainfall (linear:  $r^2 = .110$ ,  $F_{1,12} = 1.487$ ,  $p > .20$ ; quadratic:  $r^2 = .195$ ,  $F_{2,11} = 1.331$ ,  $p > .30$ ) or altitude (linear:  $r^2 = .006$ ,  $F_{1,12} = .076$ ,  $p > .75$ ; quadratic:  $r^2 = .070$ ,  $F_{2,11} = 0.415$ ,  $p > .65$ ).

Entering both temperature and the number of females into the same regression model yields the following best-fit equation:

$$\ln(\text{IBI}) = 20.736 - 2.914 \ln(F) + 0.553[\ln(F)]^2 - 8.953 \ln(T) + 1.452[\ln(T)]^2 \quad (3)$$

Including both variables results in a significant improvement in the proportion of variance explained ( $r^2 = .839$ ,  $F_{4,9} = 11.682$ ,  $p = .001$ ).



**Figure 2**  
The relationship between interbirth interval and mean annual temperature ( $^{\circ}\text{C}$ ).

## DISCUSSION

Mean annual temperature and the number of adult females in the group between them explain 84% of the variance in interbirth intervals across baboon populations. Interbirth intervals showed a significant quadratic U-shaped relationship with the number of females. Because group size is a function of the number of females in the group, there is a superficial relationship between birth rate and group size that appears to conform to the predictions of Wrangham (1980). [Note that in this analysis we are considering interbirth intervals and not birth rates as originally discussed by Wrangham (1980), so the predicted direction of the relationship is reversed.] Wrangham (1980) proposed that interbirth intervals should initially decrease with troop size because larger troops have advantages in intergroup competition over smaller troops; however, interbirth intervals should then increase again as in-group competition becomes more intense as group size increases, resulting in a U-shaped relationship.

Although Wrangham's (1980) hypothesis may have some explanatory value within populations (e.g., Japanese macaques: Takahata et al. 1998), it is difficult to see how this relationship can be extended across populations, at least with respect to intergroup competition, since most of the parameters are population dependent. Both the competitive advantage that a troop can expect to gain and the intensity of intergroup competition for a troop of a given size will depend on the range of group sizes that exist within that population. Because the range of realizable group sizes is a function of the environmental conditions experienced by a population (Dunbar 1992b, 1996), the pattern observed here may not reflect the levels of competition proposed by Wrangham (1980) but instead reflect differences in group sizes between sites due to differential resource availability.

Both number of females and group size show significant quadratic relationships with rainfall (number of females:  $r^2 = .474$ ,  $F_{2,11} = 4.952$ ,  $p < .03$ ; group size:  $r^2 = .435$ ,  $F_{2,11} = 4.238$ ,  $p < .05$ ), with these effects being independent of the relationship between interbirth interval and temperature, since there is no relationship between rainfall and temperature ( $r^2 = .002$ ,  $F_{1,12} = 0.021$ ,  $p > .85$ ). This quadratic relationship can be explained by a trade-off between two opposing effects;

namely, the effects of resource availability on the one hand and intragroup competition on the other.

Rainfall is known to be a reliable predictor of primary productivity in sub-Saharan habitats (e.g., Deshmukh, 1984; le Houérou, 1984). Populations with low group sizes and numbers of females are likely to be occupying habitats with low primary productivity. Female mammals must attain a minimum nutritional plane before they can ovulate; consequently, irrespective of the physiological mechanism involved, physical condition is likely to be a key factor determining female fertility. Females occupying poor-quality habitats are thus likely to have longer interbirth intervals. Some evidence to support the relationship between interbirth intervals and the resource base comes from the observation that birth rates decline in a number of primate species once provisioning is removed (Japanese macaques: Mori, 1979; baboons: Hall, 1963; long-tailed macaques: van Schaik and van Noordwijk, 1985), and this reduction in birth rates is attributed to correlated declines in female body weight and condition.

Food availability does not completely explain the relationship with number of females, however, because it cannot account for the observed increase in interbirth intervals with large female group sizes. If food availability alone was underlying the relationship, then interbirth intervals would decline linearly as habitats become increasingly richer. Furthermore, because primary productivity is related to rainfall, we would also expect interbirth intervals to be directly related to rainfall if food availability was the sole explanation. Since the observed relationship does not conform to either of these predictions, other factors must be important.

Intragroup competition is likely to be significant in this respect. Irrespective of the level of resource base, increasing female group size inevitably leads to increasing levels of intragroup competition. Even where resources are not monopolizable and competition is primarily of the scramble type, larger group sizes result in increased within-group competition. Some evidence for this comes from baboons in Drakensberg, South Africa, where females in larger troops spent more time feeding and may have taken lower quality food items, despite the shallow resource gradient in this mountain population (Henzi et al., 1997). Furthermore, competition levels may be independent of resource availability. Dominance rank significantly influences interbirth intervals of baboons at Gilgil (Smuts and Nicholson, 1989); although nutritional factors may underlie this relationship, stress mechanisms are also likely to be important. Evidence from baboons in the Masai Mara National Reserve indicates that, for males at least, levels of stress hormones differ markedly with dominance rank (Sapolsky and Ray, 1989). Similar patterns have been observed for gelada, in which birth rates declined with declining dominance rank (Dunbar, 1984). This relationship is also likely to be stress related because subordinate individuals experienced much higher rates of attacks than dominant animals (Dunbar, 1984), despite the virtual absence of contest feeding competition in gelada due to the nature of their grazing lifestyle. In situations where intragroup feeding competition is more intense, however, these relationships become even more pronounced. At Mikumi, Wasser and Starling (1988) reported that female attack coalitions served to reproductively suppress their recipients, such that they experienced more cycles to conception and lengthened interbirth intervals. Wasser and Starling (1988) suggested that the attack coalition behavior among females functioned to reduce competitive conditions likely to be faced by the attackers' offspring, through a decrease in birth cohort size.

Although the relationship between interbirth intervals and number of females reported here may in part reflect the pattern predicted by Wrangham (1980), we would argue that

these findings probably provide better support for the van Schaik (1983) model. We suggest that, rather than reflecting intergroup competition as proposed by Wrangham (1980), the initial decline in birth intervals with increasing group size has more to do with the fact that resource availability limits the range of permissible group sizes for populations occupying poor-quality habitats. In other words, the apparent correlation between small group size and long interbirth intervals is actually due to the fact that poor-quality habitats independently constrain both group sizes and female fecundity. This factor may not be reflected in the data sets analyzed by van Schaik (1983) and Kumar (1995), and this may account for their more straightforward linear results.

We found no evidence for the relationship between interbirth intervals and adult sex ratio reported by Dunbar and Sharman (1983). However, Dunbar and Sharman (1983) concluded that their relationship also reflected female–female competition, specifically in this respect for access to males, and that this relationship may also have been underpinned by a relationship with rainfall. Furthermore, although Dunbar and Sharman (1983) found no specific relationship between birth rate and number of females, their linear correlational approach would have masked any quadratic effects that might have been present in their data. The findings of Wasser and Starling (1988), demonstrating a proximate role for female–female competition in reproductive suppression in baboons, further supports this suggestion.

Environmental factors, through their influence on primary productivity and thus female group size, therefore appear to be important determinants of birth interval variation in baboons. However, climatic factors may also have direct effects on baboon physiology and condition, and the influence of temperature and its costs in terms of thermoregulation are significant in this respect. We found a significant quadratic relationship between interbirth interval and temperature, with birth intervals being longer at extremes of low and high mean annual temperature. This also seems to reflect a trade-off between two temperature-related effects. Thermoregulatory considerations appear to impose energetic costs on female baboons: at low temperatures, females experience elevated energy expenditures to maintain a stable body temperature, the costs of which are reflected in longer interbirth intervals as ambient temperatures decline. Ohsawa and Dunbar (1984) showed that for gelada, reduced birth rates at lower temperatures were a consequence of the females' inability to carry fetuses to term when low temperatures placed heavy energetic demands on them. Similar results have been reported for klipspringer (Dunbar, 1990). At the same time, it seems that the energetic costs of keeping the body cool (Mount 1979) have the reverse effect (interbirth intervals increase with rising temperature), resulting in the pattern of birth intervals observed in this study.

Differences in interbirth intervals between baboon populations thus result from a complex interaction between environmental factors (notably temperature and food availability, which place energetic constraints on female condition) and demographic considerations (especially female group size, which results in increased female–female competition and elevated stress levels). These factors serve to constrain a female's maximum reproductive rate for a given population and group size. While females may then exhibit a certain degree of plasticity in birth rates in response to factors such as predation risk (e.g., Lycett et al., 1998), they are ultimately constrained by the limits imposed upon them by their ecological and demographic situation. Differentiating Equations 1 and 2 indicates that, for baboons, mean birth rates are maximal in groups containing on average 14.2 females in populations with a mean annual temperature of 21.7°C. These values

might serve to define optimal habitat for baboons, at least with respect to reproductive output.

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