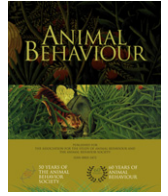


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## Do mothers prefer helpers? Birth sex-ratio adjustment in captive callitrichines

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Parental investment theory predicts that natural selection will favour a parental ability to bias the offspring sex ratio in favour of that which will yield the highest benefit–cost payoff. The local resource enhancement hypothesis posits that in cooperative breeders, parents may favour offspring that will mitigate parental effort by helping to raise younger siblings. Conversely, the fragile male hypothesis suggests that parents will adjust the sex ratio in favour of the sex that experiences higher mortality. We examined international studbook data of two cooperatively breeding primate species with differing reproductive strategies: golden lion tamarins, *Leontopithecus rosalia*, which typically give birth to twins, and callimicos, *Callimico goeldii*, which almost always give birth to singletons. The tamarins showed a stronger secondary sex-ratio bias in favour of males than did the callimicos, as predicted by the local resource enhancement hypothesis, because tamarins sustain higher per-parturition costs and because sons may invest more effort in caring for their younger siblings than do daughters. However, a generalized linear regression failed to reveal factors that may influence this variation. There was no significant predictor of male bias based on mother's age, mother's number of previous parturitions or group size. Contrary to predictions of the fragile male hypothesis, sons were no less likely to survive the postnatal period of parental investment than were daughters. A greater understanding of this phenomenon is needed because the adult sex-ratio bias in favour of males has become so pronounced, especially in golden lion tamarins, as to cause management difficulties for the conservation of these endangered species.

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Parental investment is a continuum that begins at conception and proceeds through birth, postnatal dependency and sometimes even into adulthood. Decisions regarding how much, or even whether, to invest in one's offspring may significantly impact a parent's reproductive success. Parental investment costs and benefits may vary according various factors, including offspring sex. Fisher (1930) reasoned that the population-level sex ratio at birth should reach a 50:50 equilibrium when the fitness benefits to parents of producing sons and daughters are equal. Clutton-Brock & Iason (1986) proposed that when one sex sustains higher mortality during the period of parental investment, parents would be expected to bias the birth sex ratio in favour of the more fragile sex, resulting in an equal sex ratio of individuals reaching maturity at the population level. They suggested that male offspring might be more vulnerable than females, particularly in sexually dimorphic species where males grow faster and thus may be more susceptible to starvation.

Trivers & Willard (1973), in contrast, hypothesized that a selective advantage would accrue to parents that could facultatively vary investment according to prevailing conditions. Specifically, they posited that, in polygynous animals, as long as maternal condition could impact offspring fitness, mothers in good condition should bias their birth sex ratio in favour of males, which have a higher variance in reproductive success. Support for the theory has been inconsistent (reviewed in: Clutton-Brock & Iason 1986; Cockburn et al. 2002), leading to the development of more recent models that address deviations from the Trivers & Willard hypothesis and that propose other cost–benefit scenarios for selective sex-ratio adjustment. Several models focus on the relative costs of producing males versus females. Based on observations that galago, *Galago caudatus*, daughters stay in their mother's territory, competing with her for resources, and that mothers produce more sons than daughters, Clark (1978) proposed the local resource competition hypothesis, which argues that when one sex is philopatric, local competition over resources should favour a birth sex-ratio skew in favour of the dispersing sex. Likewise, Silk (1983) reasoned that in cercopithecine monkeys, daughters are future competitors for troop resources and compete, not only with their mothers, but with all troop females as well. Daughters thereby

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deplete the food resources of relatives throughout their lives, making the dispersing sex (male) less costly. Mothers that are less able to bear these costs (e.g. due to poor physical condition or subordinate status) are predicted to skew their birth sex ratios in favour of sons.

Conversely, the local resource enhancement hypothesis argues that parents may bias the birth sex ratio in favour of the sex that mitigates the costs of parental investment by contributing to parental reproductive effort (Woolfenden & Fitzpatrick 1978; Emlen et al. 1986). Such species are termed cooperative breeders: those in which “mothers voluntarily permit access to their infants and many group members are actively engaged in active care and provisioning of infants, thereby increasing their growth and survival” (Burkart et al. 2009, page 176). Studies of sex allocation in cooperatively breeding species often have supported the local resource enhancement hypothesis (e.g. Griffin et al. 2005; McNutt & Silk 2008).

Silk & Brown (2008) tested the local resource enhancement model in cooperatively breeding primates, all of which are members of the same subfamily, the Callitrichinae. Of the 11 species in their sample, only the callimico, *Callimico goeldii*, showed no significant sex-ratio bias, which they interpreted as being due to the status of *C. goeldii* as the only noncooperatively breeding species within this clade, although this characterization is not universally accepted (Digby et al. 2011). The other 10 species all biased the birth sex ratio in favour of sons. In both marmosets and tamarins, the positive correlation found between the number of males in a group and infant survival suggests that males are particularly important as helpers (Bales et al. 2000). This apparent relationship between number of helpers and sex-ratio skew lends support to the local resource enhancement hypothesis. However, interpretation of the adaptive benefits that helpers provide is confounded in correlational studies by unmeasured factors such as territory quality and maternal experience. Studies that have directly quantified helping behaviour in callitrichines have yielded mixed results. Sons are more active alloparents than daughters in some species (cottontop tamarins, *Saguinus oedipus*: Price 1992; Refetoff Zahed et al. 2010; pygmy marmosets, *Cebuella pygmaea*: Wamboldt et al. 1988; golden lion tamarins, *Leontopithecus rosalia*: L. G. Rapaport, unpublished data) but not in others (common marmosets, *Callithrix jacchus*: Yamamoto & Box 1997).

Callimicos are not typical callitrichines because, unlike the other members of their taxonomic group, which most often give birth to twins, callimicos almost exclusively give birth to singletons (Digby et al. 2011). In fact, twinning is so uncharacteristic that twin callimicos have never been mother-reared in captivity (Warneke 2010). The callimico social system and infant care strategy, on the other hand, places the species firmly within the definition of a cooperative breeder. For instance, callimico neonates are initially carried solely by the mother but, once infants are older than 2–4 weeks of age, fathers and older offspring take over most of the carrying activity (Porter 2000; Schradin & Anzenberger 2001; Ross et al. 2010). Similarly, in the golden lion tamarin, which is a twinning callitrichine, mothers take the primary role in carrying infants during the first 3 weeks after giving birth (Tardif et al. 2002). Also typical of other callitrichines, all adult members of a callimico group regularly give food to infants (Porter & Garber 2009; Digby et al. 2011). Goldizen (1987) proposed that those callitrichine species that usually produce twins have committed themselves to a reliance on multiple caregivers for successful reproduction because the cost of rearing two offspring simultaneously in the wild is energetically prohibitive for a mother alone or even for a mated pair. Callimicos most probably sustain less per-parturition-cost to infant care because the single callimico infant weighs approximately the same, relative to adult weight, as does one infant in a

callitrichine twin litter (Hartwig 1996). Thus, the relevant question appears to be not whether callimicos are cooperative breeders, but whether the help that nonmothers provide is as beneficial to callimicos as it is in the other, twinning callitrichines.

Our aim in this study was to test sex-ratio adjustment models in two callitrichine species that have contrasting reproductive strategies: the callimico and the golden lion tamarin. Griffin et al. (2005) conducted a meta-analysis of two mammal species and nine bird species and found a correlation between the fitness benefits that helpers provide and the degree of birth sex-ratio skew. We followed their reasoning to measure the value of helpers to our two study species. Next, we sought to confirm the existence of a male sex-ratio bias in the twinning species but not in the singleton-bearing species (see also Silk & Brown 2008). We then tested predictions generated by the local resource enhancement and fragile male hypotheses to uncover the factors that drive sex-ratio skew.

The local resource enhancement hypothesis is an ultimate-level hypothesis that hinges on the relative adaptive benefits that male and female offspring may provide when they help to rear younger siblings. Natural selection may act by sensitizing mothers to conditions that predict the need for alloparental assistance. For instance, if a lower threshold for assistance exists, such that a minimum number of adults is necessary for offspring survival (Goldizen 1987), then helpers will be more critical in smaller groups. Thus, females with fewer group members should be more likely to bias the sex ratio in favour of sons (Nam et al. 2011). In golden lion tamarins, primiparous females often reproduce for the first time in a group that is formed when a lone female recruits one or two unrelated adult males to join her in an uninhabited territory (Baker & Dietz 1996; Baker et al. 2002; L. G. Rapaport, unpublished data). As a result, young and primiparous females are often found in very small groups, leading to the prediction that sex-ratio bias will vary with maternal age and parity, with younger and primiparous females giving birth to proportionally more sons.

We also tested the alternative, but not mutually exclusive, fragile male hypothesis, which predicts that the birth sex ratio will favour the sex that sustains greater mortality during the period of parental investment. If the primary sex ratio (that is, the sex ratio at conception) is equality, then in order for the overall secondary sex ratio to favour males, of necessity more mortality of female fetuses must occur. Under these conditions, a male birth-sex-ratio bias may indicate that (1) sons are more vulnerable at some point during their development and therefore receive favoured birth status from their mothers and/or (2) female mortality reflects greater female vulnerability during gestation. If male bias of the birth sex ratio reflects maternal preference for sons, then the fragile male hypothesis predicts that males will sustain higher mortality during the investment period after birth. Conversely, following the reasoning, if not the premises, of the fragile male hypothesis, if the male bias at birth signifies greater fragility of female fetuses, then one might expect higher survivorship of females during the period of postnatal investment, as a parental offset of the greater female vulnerability during gestation. In either case, males are predicted to sustain higher postnatal mortality. We assessed offspring mortality during the postnatal period of parental investment as a function of offspring sex to test these predictions.

## METHODS

### Study Subjects

Our data derive from golden lion tamarin (J. Ballou, unpublished data) and callimico (Warneke 2010) international studbooks. These international studbooks are species-specific databases that serve to record and track information on all individuals held in zoos around

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