

## REVIEW

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**Birth sex ratios in toque macaques and other mammals: integrating the effects of maternal condition and competition**

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**Abstract** Mammalian life histories suggest that maternal body condition and social dominance (a measure of resource-holding potential) influence the physical and social development of offspring, and thereby their reproductive success. Predictably, a mother should produce that sex of offspring which contributes most to her fitness (as measured by the number of her grandchildren) and that she is best able to raise within the constraints imposed by her condition, social rank, and environment. Such combined effects were investigated by monitoring variations in body condition (weight) and behavior of female toque macaques, *Macaca sinica* of Sri Lanka, in a changing forest environment over 18 years. Maternal rank, by itself, had no influence on offspring sex, but did affect maternal body condition. The combined effects of rank and condition indicated the following: mothers in robust condition bore more sons, whereas those in moderate condition bore more daughters, but both effects were expressed most strongly among mothers of high rank. Where the consequences of low rank were felt most acutely, as shown by poor condition, mothers underproduced daughters. Environmental quality directly influenced rank and condition interactions, and thus sex ratios. These relationships, and data from other mammals suggest an empirically and theoretically consistent pattern of sex allocation in mammals. New predictions integrate effects, proposed by Trivers and Willard, that are rooted in male mate competition, which is universal among polygynous mammals, with those of local resource competition

(and/or female reproductive competition), which are not universal and differ in intensity between the socioecologies and local environments of different species.

**Key words** Birth sex ratios · Sex allocation · Mammals · Natural population · *Macaca sinica* · Macaques

**Introduction**

What factors influence birth sex ratios? In polygynous mammals, maternal ability to determine the sex of her offspring, according to which sex contributes most to her fitness (as measured by the number of grandchildren produced), has been theoretically linked to either (a) maternal body condition, the Trivers and Willard (1973) (TW) model or, (b) local resource competition (LRC) among the non-dispersing sex (usually females) (Clark 1978), and (c) dominance rank, which reflects individual differences in LRC among the philopatric sex (Altmann 1980; Simpson and Simpson 1982; Silk 1983).

An additional aspect of female competition, generally ignored by the above models, concerns reproductive suppression of low-ranking females by high-ranking ones (e.g., Wasser 1983), an effect that may be independent of resource competition, but would lead to similar predictions as the LRC models alone.

A LRC hypothesis is often taken as a competing alternative to the TW model. Although empirical support exists for one or the other of these models, all too often it is marked by inconsistency and contradiction, sometimes from studies of the same species. These data and deliberations have been thoroughly reviewed (Clutton-Brock and Iason 1986; Hrdy 1987; Altmann and Altmann 1991; van Schaik and Hrdy 1991).

The roots of these inconsistencies appear to be both empirical and theoretical. For example, with few exceptions (e.g., Berman 1988), most studies attempting to test the TW model did not measure maternal condition directly. Instead, investigators used an assortment of

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secondary factors, such as diet, maternal environment, body size, dominance rank, and age, which were believed to be highly indicative of condition. Similarly, life history information critical to these models, such as maternal influence on offspring reproductive success, often remains unknown. Clearly, such limitations are not inherent to an hypothesis, but lie in its empirical application.

Secondly, the TW and LRC models are theoretically restricted, emphasizing different life history parameters and thereby underestimating others. The critical element of the TW model views differences in maternal fitness primarily as a function of maternal influence on variance in success among sons in male mate competition, with only little consideration for the additional potential effects owed to other aspects of female competition. The LRC hypotheses, on the other hand, focus on the effects of female resource competition on maternal fitness, and largely ignore those involving male mate competition. In short, among polygynous mammals, the TW model rests on male, the LRC models on female life history strategy (Emlen and Oring 1977; Wittenberger 1979).

The starting point of my argument is that a model of parental investment by offspring sex must accommodate simultaneously the life history parameters relevant to the strategies of both sexes. I wish to precede a discussion of this with an empirical integration of those factors indicated as salient to the TW model (maternal condition) and LRC models (dispersal and female dominance rank). This examination is based on an 18-year study of wild toque macaques *Macaca sinica* which inhabit natural dry evergreen forest at Polonnaruwa, Sri Lanka.

## Methods

### Study subjects and site

Toque macaques are sexually dimorphic primates, adult males and females weighing 5.2 and 3.0 kg on average, respectively. They are polygynous, organized into female-bonded, one-male or multimale groups (Eisenberg et al. 1972; Dittus 1977a; Wrangham 1980). Females are almost always philopatric, whereas all males emigrate from their natal group at adolescence (Dittus 1975, 1977a). Offspring socially inherit their rank from their mothers (Baker-Dittus 1985; Dittus 1988).

These monkeys were studied at Polonnaruwa, Sri Lanka, in their native tropical dry evergreen forest environment, which is subject to a monsoonal climate and marked seasonal and annual variations in rainfall (Dittus 1977b, 1985). The macaques' diet is based on the seasonally available foods in the forest (Dittus 1974). The study population in 1988 consisted of 24 different social groups comprising about 650 macaques, all of which were individually identified starting in 1968 following methods described by Dittus and Thorington (1981). The demographic, ecological, and social histories of all macaques have been monitored continuously since 1968 or 1971.

### Weighing and measuring wild macaques

Weights were recorded from animals in most social groups, at all months of the year, over a period of 18 years (1971–1988). Macaques were enticed to sit in a baited pan that was suspended from

a weighing pan hung in a jungle tree. All weights were recorded at dawn before animals fed. More than 250 macaques were captured and released in 1986 and 1987, and body segments were measured with calipers (Cheverud and Dittus 1992).

### Social dominance

Individuals were considered as socially 'dominant' when they consistently supplanted 'subordinates' from contested food and mates (Richards 1974) and employed typical gestures (Sade 1967). Dominance relations within groups of toque macaques were tested one or more times annually in all groups in the population over an 18-year period. Females were hierarchically ranked because dominance relations were linear and generally stable over many years (e.g., Dittus 1988). The number of females in the hierarchy within any one group was partitioned into three equal parts and the ranks of 'high,' 'mid,' and 'low' were assigned to the top, middle, and lowest thirds, respectively. To increase cell frequencies in statistical tests involving female weights, data were combined for mid- and low-ranking females. This was preferred over a simple bipartite division, because mid- and low-ranking females were somewhat underrepresented at the weighing scales, owing to competitive exclusion by high-ranking macaques.

### Female body condition

The Trivers and Willard (1973) model makes predictions about mothers whose conditions are either 'good' or 'poor': presumably they are in better or worse than mean condition. On the premise that resource competition should increase variance in condition (Hrdy and Williams 1983), it was of interest to establish additional categories corresponding to worse than 'poor' and better than 'good.' As a criterion for estimating condition, or amount of body reserves (Hanks 1981; Riney 1982), I selected deviations from the mean weight of an individual female that had been weighed at different times. I selected four objective categories of condition, demarcated by the mean and standard deviation (SD) in weight. Females weighing more than their own mean weight but less than one SD above it were considered to be in 'slightly robust' condition and as 'very robust' if their weight exceeded this. They were in 'moderate' condition if they weighed equal to their own mean weight or less than one SD below it, and were considered 'poor' if their weight was less than moderate.

I standardized the magnitude of SDs used for delimiting the condition categories. The mean SD from a well-studied subset of 33 females that had been weighed 10–20 times over an 18-year period was 0.21 kg, representing 7% of mean body weight (see Results). This value was taken as a universal norm for setting the fiducial limits around any female's own mean weight.

Sampling was limited to non-gravid, parous females aged 5.5 years or older, when female toque macaques approach mature skeletal growth (Cheverud et al. 1992). I did not use the Quetelet index (weight/height<sup>2</sup>) (Garrow 1983) to estimate condition because skeletal size was unknown for many females in my sample of long-term weight and birth records. However, skeletal trunk length was a significant predictor ( $P < 0.0001$ ) of mean body weight, accounting for about 27% of its variance (see Results). Thus, I used the direction and magnitude of deviations from a female's own mean weight to estimate condition.

### Effect of error in estimating condition on sex ratios

Estimates focus on change in condition: a score of robust indicates a recent improvement towards robust rather than static or mean robust; the score of poor points to a deterioration rather than to a chronically underweight state, and moderate points to little or no change from mean weight. I assume that an individual female's mean weight, over many years, approximates the moderate, or the phylogenetic norm (see Discussion) for females of her skeletal size.

But this would be an error for females in chronically better or worse conditions, and would have the following potential flaws.

With a large weight gain, a female in chronically poor condition might be wrongly scored as robust instead of moderate, but a typically overweight female would nevertheless be scored correctly as robust. With substantial weight loss, a usually robust female might be falsely scored as poor instead of moderate; however, a normally underweight female would still have the proper score of poor. In fact, the two potential scoring errors would be minimal, because females in a consistently stable condition were virtually absent (see Results). In this wild population, mothers (1) were subject to regular weight changes associated with year, season, and reproduction (Table 3); (2) experienced marked weight changes in relation to unusual environmental events (see Results), and (3) have low fat reserves compared to captives (see Discussion).

Nevertheless, it is important to know the effect of such *potential* scoring errors on measures of condition-specific sex ratios. They would either introduce random 'noise' into the data or, if the overall condition-related trends indicated in Table 4 were real, all errors in assigning condition would deflate the magnitude of the observed differences in sex ratios between adjacent condition classes, and their statistical significance.

Females in poor condition in this sample were not restricted to the environmentally impoverished years following the cyclone in 1978, but were distributed at random over 6 sampling years ( $G_w = 0.79$ ,  $df = 2$ ,  $P > 0.50$ ).

#### Reproductive seasons

All macaques in the population were censused monthly, and pregnant females once every few days in order to establish dates of birth for infants accurately. Conception dates were estimated from known birth dates, and generally occurred over a range of 10 months, peaking over 5 months (July to November). Any one female copulated during many months, but was normally in peak estrus for 2 weeks. The mean interval between births among mothers with surviving infants ( $n = 817$ ) was  $1.59 \pm 0.43$  years. Infants were classed as  $< 1$  year old.

#### Statistical analyses

Comparisons of all ratios were two-tailed  $G$ -tests ( $G_w$ ), with one degree of freedom (unless otherwise noted), adjusted with Williams' correction (Sokal and Rohlf 1981). The log-linear model and  $F$ -tests follow Wilkinson et al. (1996).

## Results

Variation in the birth sex ratio among toque macaques was examined in relation to (a) the independent effects of maternal rank, size, and body condition; (b) the combined influence of rank and condition, and (c) environmental change.

#### Birth sex ratios and dominance rank

The advantaged daughter (AD) corollary (Altmann 1980; Simpson and Simpson 1982; Silk 1983) of the LRC model (Clark 1978) predicts that high-ranking mothers should produce a surplus of daughters, whereas low-ranking ones should favor sons. Testing solely for the effects of maternal rank on offspring sex in the population of toque macaques, involving 1160 births, there were no significant

**Table 1** Comparison of birth sex ratios in toque macaques (*Macaca sinica*) according to differences in maternal dominance rank as measured one or more times annually from 26 different social groups over 18 years (1971–1989)

Maternal dominance rank	Number of births		Sex ratio (M:F)	$G_w$	$P$
	Male	Female			
High	218	196	1.112	1.17	$> 0.20$
Mid	182	190	0.958	0.17	$> 0.60$
Low	189	185	1.022	0.04	$> 0.80$
Total	589	571	1.032	0.28	$> 0.50$

differences in the numbers of sons and daughters born to females of different dominance ranks (Table 1).

#### Birth sex ratios and female body size

It is important to distinguish between population-wide variation in female mean weight (and body size) on the one hand, and fluctuations in individual weight over time on the other. Do females in the population differ in mean weight and size?

A well-studied subset, in which each of 33 females had been weighed 10–20 times over 18 years (443 weights), indicated that between-female variance of female weights was greater than that of repeated longitudinal measures from any one female. That is, the mean weights of individuals differed significantly ( $F_{32,410} = 29.61$ ,  $P < 0.0001$ ). Such weights were a significant function of trunk length ( $n = 58$ ,  $b_{y,x} = 0.11597$ ,  $t = 4.51$ ,  $P < 0.0001$ ). About 27% ( $r^2$ ) of variance in mean weight among females was accounted for by individual differences in body size, as measured by trunk length, among a subset of 58 females whose mean weights were based on more than two weight samples (mean = 7 samples per female).

Although a strict link between female size (or mean weight) and infant sex would be evolutionarily unstable in mammals (Fisher 1930; Maynard Smith 1982) and therefore would not be expected to occur, this relationship was nevertheless examined. The mean weights of 206 non-gravid females (each weighed 2–20 times), as well as trunk length, were tested against infant sex. Birth sex ratios did not differ significantly according to either variable (Table 2). However, such between-female comparisons are poor gauges of individual condition; for example, a small female in good health may weigh less than a large but feeble one.

#### Variation in maternal condition

Although the mean weights of females differed significantly (see above), a mature female's weight fluctuated over time within a broad range (mean range = 0.58 kg,  $SE = 0.03$ ,  $n = 33$ ), representing about 18.4% of mean body weight. The average digression from mean weight was 0.15 kg or 4.8% of mean body weight, and did not

**Table 2** Birth sex ratios in relation to the mean weights of 206 non-gravid adult female toque macaques over an 18-year period, and to the trunk lengths of 146 adult females aged 5.5 years or older at Polonnaruwa, Sri Lanka. The observed ranges of mean weights (2.35–3.99 kg) and trunk lengths (24.1–31.5 cm) were divided into three classes of equal interval

Maternal measure	Number of females	Number of births		Ratio M:F	$G_w$	$P$
		Male	Female			
<b>Weight (kg)</b>						
2.35–2.90	76	144	157	0.917	0.56	>0.45
2.91–3.44	109	280	273	1.026	0.09	>0.75
3.45–3.99	21	75	73	1.027	0.03	>0.85
<b>Trunk length (cm)</b>						
24.1–26.6	25	51	63	0.810	1.26	>0.25
26.7–29.0	92	253	252	1.004	0.00	>0.95
29.1–31.5	29	121	121	1.000	0.00	>0.95

differ significantly ( $F_{32,410} = 0.90$ ,  $P = 0.636$ ) among females weighed 10–20 times.

Female condition varied, for example, in relation to environmental dissimilarities between years and seasons (months), and by contrasts in habitat quality among social groups. It also deteriorated as a function of the age of dependent or nursing infants (Table 3).

**Birth sex ratios and maternal condition**

Although the physiological mechanism by which mothers influence fetal sex is still nebulous, it is most likely determined shortly after conception (James 1985). The

**Table 3** Long- and short-term variations in body weight among non-pregnant fully grown adult female toque macaques at Polonnaruwa, in relation to salient parameters affecting them. *Infant age classes* were by month: <1, 1–<2, 2–<4, 4–<6, 6–<8, 8–<10, 10–12. ( $F$  ANOVA  $F$ -test)

Parameter affecting female weight	Variable tested	Number of females weighed	Statistical test	$df$	$P$
Year ( $n = 21$ )	Annual means of all individual weights	941	$F = 2.91$	20	<0.001
Month ( $n = 12$ ) over 13 years	Monthly means of all individual weights	943	$F = 2.64$	11	<0.002
Social group ( $n = 14$ )	Mean of mean female weights per group	131	$F = 5.90$	13	<0.001
Age of nursing infant	Regression of weights on seven infant age classes	485	$b_{yx} = -0.042$ $t = 3.83$	5	<0.001

interest here, then, is to consider maternal condition at conception. Given the pattern of variation in condition, only those weights measured <2.5 months (mean = 1.1 months) prior to conception were considered as representative of conception. This important constraint sharply and randomly reduced the number of weights available for retrospective testing. Four classes of female condition were established (see Methods).

The column totals in Table 4 reflect the influence of condition on sex ratios. Between adjacent condition classes these totals were markedly and significantly different comparing poor with moderate condition (M:F = 12:3, 15:31;  $G_w = 10.28$ ,  $df = 1$ ,  $P = 0.001$ ), and moderate with slightly robust condition (M:F = 15:31, 29:17;  $G_w = 8.54$ ,  $df = 1$ ,  $P = 0.003$ ), but were similar and did not differ significantly between the two robust classes (M:F = 29:17, 14:10;  $G_w = 0.14$ ,  $df = 1$ ,  $P = 0.705$ ). This suggested that the underlying condition-related processes affecting sex ratios were similar for all robust females. Data from these two classes were therefore combined in further analyses, and hereafter will be referred to as simply ‘robust’ [corresponding conceptually to the ‘good’ condition of Trivers and Willard (1973)].

There were significant differences in the sex ratio in relation to maternal condition at conception, such that mothers in robust and poor conditions produced more sons, whereas those in moderate condition had more daughters (Table 4).

**Combined effects of maternal condition and dominance rank**

Does competitive ability (or rank) introduce variation in maternal condition, and thereby secondarily influence sex ratios? Female dominance relations were stable over time (Dittus 1988) and a female’s dominance rank at conception was taken as that measured on the date nearest to her conception (generally within 6 months).

A three-way log-linear model (Wilkinson et al. 1996) which incorporated the interactions between (1) rank and condition and (2) condition and sex ratios, best explained the observed sex ratios (Table 5). Conditional goodness-of-fit tests indicated that, compared to a model of independence among the three variables, rank significantly influenced condition [likelihood ratio chi-square (LRCS) = 11.09,  $df = 2$ ,  $P < 0.01$ ], which in turn

**Table 4** Toque macaque birth sex ratios (male:female) according to dominance rank and maternal body condition attained prior to conception

Maternal dominance rank	Maternal condition attained					Total
	Poor	Moderate	Slightly robust	Very robust	All robust	
High	1:0	6:15**	17:6***	6:5	23:11**	30:26
Mid + low	11:3**	9:16	12:11	8:5	20:16	40:35
Total	12:3***	15:31***	29:17* <sup>1</sup>	14:10	43:27* <sup>2</sup>	70:61

\*<sup>1</sup> $P = 0.077$ ; \*<sup>2</sup> $P = 0.056$ ; \*\* $P < 0.05$ ; \*\*\* $P < 0.02$

**Table 5** Comparison between the observed sex ratios of Table 4, and the corresponding expected frequencies and likelihood ratio residuals. The best-fitting log-linear model, estimating the latter two parameters, incorporated the effects of interactions between (1) rank and condition and (2) condition and sex ratio (likelihood chi-square = 1.84,  $df = 3$ ,  $P = 0.607$ )

Maternal dominance rank		Maernal condition					
		Poor		Moderate		Robust	
		Male	Female	Male	Female	Male	Female
High	Observed	1	0	6	15	23	11
	Expected	0.800	0.200	6.848	14.152	20.886	13.114
	Residual	0.046	0.400	0.110	0.050	0.207	0.361
Mid and low	Observed	11	3	9	16	20	16
	Expected	11.200	2.800	8.152	16.848	22.114	13.886
	Residual	0.004	0.014	0.085	0.043	0.209	0.307

affected sex ratios (LRCS = 14.54,  $df = 2$ ,  $P < 0.001$ ). It also indicated no general effect of rank on sex ratios (LRCS = 0.00,  $df = 1$ ,  $P > 0.98$ ), in accordance with the results of Table 1. But a closer examination of the data (Table 4) suggested that the bias for daughters by females in moderate condition, and that for sons by robust ones were strongest (and significant only) among high-ranking females. Similarly, where the negative rank effects were felt most strongly (as manifest by poor condition) it also underlay a strong bias against daughters.

Viewed solely in terms of the original Trivers and Willard (1973) model, 'poor'- and 'good'-condition females would encompass the poor + moderate and robust classes of Table 4, respectively (see Methods). Comparing pooled sex ratios of females above (M:F = 43:27) with those equal to or below (M:F = 27:34) mean condition only indicates a significant shift in the sex ratio in support of these authors' model ( $G_w = 3.83$ ,  $df = 1$ ,  $P = 0.050$ ).

#### Environmental effects

It follows that infant sex may be influenced by any factor, such as environmental quality, which affects maternal condition, and the negative impact of LRC on the survival of infant daughters (Dittus 1977a). At times of environmental stress and negative population growth at Polonnaruwa [a drought in 1974 and a cyclone in 1978 (Dittus 1985)], significantly greater proportions (53–91%) of 93 non-gravid females dropped below their own mean weights than during non-stress years (45% of 506 females;  $G_w = 21.84$ ,  $df = 2$ ,  $P < 0.0001$ ). During the same periods, infant (< 1 year old) mortality rose to 39.1% among males ( $n = 115$ ), and 45.5% among females ( $n = 88$ ), compared to 26.7% ( $n = 453$  males) and 30.6% ( $n = 468$  females) during normal years. Overall, among low- and mid-ranking mothers, daughters died at a greater rate (35.5% of 363 births) than sons (28.6% of 360 births); but this was not true for high-ranking mothers (30.3% of 208 sons, and 28.0% of 193 daughters). During stress periods, birth sex ratios were significantly male biased (M:F = 160:108,  $P < 0.005$ ), but not during 10 non-stress years (M:F = 429:463,  $P > 0.25$ ).

#### Discussion

The two proximal cues, maternal condition and competitive ability, indicated here as influencing sex of offspring produced in toque macaques, represent two ways by which mothers may promote their offsprings' future reproductive success. They are expected to reflect different underlying processes and evolutionary histories. I will consider the data from toque macaques in this light, and in the broader context of comparison with other polygynous mammals.

#### Information loss

Maternal rank has often been tested as the sole factor affecting mammalian sex ratios (reviews in Clutton-Brock and Iason 1986; Hrdy 1987). Considering Tables 1 and 4, when sex ratios were summed by rank only, it obscured differences owing to maternal condition (and environment), as well as the subtle effects of rank under different conditions. Such information loss had been suspected in other studies, where sex ratios were pooled over many years or social groups differing in environment, among macaques *Macaca mulatta* (Small and Smith 1985; Rawlins and Kessler 1986; Small and Hrdy 1986), *M. fuscata* (Noyes 1982), and *M. arctoides* (Rhine 1994). It may have contributed to the absence of rank-based effects on sex ratios in some other studies as well, e.g., *M. fuscata* (Fedigan et al. 1986), *M. mulatta* (Berman 1988).

#### Cue for maternal condition relative to others

'Maternal condition' implies a quality, such as ample body reserves (Hanks 1981; Riney 1982), enabling mothers to contribute to the health and growth of their offspring. In the TW model, it is a trait serving inter-maternal competition to produce the strongest sons as contestants for mates. In toque macaques and most other mammals (Greenwood 1980), sons disperse and mate distant from their natal areas, competing not only with peers, but also with rivals conceived in different years, social groups, and under potentially disparate

ecological conditions. When a mother determines which sex of offspring to produce, based solely on conditional cues, how does she compare herself to the mothers of her son's future rivals, when these mothers are possibly too remote for communication and subject to different environments? The mechanism for making efficient comparisons with contemporary females in the local breeding population is elusive, even if dispersal were highly localized.

A broader interpretation of the TW model suggests that a cue to a mother's condition relative to others emanates from changes within her own body in comparison to a predictable species-specific 'reference point' of mean adult condition, which has been adapted to the historical modal social organization and natural environment of the species. This reference point would be subject to natural selection and indicates that condition which, on average, contributes most to fitness.

Accordingly, chronically overweight adults, as are commonly found in provisioned settings (e.g., Berman 1988) would represent outliers of adult condition in the ecological history to which parental investment patterns presumably are adapted.

In mammals, the most variable constituent of the body is adipose tissue (Pond 1984) and it has a consequential effect on reproduction (Frisch and McArthur 1974; McFarland 1992). It seems logical that fatness should be an important cue for condition. The mean fatness (percent of body weight contributed by fat) normally seen in cercopithecine females living in food-enriched captivity was 12.7% among pig-tailed macaques *M. nemestrina*, (Walike et al. 1977; McFarland 1992), 12.6% in *M. fascicularis* (Pond and Mattacks 1987), 17.1% for rhesus *M. mulatta* (Kemnitz et al. 1989), 16.8% among baboons *Papio cynocephalus* (Rutenberg et al. 1987), and 23% for garbage-feeding feral baboons (Altmann et al. 1993). The average maximum weight change (range) in female toque macaques was 18.4% of mean body weight, corresponding more or less to the mean fatness of provisioned cercopithecine females. The range (9.6% of mean weight) of the average digression from mean weight in toque macaques was less than the above measures but more than the mean fatness (2%) of wild-feeding baboons (Altmann et al. 1993). These comparisons suggest that condition in toque macaques (1) was probably mostly a function of fatness and (2) typically was less than that of provisioned counterparts.

The weight of all female toque macaques was subject to regular change, and the mean magnitude of such fluctuations did not differ significantly ( $P=0.636$ ) among females. Nevertheless, females differed significantly ( $P<0.0001$ ) in their mean weights, and only 27% of the sample variance was attributed to size (skeletal height), suggesting that some females were persistently in better or worse condition than others. The potential error of this on analyses was minimal (see Methods). Females whose mean condition was persistently different from the norm would be expected to behave

most frequently in the manner typical of their usual condition.

#### Assumptions and the TW model

The TW model requires that male condition (usually body size) is linked to success in male mate competition (often measured in terms of dominance rank) and therefore to male fitness. In male toque macaques, high rank was positively associated with body weight (Dittus 1979), as well as reproductive success (Keane et al. 1997). Similar links have been observed in red deer (Clutton-Brock et al. 1988) and elephant seals *Mirounga angustirostris* (Le Boeuf 1972, 1974). Male size covaried with dominance (and plausibly reproductive success) in red deer *Cervus elephus* (Scuttie 1982), reindeer *Rangifer tarandus* (Skogland 1983), mountain sheep *Ovis canadensis* (Geist 1971), bison *Bison bison* (Maher and Byers 1987; Wolff 1988), heteromyid rodents (Fleming 1974), and marsupials (Kaufmann 1974). Male size relations were unknown in other studies of primates, but male rank was associated with reproductive success in wild howler monkeys *Alouatta seniculus* (Pope 1990), long-tailed macaques *Macaca fascicularis* (de Ruiter et al. 1993) and baboons *P. cynocephalus* (Altmann et al. 1996). In captivity, a similar relation was evident among mandrills *Mandrillus sphinx* (Dixson et al. 1993; Wickings et al. 1993), Barbary macaques *Macaca sylvanus* (Paul et al. 1993), patas monkeys *Erythrocebus patas* (Oshawa et al. 1993), but not rhesus *M. mulatta* (Berard et al. 1993; Smith 1993) or Japanese macaques *M. fuscata* (Inoue et al. 1993).

The TW model also rests on the assumption that maternal condition influences that of offspring at the end of the period of parental care. This has been demonstrated in a broad spectrum of mammals [marsupial mouse *Antechinus stuartii* (Dickman 1988); rodents *Mesocricetus auratus* (Labov et al. 1986), *Myocastor coypus* (Gosling 1986); red deer (Clutton-Brock et al. 1988); bighorn sheep *O. canadensis* (Hogg et al. 1992); and see citations in Trivers and Willard (1973)]. Similarly, good condition enhanced survival [e.g., macaques (Mori 1979); marsupials (Austad and Sunquist 1986); red deer (Clutton-Brock et al. 1982)] and persisted to influence offspring condition at breeding age (Trivers and Willard 1973; Gosling 1986; Clutton-Brock 1988). Although these relationships, especially the last, have not been tested among many species (reviewed by Clutton-Brock and Iason 1986; Hrdy 1987), including toque macaques, I made this assumption here.

Finally, the TW model supposes greater variance in the reproductive success of males than females (Wade 1979). In toque macaques, sex differences in age-specific reproductive values (Dittus 1979), as well as variation in male reproductive success (Keane et al. 1997) imply greater variance in male than female reproduction. Such differences have been found in other mammals [red deer (Clutton-Brock et al. 1988); elephant seals (Le Boeuf and Reiter 1988); lions (Packer et al. 1988)]. But, this

pattern was either absent or obscured in vervet monkeys *Cercopithecus aethiops*, where predation caused high mortality (Cheney et al. 1988).

Given the known life history of toque macaques, and assuming that mothers in robust condition produce reproductively superior sons, the results (Table 4) are consistent with the TW model. But they also indicate a more complex pattern of sex allocation, wherein maternal dominance plays a role.

### Competition and the TW and LRC hypotheses

Dominance rank, often measured in terms of priority of access to resources (Richards 1974), reflects an individual's ability to monopolize resources relative to other members of its society. In species with well-developed dominance hierarchies, rank may influence (1) maternal condition and that of offspring, (2) sex differences in offspring survival, and (3) female birth rates (or degree of socially induced reproductive suppression) as detailed below.

The log-linear test (Table 5) indicated a significant ( $P < 0.01$ ) positive effect of maternal rank on condition in toque macaques. Similarly, maternal rank correlated with body weight in other cercopithecine primates *M. fuscata* (Mori 1979), *M. mulatta* (Small 1981), *C. aethiops* (Whitten 1983), and red deer (Clutton-Brock et al. 1988). High-ranking mothers also produced heavier offspring [*M. fuscata* (Mori 1979) and *M. mulatta* (Meikle and Vessey 1988)] and reproductively superior sons [*C. elaphus* (Clutton-Brock et al. 1984); *M. mulatta* (Meikle and Vessey 1988); *M. sylvanus* (Paul et al. 1992)]. The general pattern is consistent with the suggestion that maternal rank accentuates variance in maternal condition (Hrdy and Williams 1983) and so the effects as postulated by the TW hypothesis.

The significance of the effect of rank on body condition, and so to the TW model, has generally been underestimated. Instead, competition was viewed solely in light of LRC hypotheses.

In toque macaques (Dittus 1979) and other cercopithecine primates, success in resource competition and reproduction was determined by a female's rank in the dominance hierarchy (Drickamer 1974; Silk et al. 1981; Fairbanks and McGuire 1984; Simpson and Simpson 1985; Meikle and Vessey 1988; Gomendio et al. 1990). Daughters inherited their mother's rank and remained in their natal group for life and so competed with resident females for locally limited resources (Kawamura 1958; Sade 1967; Missakian 1972; Cheney 1977; Dittus 1977a; Berman 1980; Hausfater et al. 1982; Baker-Dittus 1985). Low-ranking daughters typically experienced high mortality owing to harassment from dominant residents, whereas all sons emigrated and were spared such a fate (Dittus 1977a, 1979, 1980; Silk 1983; Simpson and Simpson 1985; Rhine et al. 1988). Such harassment of subordinate females may also involve fitness loss through reproductive suppression, in lieu of

strict resource competition, as has been suggested for baboons *Theropithecus gelada* (Dunbar and Dunbar 1977) and *P. cynocephalus* (Wasser 1983). Similarly, white-tailed deer *Odocoileus virginianus* suffered a drop in fecundity and fawn survival when they were expelled by dominant does from limited birthing refuges (Ozoga et al. 1982) and food resources (Verme 1985; Caley and Nudds 1987).

Toque macaques precisely fit the requirements for LRC and AD effects on sex ratios, yet maternal rank had no direct impact on the sex of infants produced (Tables 1 and 5), thus seeming to refute LRC predictions. But when the effects of dominance rank were considered together with those of condition, LRC effects were indeed evident.

### Integrated effects of condition and rank on sex ratios

The following interpretations of the results (Table 4) integrate the life history relationships as outlined above. (1) Among dominant robust mothers, the effects of rank and condition coincide in a synergy leading to the overproduction of sons (presumably physically and socially superior), in support of TW predictions. (2) One would expect subordinate rank to weaken this synergy (to produce superior sons) among robust mothers and thus, the tendency to overproduce sons. (3) Lack of robust condition is a greater handicap for raising superior sons than daughters, whose future fitness is less dependent upon physical strength than high rank. Dominant mothers in moderate condition overproduced daughters in support of both TW and LRC predictions. Although dominant mothers were rarely in poor condition, one would expect them to behave like those in moderate condition. (4) The absence of a strong tendency in favor of either sex is consistent with the simultaneous, but opposing action of TW and LRC effects among subordinate mothers in moderate condition. (5) Low-ranking mothers in poor condition are expected to produce poor-quality offspring, among which sons should predominate because they are subject to less LRC-induced mortality than daughters. This effect was accentuated during years of environmental impoverishment.

### Phylogeny of maternal investment: predictions

The life history parameters of toque macaques considered here are also typical of other polygynous mammals with highly structured societies. The pattern found here, therefore, should be of broader relevance. But, in generalizing these predictions to other polygynous mammals, the relative importance of maternal condition and rank is expected to vary with differences in sexual dimorphism, social organization, ecology, and environment among species (and populations).

Phylogenetically, the effects predicted by TW coincide with the evolution of polygyny and sexual dimor-

phism. From the relatively dispersed and asocial life styles to the more cohesive and hierarchically ordered matrifocal societies, most mammals have retained these features, regardless of the many ecological and behavioral variants in social organization (Eisenberg 1981). Therefore, *the TW effects should be nearly universal among mammals to the extent that sexual dimorphism is expressed or polygyny is practiced* (except see Ralls 1976; Kleiman 1977).

Polygynous mammals differ, however, both in the manner and degree to which resource competition affects female fitness (Eisenberg 1966, 1981; Emlen and Oring 1977; Wittenberger 1979; Clutton-Brock 1988). Secondly, therefore, *additional refinements in maternal behavior should be expressed solely in those species whose social order involves resource competition (or female reproductive competition) and whose ecologies permit the monopolization and defense of limited resources* (Dittus 1977a, 1979; Wrangham 1980; Armitage 1987). The effects of LRC reflect supplemental, not alternative, social adaptations typical of complex social derivatives.

The different LRC models trace social evolution. The original LRC model (Clark 1978) referred to prosimians (*Galago crassicaudatus*) and suggested that when mothers compete with their philopatric daughters for limited resources, but not with their dispersing sons, mothers produce more sons. The AD hypothesis – high-ranking mothers should produce daughters, low-ranking ones sons (Altmann 1980; Simpson and Simpson 1982) – is a refinement of LRC to accommodate differences in competitive ability among females living in cohesive hierarchically ordered matrifocal societies typical of macaques and baboons, which evolved from the more conservative prosimian stocks (Eisenberg et al. 1972). Neither the LRC or the AD model can invalidate the TW hypothesis because they emphasize separate aspects of mammalian life histories.

Empirical tests have predictable constraints. Chronically overweight females, as are common in captive settings, represent evolutionary outliers of condition and therefore are biased test samples. Berman (1988), for example, estimated degrees of obesity in colony-raised rhesus macaques (*M. mulatta*), and found no relationship between fatness and sex ratios. She suggested that provisioned females were rarely lean enough to show condition-related sex ratio adjustments. Likewise, in captivity, the effects of rank and competition on survival and sex ratios are likely to be attenuated or eliminated, depending upon the amount and the temporal and spatial distribution of food resources (Wolfe 1984).

#### Relevant variables and levels of analysis

Facultative adjustment of sex ratios is advantageous for species in which there are contingent benefits of producing either male or female offspring and for which these contingencies change both during the reproductive lifespan of an individual and between generations. It

presumes an inherited sensitivity to contingent cues that may be subject to natural selection. The myriad of potential cues for a species (social, demographic, physiological, environmental) pose a problem for identifying the appropriate level for analysis. Those highlighted here, body condition (predicting body reserves) and social rank (competitive ability), being intrinsic to the individual, are proximate to the physiological mechanisms which affect offspring sex, even though the mechanism itself is unclear (James 1985). Also, condition and rank are sensitive to extrinsic (environmental) effects (Dittus 1988) and this responsiveness can be measured.

Pointing to the importance of LRC or rank (predictors of offspring survival) and body condition, however, does not imply an exclusive interaction. Conceivably, any agent linked to offspring sex, enhancing maternal fitness, and predictable by the mother at conception may be a cue for adaptive maternal adjustments of the sex ratio and modification of TW effects. The production of one sex may be favored when there is local resource enhancement through cooperation of individuals of that sex (Emlen et al. 1986), or when such cooperation augments success in male-male competition for mates, as evident in lions (Packer and Pusey 1987). Likewise, predictors of sex-specific offspring survival, other than LRC, may also be involved, as in some studies of baboons *P. cynocephalus* (Wasser and Norton 1993) and horses *Equus caballus* (Monard et al. 1997). Unusual environments may swamp the norms discussed here: Cheney et al. (1988) suggested that vervets *C. aethiops* showed no sex ratio bias under intense predation or disease, because female rank had little or no influence on offspring survival. Or, in small groups, additional female members collaborate in intergroup competition and thereby contribute to female fitness through local resource enhancement.

#### Other polygynous mammals

As condition has rarely been measured, it is impossible to assess its influence on most extant data. I have selected a few studies here, where a reasonable prediction of female condition might be attempted.

In well-provisioned environments, the effect of rank on resource acquisition ability and condition should be relaxed and accompanied by a shift of all mothers to a relatively higher nutritional plane (and ability to invest). Hence, a greater proportion of mothers would be in robust condition, and the negative competitive effects on low-ranking females and their philopatric daughters would be attenuated (although reproductive suppression may still operate). The sex ratios of such well-fed high-ranking cercopithecine females (presumably robust) favored sons, whereas those of low-ranking ones favored daughters in *M. sylvanus* (Paul and Kuester 1987), *M. mulatta* (Meikle and Vessey 1988), and *M. fascicularis* (van Schaik et al. 1989), there being a positive correlation between the proportions of sons from high-ranking

mothers and food-driven positive population growth rate (reduced competition and increased probability of robustness) as measured across several cercopithecine species (van Schaik and Hrdy 1991). Robust female white-tailed deer *O. virginianus* inhabiting agricultural “corn-forests” (Nixon 1971; Haugen 1975), and well-fed captive wolves *Canis lupus* (Mech 1975) likewise overproduced sons.

Well-fed robust females are likely to be scarce in nature. This may explain why, among wild baboons *P. cynocephalus*, dominant mothers (on average, presumably not robust) overproduced daughters and low-ranking ones sons (Altmann 1980; Altmann et al. 1988). Similar sex ratio trends were evident where resource competition was judged to be well expressed across several primate genera (Johnson 1988), including captive macaques *Macaca radiata* (Silk 1983) and *M. mulatta* (Simpson and Simpson 1982; Nevison et al. 1996) and other mammals where resource competition strongly influences their reproductive success: marmots *Marmota flaviventris* (Armitage 1987), white-tailed deer (Verme 1985; Caley and Nudds 1987), reindeer (Skogland 1986), zebras *Equus zebra* (Lloyd and Rasa 1989) and wolves (Mech 1975).

The influence of female competition on maternal investment should be absent or attenuated in mammals where the social and ecological bases for such competition are lacking or poorly developed. Nevertheless, investment should still be influenced in accordance with the TW model. Data from such species support this prediction. An overproduction of sons by mothers in robust condition, and of daughters by non-robust mothers, has been found consistently among marsupials *Didelphis marsupialis* (Austad and Sunquist 1986); rodents *Mus* spp. (Rivers and Crawford 1974), *Myocastor coypus* (Gosling 1986) and *Mesocricetus auratus* (Labov et al. 1986); seals *Arctocephalus galapagoensis* (Trillmich 1986) and *Zalophus californianus* (Ono et al. 1987), and some ungulates *C. elaphus* (Clutton-Brock et al. 1984) and *B. bison* (Rutberg 1986).

During their lifetimes, mothers are expected to alter their behavior in tune with variations in social structure and LRC. Female dasyurid marsupials *Antechinus* may breed one or more seasons depending on their longevity. Competition among philopatric mothers and daughters for limited resources and breeding space is therefore either absent (when semelparous) or common in varying degrees (when iteroparous). In normal environments, and in the absence of competitors, primiparous mothers (presumably in average condition) overproduced daughters but then switched to sons (which emigrate) as increasing numbers of daughters competed and so diminished maternal fitness (Cockburn et al. 1985). In the presence of food superabundance, *A. stuartii* mothers were robust and overproduced sons whose weights and survival were greater than normal (Dickman 1988). These data point to shifts in investment strategy (TW and LRC) to maximize maternal fitness under different social and environmental conditions (see also Cockburn 1994).

## Other models and empirical limitations

Independently, van Schaik and Hrdy (1991) had also suggested that sex ratios are influenced simultaneously by TW and LRC effects, with respect to mostly food provisioned captive primates. In a top-down analysis, using population growth rate as a proxy for resource availability and intensity of competition, they showed that the proportion of males produced by high-ranking females (compared to that by low-ranking ones) increases with population growth rate. Data from toque macaques during different phases of population growth support this view largely because, in this instance, the population growth rate was tracked by female condition (see Results: Environmental effects). The advantage of their model is ease of measurement of the proxy, which at the same time, however, is also its limitation: (1) it falters when population growth is influenced primarily by factors other than LRC, such as predation, disease, human disturbance (e.g., Cheney et al. 1988; Rhine et al. 1992), or reproductive suppression (Dunbar and Dunbar 1977; Wasser 1983); (2) in particular, it confines the TW effect to situations of reduced LRC (presumed prevalent in resource-rich and growing primate populations), whereas the model proposed here views the TW effect as applicable to a broad spectrum of socioecological conditions, including intense LRC (as in toque macaques), among all polygynous mammals whose traits concur with the underlying assumptions of the TW model; (3) it regards the TW and LRC effects as products of counteracting selection, whereas the model here regards LRC as a modifier of TW effects, in a way either to corroborate or to oppose them (depending upon the combination of maternal condition and rank in relation to the local environment). The present model regards LRC as one important predictor among others that anticipate differences in fitness between sons and daughters, which may modify TW effects and maternal allocation by offspring sex.

Like other models of sex allocation, the present one also has its limitations insofar as it is built partly on key assumptions. The following questions, in particular, need broader testing. (1) Does maternal condition affect that of their sons at breeding age, and how is this modified by male dispersal? (2) Does the reproductive success of sons born to low-ranking mothers in poor condition indeed outweigh loss of maternal fitness through mortality among daughters? Similarly, the impact of extrinsic factors is rarely measured; for example, do mothers adjust their investment according to (1) sex differences in mortality over which mothers have no control, such as predation (e.g., Cheney et al. 1988) or unknown causes (Wasser and Norton 1993) or (2) socioecological contrasts among social groups which affect individual fitness (e.g., Dittus 1986; Cheney and Seyfarth 1987; O'Brien and Robinson 1987; Robinson 1988)?

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## References

- Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, Mass
- Altmann M, Altmann J (1991) Models of status-correlated bias in offspring sex ratio. *Am Nat* 137:542–555
- Altmann J, Hausfater G, Altmann SA (1988) Determinants of reproductive success in savannah baboons, *Papio cynocephalus*. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 403–418
- Altmann J, Schoeller D, Altmann SA, Muruthi P, Sapolsky RM (1993) Body size and fatness of free-living baboons reflect food availability and activity levels. *Am J Primatol* 30:149–161
- Altmann J, Alberts SC, Haines SA, Dubach J, Muruthi P, Coote T, Geffen E, Cheesman DJ, Mututua RS, Saiyalel SN, Wayne RK, Lacy RC, Bruford MW (1996) Behavior predicts genetic structure in a wild primate group. *Proc Natl Acad Sci USA* 93:5797–5801
- Armitage KB (1987) Do female yellow-bellied marmots adjust the sex ratios of their offspring? *Am Nat* 129:501–519
- Austad SN, Sunquist ME (1986) Sex-ratio manipulation in the common opossum. *Nature* 324:58–60
- Baker-Dittus AM (1985) Infant- and juvenile-directed care behaviors by adult toque macaques, *Macaca sinica*. PhD thesis, University of Maryland, College Park
- Berard JD, Nuernberg P, Epplen JT, Schmidtke J (1993) Male rank, reproductive behavior, and reproductive success in free-ranging rhesus macaques. *Primates* 34:481–489
- Berman CM (1980) Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. *Int J Primatol* 1:153–170
- Berman CM (1988) Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. *Am Nat* 131:307–328
- Caley MJ, Nudds TD (1987) Sex-ratio adjustment in *Odocoileus*: does local resource competition play a role? *Am Nat* 129:452–457
- Cheney DL (1977) The acquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. *Behav Ecol Sociobiol* 2:303–318
- Cheney DL, Seyfarth RM (1987) The influence of intergroup competition on the survival and reproduction of female vervet monkeys. *Behav Ecol Sociobiol* 21:375–386
- Cheney DL, Seyfarth RM, Andelman SJ, Lee PC (1988) Reproductive success in vervet monkeys. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 384–402
- Cheverud JM, Dittus WPJ (1992) Primate population studies at Polonnaruwa. II. Heritability of body measurements in a natural population of toque macaques (*Macaca sinica*). *Am J Primatol* 27:145–156
- Cheverud JM, Wilson P, Dittus WPJ (1992) Primate population studies at Polonnaruwa. III. Somatometric growth in a natural population of toque macaques (*Macaca sinica*). *J Hum Evol* 23:51–77
- Clark AB (1978) Sex ratio and local resource competition in a prosimian primate. *Science* 201:163–165
- Clutton-Brock TH (ed) (1988) Reproductive success. University of Chicago Press, Chicago
- Clutton-Brock TH, Iason GR (1986) Sex ratio variation in mammals. *Q Rev Biol* 61:339–374
- Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago
- Clutton-Brock TH, Albon SD, Guinness FE (1984) Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308:358–360
- Clutton-Brock TH, Albon SD, Guinness FE (1988) Reproductive success in male and female red deer. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 325–343
- Cockburn A (1994) Adaptive sex allocation by brood reduction in antechinuses. *Behav Ecol Sociobiol* 35:53–62
- Cockburn A, Scott MP, Dickman CR (1985) Sex ratio and intra-sexual kin competition in mammals. *Oecologia* 66:427–429
- Dickman CR (1988) Sex ratio variation in response to interspecific competition. *Am Nat* 132:289–297
- Dittus WPJ (1974) The ecology and behavior of the Ceylon toque monkey, *Macaca sinica*. PhD thesis, University of Maryland, College Park
- Dittus WPJ (1975) Population dynamics of the toque monkey (*Macaca sinica*). In: Tuttle RH (ed) Socioecology and psychology of primates. Mouton, The Hague, pp 125–152
- Dittus WPJ (1977a) The social regulation of population density and age-sex distribution in the toque monkey. *Behaviour* 63:281–322
- Dittus WPJ (1977b) The ecology of a semi-evergreen forest community in Sri Lanka. *Biotropica* 9:268–286
- Dittus WPJ (1979) The evolution of behaviors regulating density and age-specific sex ratios in a primate population. *Behaviour* 69:265–302
- Dittus WPJ (1980) The social regulation of primate populations: a synthesis. In Lindburg DG (ed) The macaques: studies in ecology, behavior and evolution. Van Nostrand Reinhold, New York, pp 263–286
- Dittus WPJ (1985) The influence of cyclones on the dry evergreen forest of Sri Lanka. *Biotropica* 17:1–14
- Dittus WPJ (1986) Sex differences in fitness following a group take-over among toque macaques: testing models of social evolution. *Behav Ecol Sociobiol* 19:257–266
- Dittus WPJ (1988) Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. *Anim Behav* 36:1626–1645
- Dittus WPJ, Thorington RW Jr (1981) Techniques for aging and sexing primates. In: Subcommittee on Conservation of Natural Primate Populations (ed) Techniques for the study of primate population ecology. National Academy of Science, Washington, DC, pp 81–134
- Dixon AF, Bossi T, Wickings EJ (1993) Male dominance and genetically determined reproductive success in the mandrill (*Mandrillus sphinx*). *Primates* 34:525–532
- Drickamer LC (1974) A ten-year summary of reproductive data for free-ranging *Macaca mulatta*. *Folia Primatol* 21:61–80
- Dunbar RIM, Dunbar EP (1977) Dominance and reproductive success in female gelada baboons. *Nature* 266:351–352
- Eisenberg JF (1966) The social organization of mammals. *Handb Zool*, vol 8, 10:1–92
- Eisenberg JF (1981) The mammalian radiations. University of Chicago Press, Chicago
- Eisenberg JF, Muckenhirn NA, Rudran R (1972) The relation between ecology and social structure in primates. *Science* 176:863–874
- Emlen ST, Oring LW (1977) Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223
- Emlen ST, Emlen JM, Levin SA (1986) Sex ratio selection in species with helpers-at-the-nest. *Am Nat* 127:1–8
- Fairbanks LA, McGuire MT (1984) Determinants of fecundity and reproductive success in captive vervet monkeys. *Am J Primatol* 7:27–38

- Fedigan LM, Fedigan L, Gouzoules S, Gouzoules H, Koyama N (1986) Lifetime reproductive success in female Japanese macaques. *Folia Primatol* 47:143–157
- Fisher RA (1930) The genetical theory of natural selection. Clarendon, Oxford
- Fleming TH (1974) Social organization in two species of Costa Rican heteromyid rodents. *J Mammal* 55:543–561
- Frisch RE, McArthur JW (1974) Menstrual cycles: fatness as a determinant of minimum weight for height necessary for their maintenance or onset. *Science* 185:949–951
- Garrow JS (1983) Indices of adiposity. *Nutr Abstr Rev* 53:697–707
- Geist V (1971) Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago
- Gomendio M, Clutton-Brock TH, Albon SD, Guinness FE, Simpson MJ (1990) Mammalian sex ratios and variation in costs of rearing sons and daughters. *Nature* 343:261–262
- Gosling LM (1986) Selective abortion of entire litters in the coypu: adaptive control of offspring production in relation to quality and sex. *Am Nat* 127:772–795
- Greenwood PJ (1980) Mating systems, philopatry, and dispersal in birds and mammals. *Anim Behav* 28:1140–1162
- Hanks J (1981) Characterization of population condition. In: Fowler CW, Smith TD (eds) Dynamics of large mammal populations. Wiley, New York, pp 47–83
- Haugen AO (1975) Reproductive performance of white-tailed deer in Iowa. *J Mammal* 56:151–159
- Hausfater G, Altmann J, Altmann S (1982) Long-term consistency of dominance relations among female baboons (*Papio cynocephalus*). *Science* 217:752–754
- Hogg JT, Haas CC, Jenni DA (1992) Sex-biased maternal expenditure in Rocky Mountain bighorn sheep. *Behav Ecol Sociobiol* 31:243–251
- Hrdy SB (1987) Sex-biased parental investment among primates and other mammals: a critical evaluation of the Trivers-Willard hypothesis. In: Geller R, Lancaster J (eds) Child abuse and neglect: biosocial dimensions. Aldine, New York, pp 97–147
- Hrdy SB, Williams GC (1983) Behavioral biology and the double standard. In: Wasser SK (ed) Social behavior of female vertebrates. Academic Press, New York, pp 3–17
- Inoue M, Misunaga F, Nozaki M, Oshawa H, Takenaka A, Sugiyama Y, Shimizu K, Takenaka O (1993) Male dominance rank and reproductive success in an enclosed group of Japanese macaques: with special reference to post-conception mating. *Primates* 34:503–511
- James WH (1985) Sex ratio dominance status and maternal hormone levels at the time of conception. *J Theor Biol* 114:505–510
- Johnson CN (1988) Dispersal and the sex ratio at birth in primates. *Nature* 332:726–728
- Kaufmann JH (1974) The ecology and evolution of social organization in the kangaroo family (Macropodidae). *Am Zool* 14:51–62
- Kawamura S (1958) Matriarchal social order in the Minoo-B group: a study of the rank system of Japanese macaques. *Primates* 1:149–156
- Keane B, Dittus WPJ, Melnick DJ (1997) Paternity assessment in wild groups of toque macaques *Macaca sinica* at Polonnaruwa, Sri Lanka using molecular markers. *Mol Ecol* 6:267–282
- Kennitz JW, Goy RW, Flitsch RJ, Lobmiller JJ, Robinson JA (1989) Obesity in male and female rhesus monkeys: fat distribution, glucoregulation and serum androgen levels. *J Clin Endocrinol Metabol* 69:287–293
- Kleiman DG (1977) Monogamy in mammals. *Q Rev Biol* 52:39–69
- Labov JB, Huck UV, Vaswani P, Lisk RD (1986) Sex ratio manipulation and decreased growth of male offspring of undernourished golden hamsters (*Mesocricetus auratus*). *Behav Ecol Sociobiol* 18:241–249
- Le Boeuf BJ (1972) Sexual behavior in the northern elephant seal, *Mirounga angustirostris*. *Behaviour* 41:1–26
- Le Boeuf BJ (1974) Male-male competition and reproductive success in elephant seals. *Am Zool* 14:163–176
- Le Boeuf BJ, Reiter J (1988) Lifetime reproductive success in northern elephant seals. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 344–362
- Lloyd PH, Rasa OAE (1989) Status, reproductive success and fitness in Cape mountain zebra (*Equus zebra zebra*). *Behav Ecol Sociobiol* 25:411–420
- Maher CR, Byers JA (1987) Age related changes in reproductive effort of male bison. *Behav Ecol Sociobiol* 21:91–96
- Maynard Smith J (1982) Evolution and the theory of games. Cambridge University Press, Cambridge, UK
- McFarland RK (1992) Body composition and reproduction in female pigtail macaques. PhD thesis, University of Washington
- Mech LD (1975) Disproportionate sex ratios of wolf pups. *J Wildl Manage* 39:737–740
- Meikle DB, Vessey SH (1988) Maternal dominance rank and lifetime survivorship of male and female rhesus monkey. *Behav Ecol Sociobiol* 22:379–383
- Missakian EA (1972) Genealogical and cross-genealogical dominance relations in a group of free-ranging monkeys (*Macaca mulatta*) on Cayo Santiago. *Primates* 13:169–180
- Monard A-M, Duncan P, Fritz H, Feh C (1997) Variations in the birth sex ratio and neonatal mortality in a natural herd of horses. *Behav Ecol Sociobiol* 41:243–249
- Mori A (1979) Analysis of population changes by measurement of body weight in the Koshima troop of Japanese monkeys. *Primates* 20:371–397
- Nixon CM (1971) Productivity of white-tailed deer in Ohio. *Ohio J Sci* 71:217–225
- Noyes MJS (1982) The association of maternal attributes with infant gender in a group of Japanese monkeys. *Int J Primatol* 3:320
- Nevison CM, Rayment FDG, Simpson MJA (1996) Birth sex ratios and maternal social rank in a captive colony of rhesus monkeys (*Macaca mulatta*). *Am J Primatol* 39:123–138
- O'Brien TG, Robinson JG (1987) The effects of group size and female rank on sex ratio at birth in capuchins *Cebus olivaceus*. *Int J Primatol* 8:499
- Ono KA, Boness DJ, Oftedal OT (1987) The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Behav Ecol Sociobiol* 21:109–118
- Oshawa H, Inoue M, Takenaka O (1993) Mating strategy and reproductive success of male patas monkeys (*Erythrocebus patas*). *Primates* 34:533–544
- Ozoga JJ, Verme LJ, Bienz CS (1982) Parturition behavior and territoriality in white-tailed deer: impact on neonatal mortality. *J Wildl Manage* 46:1–11
- Packer C, Pusey AE (1987) Intrasexual cooperation and the sex ratio in African lions. *Am Nat* 130:636–642
- Packer C, Herbst L, Pusey AE, Bygott D, Hanby JP, Cairns SJ, Borgerhoff Mulder M (1988) Reproductive success in lions. In: Clutton-Brock TH (ed) Reproductive success. University of Chicago Press, Chicago, pp 363–383
- Paul A, Kuester J (1987) Sex ratio adjustment in a seasonally breeding primate species: evidence from the Barbary macaque population at Affenberg Salem. *Ethology* 74:117–132
- Paul A, Kuester J, Arnemann J (1992) Maternal rank affects reproductive success of male Barbary macaques (*Macaca sylvanus*): evidence from DNA fingerprinting. *Behav Ecol Sociobiol* 30:337–341
- Paul A, Kuester J, Timme A, Arnemann J (1993) The association between rank, mating effort, and reproductive success in male Barbary macaques (*Macaca sylvanus*). *Primates* 34:491–502
- Pond CM (1984) Physiological and ecological importance of energy storage in evolution of lactation: evidence for a common pattern of anatomical organization of adipose tissue in mammals. *Symp Zool Soc Lond* 51:1–32
- Pond CM, Mattacks CA (1987) The anatomy of adipose tissue in captive *Macaca* monkeys and its implication for human biology. *Folia Primatol* 48:164–185

- Pope TR (1990) The reproductive consequences of male cooperation in the red howler monkey: paternity exclusion in multi-male and single-male troops using genetic markers. *Behav Ecol Sociobiol* 27:439–446
- Ralls K (1976) Mammals in which females are larger than males. *Q Rev Biol* 51:245–276
- Rawlins RG, Kessler MJ (1986) Secondary sex ratio variation in the Cayo Santiago macaque population. *Am J Primatol* 10:9–23
- Rhine RJ (1994) A twenty-one-year study of maternal dominance and secondary sex ratio in a colony group of stump-tailed macaques (*Macaca arctoides*). *Am J Primatol* 32:145–148
- Rhine RJ, Wasser SK, Norton GW (1988) Eight-year study of social and ecological correlates of mortality among immature baboons of Mikumi National Park, Tanzania. *Am J Primatol* 16:199–212
- Rhine RJ, Norton GW, Rogers J, Wasser SK (1992) Secondary sex ratio and maternal dominance rank among wild yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. *Am J Primatol* 27:261–273
- Richards SM (1974) The concept of dominance and methods of assessment. *Anim Behav* 22:914–930
- Riney T (1982) Study and management of large mammals. Wiley, New York
- Rivers JPW, Crawford MA (1974) Maternal nutrition and the sex ratio at birth. *Nature* 252:297–298
- Robinson JG (1988) Group size in wedge-capped capuchin monkeys *Cebus olivaceus* and the reproductive success of males and females. *Behav Ecol Sociobiol* 23:187–197
- Ruiter JR de, Van Hoof JARAM (1993) Male dominance rank and reproductive success in primate groups. *Primates* 34:513–523
- Rutberg A (1986) Lactation and fetal sex ratios in American bison. *Am Nat* 127:89–94
- Rutenberg GW, Coehlo AM, Lewis DS, Carey KD, McGill HC (1987) Body composition in baboons: evaluating a morphometric method. *Am J Primatol* 12:275–285
- Sade DS (1967) Determinants of dominance in a group of free-ranging rhesus monkeys. In: Altmann SA (ed) Social communication among primates. University of Chicago Press, Chicago, pp 99–114
- Schaik CP van, Netto WJ, Amerongen AJJ van, Westland H (1989) Social rank and sex ratio of captive long-tailed macaque females (*Macaca fascicularis*). *Am J Primatol* 19:147–162
- Schaik CP van, Hrdy SB (1991) Intensity of local resource competition shapes the relationship between maternal rank and sex ratios at birth in cercopithecine primates. *Am Nat* 138:1555–1562
- Scuttie JM (1982) Body size: dominance relationships in red deer stag calves. *Anim Behav* 31:610–611
- Silk JB (1983) Local resource competition and facultative adjustment of sex ratios in relation to competitive abilities. *Am Nat* 121:56–64
- Silk JB, Clark-Wheatley CB, Rodman PS, Samuels A (1981) Differential reproductive success and facultative adjustment of sex ratios among female bonnet macaques (*Macaca radiata*). *Anim Behav* 29:1106–1120
- Simpson AE, Simpson MJA (1985) Short-term consequences of different breeding histories for captive rhesus macaque mothers and young. *Behav Ecol Sociobiol* 18:83–89
- Simpson MJA, Simpson AE (1982) Birth sex ratios and social rank in rhesus monkey mothers. *Nature* 300:400–401
- Skogland T (1983) The effects of density dependent resource limitation on size of wild reindeer. *Oecologia* 60:156–168
- Skogland T (1986) Sex ratio variation in relation to maternal condition and parental investment in wild reindeer *Rangifer t. tarandus*. *Oikos* 46:417–419
- Small MF (1981) Body fat, rank, and nutritional status in a captive group of rhesus macaques. *Int J Primatol* 2:91–95
- Small MF, Hrdy SB (1986) Secondary sex ratios by maternal rank, parity and age in captive rhesus macaques. *Am J Primatol* 11:359–365
- Small MF, Smith DG (1985) Sex of infants produced by male rhesus macaques. *Am Nat* 126:354–361
- Smith DG (1993) A 15-year study of the association between dominance rank and reproductive success of male rhesus macaques. *Primates* 34:471–480
- Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco
- Trillmich F (1986) Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. *Behav Ecol Sociobiol* 19:157–164
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90–92
- Verme LJ (1985) Progeny sex ratio relationships in deer: theoretical vs observed. *J Wildl Manage* 49:134–136
- Wade MJ (1979) Sexual selection and variance in reproductive success. *Am Nat* 114:742–746
- Walike BC, Goodner CJ, Koerker DJ, Chideckel EW, Kalnasy LW (1977) Assessment of obesity in pigtail monkeys. *J Med Primatol* 6:151–162
- Wasser SK (1983) Reproductive competition and cooperation among female yellow baboons. In: Wasser SK (ed) Social behavior of female vertebrates. Academic Press, New York, pp 349–390
- Wasser SK, Norton G (1993) Baboons adjust secondary sex ratio in response to predictors of sex-specific offspring survival. *Behav Ecol Sociobiol* 32:273–281
- Whitten PL (1983) Diet and dominance among female vervet monkeys (*Cercopithecus aethiops*). *Am J Primatol* 5:139–159
- Wickings EJ, Bossi T, Dixon AF (1993) Reproductive success in the mandrill, *Mandrillus sphinx*: correlations of male dominance and mating success with paternity, as determined by DNA fingerprinting. *J Zool (Lond)* 231:563–574
- Wilkinson L, Blank G, Gruber C (1996) Desktop data analysis with SYSTAT. Prentice Hall, Princeton, NJ
- Wittenberger JF (1979) The evolution of mating systems in birds and mammals. In: Master P, Vandenburgh J (eds) Handbook of behavioral neurobiology: social behavior and communication. Plenum, New York, pp 271–349
- Wolfe LD (1984) Female rank and reproductive success among Arashiyama B Japanese macaques (*Macaca fuscata*). *Int J Primatol* 5:133–143
- Wolff JO (1988) Maternal investment and sex ratio adjustment in American bison calves. *Behav Ecol Sociobiol* 23:127–133
- Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75:262–300

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