which the first 15.6 trials (2 days) were spent in cue-assisted training. On the day of testing after the 2-week holding period, all animals met criterion, passing four consecutive trials, the last of which was a retention test. The mean time to complete a successful trial was 19.8 seconds.

9. In this experiment, medial septal lesions were used to eliminate theta rhythm. Cells of the medial septal nucleus are known to project to the hippocampus [G. Raisman, *Brain* **89**, 317 (1966); S. Mosko, G. Lynch, C. W. Cotman, *J. Comp. Neurol.* **152**, 163 (1973); L. W. Swanson and W. M. Cowan, in *The Septal Nuclei*, J. DeFrance, Ed. (Plenum, New York, 1976), p. 37] and medial septal lesions can abolish theta rhythm [C. Mayer and C. Stumpf, *Arch. Exp. Pathol. Pharmakol.* **234**, 490 (1958)]. The lesioning electrode was a No. 00 stainless steel insect pin coated with Epoxylite insulating lacquer and cleared of insulation for a distance of 400 μm from the tip. The animal was positioned in a stereotaxic device so that skull flat plane (passing through bregma and lambda and parallel to the interaural line) was level, and the electrode was implanted 1 mm anterior to bregma and 6.3 mm below the surface of the skull. The electrode was implanted 1 mm to the left of the midline to avoid the superior sagittal sinus and was inclined in the frontal plane toward the midline at an angle of 15° from the vertical so as to position its tip in the midline area. Lesions were made by passing 2 mA of current to the lesioning electrode from an anal ground for 8 seconds (septal electrode negative). These lesioning parameters were chosen to be marginally effective in eliminating theta rhythm.
10. Details of electrode construction, implantation, and recording were as in J. Winson, *Electroencephalogr. Clin. Neurophysiol.* **36**, 241 (1974); and (*11*).
11. J. Winson, *Brain Res.* **103**, 71 (1976).
12. ———, *Behav. Biol.* **7**, 479 (1972).
13. From the recordings taken on the third day of testing, six samples of theta rhythm constituting approximately 10 cycles each were selected during voluntary movement, and six samples were selected during REM sleep. For each behavior, the average amplitude and the average frequency of the theta rhythm were determined from the totality of these samples, by measurements taken directly from the polygraph records (*10*). The criterion used for selecting a control animal was that, within each behavior, the average amplitudes and frequencies after placement of lesions did not differ from the prelesion values by more than 15 percent.
14. In these rats, lesions resulted either in a stable, intermediate condition in which theta rhythm was diminished in amplitude but not eliminated, or a condition in which the amplitudes were initially attenuated but recovered to some extent over a period of several days to 2 weeks.
15. N. V. Brady and W. J. H. Nauta, *J. Comp. Physiol. Psychol.* **56**, 339 (1953).
16. All lesions were rostral to the decussation of the anterior commissure. Lesions in the experimental animals had in common the bilateral destruction of the major part of the medial septal nucleus anterior to the decussation. Damage to the lateral septum was in almost all cases confined to the medial half of the lateral septal nucleus (partes dorsalis, intermedialis, and ventralis) where it was generally bilateral. In two animals there was unilateral destruction extending to the lateral aspects of the lateral septal nucleus (intermedialis and ventralis). Lesions in the control animals were generally slightly displaced from the midline. Damage to the medial septal nucleus either was unilateral or, when bilateral, was restricted to the more anterior parts of the nucleus. In all cases there was unilateral destruction of both medial and lateral portions of the lateral septal nucleus (dorsalis, intermedialis, and ventralis) and, in some instances, bilateral damage to the more medial portion of this nucleus.
17. There was no apparent pattern in the behavior of four of the animals. Two poked in every cup around the track, a behavior previously noted in rats with fornical lesions tested on a similar maze (*4*).
18. On the seventh trial of the tests performed on the day after the lesions, as well as on the seventh trial of the tests 1 week later, water was withheld when the rat, after poking in a number of other cups, finally poked in the goal cup. In contrast to their behavior at nongoal cups where rats activated the photoelectric detector and then moved on, when animals arrived at the goal cup, in some instances they in effect passed a retention test. They either did not move away from the goal cup, in which case they were given water after 10 seconds, or they moved to an adjacent cup and immediately returned to poke again in the goal cup and were given water. Five of the six rats displayed this behavior, one rat on the trial performed on the day after lesioning, two rats on the trial given 1 week later, and two rats on both occasions.
19. The destruction of pathways which originate in or pass through the medial septum, other than those responsible for generating theta rhythm, may also contribute to the deficit. Among the fibers which traverse the medial septal area are serotonergic [L. C. A. Conrad, C. M. Leonard, D. W. Pfaff, *J. Comp. Neurol.* **156**, 179 (1974)] and noradrenergic [L. W. Swanson and B. K. Hartman, *J. Comp. Neurol.* **163**, 467 (1975); B. E. Jones and R. Y. Moore, *Brain Res.* **127**, 23 (1977)] fibers which provide part of the monoamine innervation of the hippocampus.
20. J. F. R. König and R. A. Klippel, *The Rat Brain* (Krieger, New York, 1970).
21. Supported by a grant from the Harry F. Guggenheim Foundation. I thank J. Caguiat for technical assistance.

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# Sex Ratio and Local Resource Competition in a Prosimian Primate

Abstract. *Competition between female kin for local limiting resources may explain a male-biased secondary sex ratio in the prosimian* Galago crassicaudatus. *Data demonstrating the skewed sex ratio, a brief summary of field observations on the species, and a simple mathematical statement of the hypothesis are presented. Local resource competition may influence sex ratio in other mammals.*

The African galagos comprise a family (Galagidae) of nocturnal, arboreal prosimian primates. I report a secondary sex ratio skewed toward males in the largest-sized species, *Galago crassicaudatus*, and possibly also in some of its congeners. The results of a worldwide survey of museum collections (*1*), a survey of births in captivity, and a 1½-year field study all demonstrate a preponderance of males. The inequality is present at birth and is neither the result of nor compensated for by differential death of sexes after birth. This inequality is not satisfactorily explained by existing hypotheses on high sex ratios. Rather, I suggest that it results from a social structure which produces sibling and mother-offspring competition for limiting resources that involves only one sex (in this case, female).

Evidence for a high sex ratio in *G. crassicaudatus* is presented in Tables 1 to 3. In all cases, samples were analyzed by the chi square goodness-of-fit test, discounting "unknowns" from the analysis.

Collections from worldwide museums comprise the museum data (Table 1). Specimens were classified as to subspecies in accord with Hill (*2*) and tabulated as "♂," "♀," or "?" (no record present with the specimen). It is clear that, where sample size is sufficient, numbers of individual subspecies are often significantly skewed toward males, never toward females, and that the overall museum count is significantly male-biased.

Obviously, there may be sampling error problems: either sex may be more conspicuous, trappable, or desirable as a trophy. However, personal experience with trapping, retrapping, and observing this galago species suggests that females are at least as trap-prone and conspicuous as males (*3*, *4*); indeed, older adult males are hardest to trap and quickest to flee. The slight sex difference (*5*) is hardly discernible in the field and unlikely to influence the nocturnal hunter, who locates animals by light reflecting from the tapeta of their eyes. Thus, I propose that the data do accurately approximate the sex ratio of subadult and adult galagos.

Records of captive births (Table 2) demonstrate a significant preponderance of males born. Questionnaires were sent to institutions known to be breeding *G. crassicaudatus* or reporting births in the *International Zoo Yearbook*. Some of the latter stated that they had no breeding galagos at present (1976) and, since it was often impossible to tell whether an institution reported the same data in the questionnaire that it had presented in the *International Zoo Yearbook*, yearbook birth reports (1970 to 1974) are given separately (Table 2). The number of unknowns includes animals on which sex determination was simply not made and dead infants that were partially consumed before they were found. In testing the captive birth data, I found no evidence for differential death before maturity (*6*). Thus, I suggest that the museum data represents the secondary sex ratio in those populations sampled.

Finally, my 1.5-year field study of a population of *G. crassicaudatus umbrosus* in North Transvaal, South Africa, yielded both birth data and a total population ratio for June 1977 (Table 3). All animals on the site plus those in immediately adjacent bush were trapped, their sex was recorded, and they were individually marked. Where I had not observed the mother at or soon after parturition, I assumed that multiparous females had

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three young per litter and primiparous females two. This is at worst an overestimate of the number born; all of the multiparous females observed within 2 weeks of parturition have had three young, and the lower primipara litter size is a well-known phenomenon for this and other mammal species. Such assumed young together with two known young which disappeared before a sex determination was made comprise the "unknown" category of Table 3.

Theoretical explanations for skewed secondary sex ratios derived from social insects (7) are inapplicable to the degree that they depend on haplo-diploid breeding systems. Since the sex ratio bias applies to all the samples for this species, models predicting sex ratio adjustment depending on individual variation in parental ability to invest in one sex (8, 9) do not explain this case. Finally, both male and female offspring interact equally with their younger siblings and neither sex acts as classical "helpers," so that differential contribution of one sex to the next parental brood does not offer a reason. My explanation of the skewed sex ratio involves a difference between male and female offspring in their use of local, high-productivity areas which are essential for female reproduction. Closely related females compete for this resource during the birth season when their movements are restricted by the burden of raising offspring. Males are never restricted to these high-productivity areas and do not compete intensively for them. I term this "local resource competition" (10). This hypothesis is based on the results of my field study of the social and spatial organization of *G. crassicaudatus*.

*Galago crassicaudatus* lives in neighborhoods (11) of loosely bonded animals of both sexes. Individuals' home ranges are highly overlapping. Grooming or playful interactions between members of all age-sex classes (except between males of ≥ 2.5 years) are frequent, even nightly. Female ranges are usually smaller than male ranges and daughters remain in the maternal range longer than sons (12). Even after reaching maturity, daughters may share large portions of the maternal range and remain closely associated as frequent sleeping and grooming companions of their mothers or sisters (or both). At the same time, adult females can be extremely antagonistic to young females that are not their daughters. Thus, a population structure exists in which female kin will be closely associated spatially and socially for much of their lives.

Diet in this omnivorous species consists mostly of fruits, gums from *Acacia* sp., and insects (12). At the study site, *Acacia karroo* gum and insects comprise most of the food. Both *Acacia* gum and fruits such as figs taken by other populations (12) occur in local abundance. Insects, at the time of galago births in South Africa (October to November, the end of the dry cold season), are also localized on a few flowering bushes (*Rhus* sp.). Both gum and insects visiting flowering bushes are fairly rapidly renewing resources. During one night, any one feeding site may be used by several galagos in succession. However, galagos seldom feed longer than 3 or 4 minutes at a single gum source before moving on. A reasonable time between profitable visits to a single source may be several hours.

Table 1. Sex ratios of *Galago crassicaudatus* in museum collections. (♂) males; (♀) females; (?) sex not determined.

| Subspecies | ♂ | ♀ | ? | ♂ (%) | $\chi^2$ |
|---|---|---|---|---|---|
| *agisymbanus* | 36 | 44 | 10 | 45 | 0.80 |
| *argentatus* | 7 | 2 | 8 | 78 | 2.78 |
| *badius* | 0 | 1 | 0 | | |
| *crassicaudatus* | 16 | 10 | 2 | 62 | 1.38 |
| *garnetti* | 46 | 21 | 9 | 69 | 9.38* |
| *kikuyensis* | 22 | 9 | 2 | 71 | 5.45† |
| *lasiotis* | 41 | 15 | 16 | 73 | 12.1* |
| *lestradi* | 3 | 1 | 5 | | 0 |
| *lonnbergi* | 38 | 34 | 3 | 53 | 0.22 |
| *monteiri* | 100 | 73 | 92 | 58 | 4.21† |
| *panganiensis* | 37 | 13 | 12 | 74 | 11.5* |
| *umbrosus* | 1 | 0 | 0 | | |
| Unidentified | 91 | 50 | 23 | 65 | 11.9* |
| Total | 483 | 273 | 182 | 62 | 38.3* |

*$P < .005$. †$P < .05$.

Table 2. Births in captivity compiled from *International Zoo Yearbook*, 1970–1974 and from 1976 questionnaire replies of ten institutions reporting births. Deaths before maturity are shown in parentheses and *N* is the number of zoos reporting that year.

| Year | *N* | ♂ | ♀ | ? | ♂ (%) | $\chi^2$ |
|---|---|---|---|---|---|---|
| *Data from* International Zoo Yearbook | | | | | | |
| 1970 | 17 | 25 | 16 | 9 | 61 | 1.98 |
| | | (7) | (4) | (4) | | |
| 1971 | 15 | 23 | 15 | 13 | 61 | 1.68 |
| | | (2) | (0) | (14) | | |
| 1972 | 9 | 33 | 20 | 21 | 62 | 3.19 |
| | | (11) | (5) | (11) | | |
| 1973 | 16 | 28 | 32 | 11 | 47 | 0.27 |
| | | (12) | (5) | (2) | | |
| 1974 | 10 | 17 | 13 | 11 | 57 | 0.53 |
| | | (4) | (4) | (4) | | |
| Total | | 126 | 96 | 65 | 57 | 4.05* |
| | | (36) | (18) | (35) | | |
| *Data from questionnaire* | | | | | | |
| 1976 | 10 | 209 | 141 | 100 | 60 | 13.21† |

*$P < .05$. †$P < .005$.

Table 3. Field study sex ratio results.

| Sample | ♂ | ♀ | ? | ♂ (%) | $\chi^2$ |
|---|---|---|---|---|---|
| Born | 13 | 4 | 5–8* | 76 | 4.76† |
| Total living | 21 | 9 | 3–4 | 70 | 4.80† |

*Includes young presumed born but dead before 5 weeks. †$P < .05$.

During late gestation and 3 to 4 weeks postpartum, up to three new young greatly reduce maternal mobility. Infants are either carried or "parked" on branches for short periods, and though predation on infants appears to be light, females do not go far or leave them for long. Mothers remain in small portions of the normal ranges that boast high gum production and insect-attracting bushes. Females with overlapping ranges may share an area, even during the initial postpartum antagonism toward all other galagos. This supports the evidence, derived from observable long-term gum production of individual trees in these and other parts of galago ranges, that such small areas of prolific food supply, capable of supporting pregnant or lactating females, are uncommon. One such area may often be capable of supporting more than one sedentary female as well as less frequent foragers (males and subadult females) who sample the trees lightly as a small portion of their much larger resource base. The upper limit on female use will be determined by the rate of gum flow from the trees.

Females may also gain from sharing such areas. After initial antagonism has gone, they groom each other regularly as well as groom, lead, or sit with the other's young. Circumstantial evidence, such as relative ages and close resemblances of the female pairs observed, suggests that they are likely to be mothers and daughters.

I propose, therefore, that the existence of such an area within a female's range is essential to her reproductive success. Female offspring must either share such an area with an established female or find a spot of their own. A low adult death rate, the antagonism of nonmaternal females, and the sedentary nature of daughters, all mean that daughters are most likely to compete with their mothers and sisters for these spots.

Sons have a chance to breed as soon as daughters, at 1.75 years during the annual season. They range widely, and are seldom seen in the local rich patches while infants are very young. Neither their presence nor their reproductive success inhibits their mother's, sisters', or brothers' chances and a female would be expected to enhance her own and her daughters' fitness by producing sons over and above the number of daughters that can share the local resource or secure a new one nearby.

A mathematical statement of the hypothesis is as follows (*13*). Using MacArthur's product theorem (*14*), we assume that natural selection maximizes $m \cdot f$, where $m$ is the number of sons alive at breeding age and $f$ is the number of daughters alive at breeding age.

Let

$$m = c \cdot r \cdot S_m$$
$$f = c(1 - r)S_f \qquad (1)$$

where $c$ is clutch size, $r$ is proportion of males in clutch, $S_m$ is the average survival (fitness) of males, and $S_f$ is the average survival (fitness) of females. Natural selection will maximize

$$m \cdot f = c^2 r(1 - r)S_m S_f \qquad (2)$$

However, since sons move farther and sooner from the maternal range, a son's fitness is unlikely to depend on the sex ratio of his siblings, while a daughter's fitness will vary inversely with the number of sisters that require the same local resource as she. Under these conditions, the equation becomes

$$m \cdot f = c^2 r(1 - r)S_m S_f(r), \qquad (3)$$

where

$$\delta S_f(r)/\delta r > 0$$

In this case, the product $m \cdot f$ is maximized at

$$\frac{\delta(m \cdot f)}{\delta r} = r(1 - r)\frac{\delta S_f(r)}{\delta r} + (1 - 2r)S_f(r) = 0 \qquad (4)$$

or

$$\frac{\delta S_f(r)}{\delta r} = \frac{(2r - 1)S_f(r)}{r(1 - r)} \qquad (5)$$

The right-hand side of Eq. 5 will be positive (that is, $> 0$) only when $r > 1/2$ or, in other words, when the sex ratio is skewed toward males. Although the equations deal only with sibling competition, competition between mother and daughter is just as likely and can only increase the relative fitness of females that produce sons.

The limited data for other galago species suggest that most of them may also adhere to the pattern. Interestingly, although a greater degree of organized territoriality is reported for the West African species, female association in sleeping groups and range sharing, especially of mothers and daughters, are also reported (*4, 15*). Female *G. senegalensis*, the only species found sympatrically with *G. crassicaudatus*, associate frequently and even produce young in one nest (*16*).

A number of mammals, especially eutherian species, are reported to have male-biased sex ratios at birth (*17*). Examples include African wild dogs, wolves, brush-tailed possums (*Trichocerus vulpecula*), tree squirrels, and golden-lion marmosets in captivity (*18, 19*). Female kin association is not an unusual pattern for many mammals (*20*), and local resource competition might help explain instances of male-biased sex ratios among them (*9, 21*).

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## References and Notes

1. Museum data was provided by T. Olson, who collected it as part of a larger survey and revision of the Galagidae.
2. W. C. O. Hill, *Primates: Comparative Anatomy and Taxonomy* (Univ. of Edinburgh Press, Edinburgh, 1953), vol. 1.
3. However, P. Charles-Dominique (*4*) states that the tiny *G. demidovii* males were more trappable than females, as a result of greater activity at night.
4. P. Charles-Dominique, *Z. Tierpsychol. Suppl.* **9**, 7 (1972).
5. Size varies with subspecies, but, as an example from the study population: of all animals $\geq 1$ year old trapped in March through May 1977, female weight averaged 1217 g (S.D. = 71.35, $N = 7$) and male weight averaged 1439 g (S.D. = 65, $N = 10$). The slight difference is significant ($t = 6.67$, $P < .01$).
6. $\chi^2 = 1.76$ for questionnaire results; $\chi^2 = 0.23$ for *International Zoo Yearbook* results.
7. W. D. Hamilton, *Science* **156**, 477 (1967).
8. R. L. Trivers, in *Sexual Selection and the Descent of Man, 1871–1971*, B. Campbell, Ed. (Aldine-Atherton, Chicago, 1972), pp. 136–179.
9. R. L. Trivers and D. E. Willard, *Science* **179**, 90 (1973).
10. The term "local resource competition" was suggested to me by E. Charnov.
11. Neighborhood is used here to denote animals that are familiar with and interact frequently with any given individual, without connoting membership in a closed or bounded society.
12. S. K. Bearder, thesis, Witwatersrand University (1975); A. B. Clark, in preparation.
13. I am indebted to E. Charnov and D. S. Wilson for this formulation.
14. R. H. MacArthur, in *Theoretical and Mathematical Biology*, T. H. Waterman and H. J. Morowitz, Eds. (Blaisdell, New York, 1965), pp. 388–397. This model assumes discrete generations, random matings, and large populations. Relaxation of the first assumption could only increase the effect of local resource competition in the direction described.
15. P. Charles-Dominique, *Ecology and Behaviour of Nocturnal Prosimians* (Duckworth, London, 1976).
16. S. K. Bearder, thesis, Witwatersrand University (1969); personal communication.
17. S. A. Asdell, *Patterns of Mammalian Reproduction* (Cornell Univ. Press, Ithaca, N.Y., ed. 2, 1964).

→ R. Estes and J. Goodard, *J. Wildl. Manage.* **31** (No. 1), 52 (1967); G. B. Schaller, *The Serengeti Lion* (Univ. of Chicago Press, Chicago, 1972); R. M. Hope, *Aust. J. Zool.* **20** (No. 2), 131 (197→ C. C. Smith, *Ecol. Monogr.* **38**, 31 (1968); *Int. Zoo. Yearb.* **12–16** (1970–1974).

19. D. L. Mech, *J. Wildl. Manage.* **39** (No. 4), 73 (1975).
20. J. Eisenberg, *Hand. Zool.* **8** (No. 39), 1 (1966); in *The Phylogeny of the Primates: A Multidisciplinary Approach*, W. P. Luckett and F. E. Szalay, Eds. (Plenum, New York, 1975), pp. 47–68.
21. Male-bias is positively correlated with female malnutrition or high population density (or both) in white-tailed deer [L. J. Verme, *North Am. Wildl. Nat. Resources Conf. Trans.* **32**, 405 (1967)] and some wolf populations (*19*); it is negatively correlated with increasing maternal age in humans [A. S. Parkes, in *Man and his Future*, G. E. W. Wolstenholme, Ed. (Churchill, London, 1963]. High population density would be likely to increase competition for limiting resources, and increasing maternal age increases the chances that the mother's death might open up a space for a female offspring. Thus, these examples suggest that sex ratio adjustment mechanisms in some species might be sensitive to the probability of intense female competition, shifting the ratio in a direction opposite to that predicted by Trivers and Willard (*9*) for females in poor condition.

22. I acknowledge the support of Professor G. A. Doyle and the Primate Behaviour Research Group, Witwatersrand University, during the field study; the help, advice, and enthusiasm of S. K. Bearder, E. Charnov, T. Olson, and D. S. Wilson; and the sincere interest shown by all institutions that gave their time to answer the questionnaire. E. Charnov, D. Hart, W. A. Mason, and D. S. Wilson made valuable comments on the paper.

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# The Stomach Signals Satiety

Abstract. *Inflatable pyloric cuffs and stomach tubes were implanted in rats. With the cuff inflated and a valve to limit intragastric pressure to that accompanying normal satiety, they drank only as much when they had been deprived of food for 12 hours as without inflation of the cuff. However, they overdrank with the cuff inflated when they had been water deprived for 12 hours. When 10 ml of milk was withdrawn from the stomach with the cuff inflated, compensatory drinking occurred. Further, compensatory drinking also occurred when milk escaped from the stomach into the duodenum. Satiety signals thus arise from the stomach.*

When animals eat and food either does not reach the stomach or is rapidly removed, exaggerated feeding occurs (*1–3*). Further, when food is withdrawn from the stomach after a meal is finished, rats will compensate for the amount withdrawn (*1, 3*). While such findings indicate that some signal from the upper gastrointestinal tract produces satiety, it is not clear whether such signals emanate from the stomach, the duodenum, or both, although it has been strongly argued that such signals arise from the duodenum (*4*). Here we describe a series of experiments that isolate the stomach from the duodenum while the rat ingests nutrient. These show for what we believe to be the first time that it is the stomach and not the duodenum that regulates the amount eaten during a meal. The stomach was isolated from the duodenum by the use of an inflatable cuff (*5*)

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