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

$$m = c \cdot r \cdot S_{\mathrm{m}}$$
$$f = c(1 - r)S_{\mathrm{f}} \qquad (1)$$

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

$$m \cdot f = c^2 r(1 - r)S_{\mathrm{m}}S_{\mathrm{f}} \qquad (2)$$

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

$$m \cdot f = c^2 r(1 - r)S_{\mathrm{m}}S_{\mathrm{f}}(r), \qquad (3)$$

where

$$\delta S_{\mathrm{f}}(r)/\delta r > 0$$

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

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

or

$$\frac{\delta S_{\mathrm{f}}(r)}{\delta r} = \frac{(2r - 1)S_{\mathrm{f}}(r)}{r(1 - r)} \qquad (5)$$

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 ≥ 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).
18. 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 (1972); 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*) implanted around the pylorus. Blocking the exit from the stomach while the animal eats could prevent eating through excessive distention or pressure in the stomach and thus create artefactual results. This difficulty was avoided by connecting the stomach to a valve through which the stomach contents flow out when a certain pressure is exceeded (*6*). This pressure was set to equal the normal pressure in the stomach measured when the rats drank to satiety with the cuff uninflated.

In experiment 1, eight rats (Sprague-Dawley, Charles River, 350-g males) accustomed to drinking milk while in a restraining cage, were implanted with a pyloric cuff and a stomach tube (Silastic, 0.125 inch outside diameter, 0.075 inch inside diameter). After recovery, they were put on a 12-hour food-deprivation schedule for a week. The deprived animals were placed in a restraining cage and connected to a water manometer to measure intragastric pressure with the cuff uninflated. They drank a mean of 13.6 ml of milk. On the following day, the stomach tube was connected to the overflow pressure valve and the pyloric cuff was inflated with water. Otherwise, conditions were the same as on the first day. The rats drank a mean of 11.5 ml of milk. This amount was not significantly different from that on the first day ($t = .6$).

In experiment 2, six rats were run under the same conditions plus two additional ones. In the additional two conditions the rats were run with and without the cuff after 12 hours of water deprivation. The 12-hour food-deprived rats drank a mean of 15.8 ml of milk with the cuff uninflated and a mean of 14.76 ml with the cuff inflated. Again, this difference was not significant ($t = .11$). However, when water deprived, the rats drank a mean of 14.3 ml with the cuff uninflated and 30.7 ml with the cuff inflated ($t = 2.35$, $P < .05$, one-tailed). The lack of overdrinking by the food-deprived rats was therefore unlikely to be due to discomfort resulting from an inflated cuff. In this experiment, the amount of fluid escaping through the pressure overflow valve in the cuff-inflated condition was also recorded—a mean of 1.3 ml in the food-deprived condition and 17 ml in the water-deprived condition. The amount of fluid remaining in the stomach under the two conditions was therefore approximately equal. The amounts drunk in the two food-deprived conditions (cuff inflated, cuff not inflated) did not differ, even though the duodenum remained empty when the cuff was inflated. Eating stopped normally even though abnormal pressure can be ruled out as a cause.

Table 1. Amounts drunk (in milliliters) in the last 25 minutes of experiment 3 under conditions C1 through C4. A pyloric cuff either was or was not inflated, and 10 ml of milk either was or was not withdrawn from the stomach.

Cuff inflated	Milk withdrawn	
	Yes	No
Yes	C1: 8.9	C2: 1.9
No	C3: 15.1	C4: 7.7

In experiment 3, the respective roles of the stomach and duodenum in signaling satiety were investigated according to yet another paradigm. In this design, another four rats (550 to 650 g, but otherwise the same as in experiments 1 and 2) were trained and surgically prepared as in the previous experiments. They were allowed to drink milk for 20 minutes without inflation of the cuff in all the experimental conditions. The milk was then removed from the restraining cage for 5 minutes. In condition 1, the cuff was immediately inflated when the milk was removed, and 10 ml of milk was pumped out of the stomach through the implanted tube. At the end of the 5 minutes, milk was again offered and the amount of drinking was measured for the next 25 minutes. Condition 2 was the same except that no milk was withdrawn from the stomach. In condition 3, the cuff was not inflated when 10 ml of milk was pumped out of the stomach. As in condition 1, the amount of drinking was measured for the 25 minutes after milk was again offered. Condition 4 was like the third except that no milk was withdrawn from the stomach. The experiment was designed to show whether drinking in compensation for nutrient removed from the stomach is in response to signals from the duodenum or the stomach (*1, 3*).

The four conditions were repeated once, the second time in reverse order. The data were treated by analysis of variance [A by B by C, with C (subjects) being a random factor]. Both the first fixed factor A (cuff inflation) and the second fixed factor B (milk withdrawal) were significant [A: $F\ (1, 3) = 22.86$, $P < .05$; B: $F\ (1, 3) = 48.62$, $P < .01$] (Table 1). None of the interactions approached significance. The interaction of most interest (AB, between cuff and pumping) attained an $F\ (1, 3)$ of 1.65, which shows that compensatory drinking is unaffected by the status of the cuff. If the amount drunk under condition 2 is taken as a baseline for the cuff-inflated conditions, the amount drunk in compensation for the withdrawal of milk in condition 1 was 7.0 ml. When the cuff was not inflated, condition 4 serves as a baseline; then the amount drunk in compensation (condition 3) was 7.4 ml. If the inflated cuff had been causing discomfort we would expect an interaction to appear in the analysis because such discomfort should reduce the amount of milk drunk in compensation. An interpretation of the results requiring no interaction is that when the cuff is left uninflated, nutrient escapes from the stomach into the duodenum for 30 minutes. This has the same effect as pumping out nutrient from the stomach, so that the rat drinks more to compensate.

This interpretation was tested in experiment 4. The same four rats were permitted to drink for 20 minutes with the cuff inflated (*7*). The cuff was then deflated for the next 30 minutes under two conditions, thus permitting some of the stomach contents to escape into the duodenum. In the first condition, milk was unavailable during the 30 minutes when the cuff was off. After this 30 minutes of drainage, the cuff was inflated again to stop further drainage, and the rat was permitted to drink for another 20 minutes. The mean amount drunk by each rat during two repetitions of this condition was 12.8 ml. In the second condition, the cuff was again left uninflated for 30 minutes, but the rat was permitted to drink milk during the last 20 minutes of this period. The mean amount drunk was 12.7 ml ($t = .03$, not significant). This means that cuff inflation has no effect on the amount consumed during compensatory drinking (as was also shown by the statistical analysis of experiment 3). Further, as amounts drunk are nearly equal when the stomach is allowed to drain into the duodenum for equal amounts of time in experiment 4, we may conclude that it is stomach drainage that produces the increased drinking in the cuff-off condition in experiment 3. The lack of difference in drinking during the last 20 minutes of the two conditions of experiment 4 further negates the possibility that cuff inflation is aversive.

These results demonstrate that signals arising from the stomach itself (as distinct from the duodenum and jejunum) regulate meal size and produce satiety.

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References and Notes

1. J. D. Davis and C. S. Campbell, *J. Comp. Physiol. Psychol.* **83**, 379 (1973).
2. C. L. Hull, J. R. Livingston, R. O. Rouse, A. N. Barker, *ibid.* **44** 236 (1951); D. G. Mook, *ibid.* **56**, 645 (1963); H. D. Hanowitz and M. I. Grossman. *Am. J. Physiol.* **159**, 143 (1949); I. Share, E. Martyniuk, M. I. Grossman, *ibid.* **169**, 229 (1952).
3. C. T. Snowdon, *J. Comp. Physiol. Psychol.* **71**, 68 (1970).
4. R. C. Young, J. Gibbs, J. Antin, J. Holt, G. P. Smith, *ibid.* **87**, 795 (1974).
5. J. A. Deutsch and M.-L. Wang, *Science* **195**, 89 (1977).
6. This valve was made of a Plexiglas tube ($^{1}/_{8}$ inch inside diameter), which was attached to the implanted stomach tube, bent so as to spill over when the fluid in the vertical tube reached a predetermined height. To prevent the possibility of a siphoning effect, a perforation was made at the top of the bend in the pressure tube.
7. During this initial 20-minute period, the rats drank a mean of 25.8 ml [standard deviation (S.D.) = 4.57] of milk while the cuff was inflated. During the initial 20-minute period of experiment 3, they drank a mean of 24.8 ml (S.D. = 6.7) with cuff uninflated.
8. This work was supported by Academic Senate Grant R-B10 to J.A.D. We thank M. Hayhoe and N. Y. Walton for help with the statistical treatment of the data and Dr. N. M. White for helpful comment.

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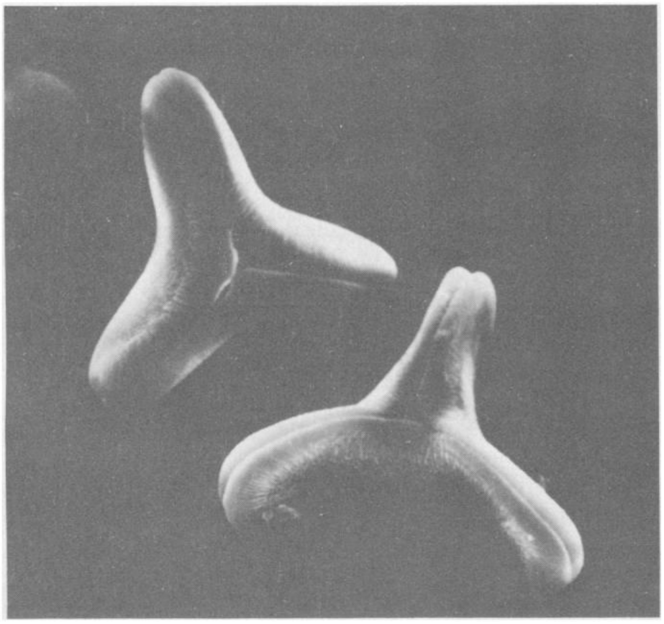
Avian Pollination Studies: A Simple Scanning Electron Microscopic Technique

Abstract. *Identifying ornithophilous plant species utilized by several different flower-visiting birds is simplified by the scanning electron microscope. The technique involves comparing pollen samples taken from the birds' head feathers with pollen reference standards collected in the same area, which simplifies analysis of pollination patterns in a complex community.*

Pollination patterns of avian flower visitors, especially in tropical montane forests, are difficult to study and quantitate by simple observation. We attempted to solve this problem by collecting the pollen carried by hummingbirds and a flower-piercer and identifying the samples with the aid of the scanning electron microscope (SEM). Pollination patterns may be inferred from such data.

Insect (*1*) and bat (*2, 3*) pollination have been studied by analyzing the pollen actually carried by the organisms, but optical microscopy was used in those studies. Our own preliminary attempts to identify pollen with light microscopy proved tedious, and the large quantities of pollen required precluded studying the pollen actually carried by a pollinating bird. However, the small amount of pollen remaining on a bird collected by shooting or mist-netting can easily be retrieved on a small (12 mm^2) piece of double-stick tape. This can be stored in a dust-proof vial, where it will dry spontaneously within a few days, and later prepared for SEM study by coating it with gold. This tape-collecting method is also desirable because the tape can be quickly monitored in the field with a compound microscope, although proper identification of pollen types is obviously impossible at that stage. Study of these pollen collections by SEM makes it possible in most cases to identify the plant or plants the bird visited by comparing the pollen from the bird with pollen standards collected from ornithophilous plants found in the bird's feeding area.

We tested this technique on five species of avian flower visitors in a second-growth montane forest called Yanasacha, near Cuenca, Ecuador (altitude approximately 3000 m). All of the birds collected were hummingbirds except for one masked flower-piercer, *Diglossa cyanea*, which is primarily a nectar robber and a poor pollinator. The pollen grains collected were easily identifiable in the case of the hummingbirds (Figs. 1 and 2), as if they had been shaken directly from the flower. The grains collected from the *Diglossa*, although identifiable, were coated with nectar, which tended to obscure some surface detail and made identification more difficult. The longer bills of the hummingbirds seemed to keep the pollen more nectar-free. The SEM technique is probably less useful for studies of *Diglossa* and related groups because these nectar robbers usually do not become as well dusted with pollen as the trochilids; in fact, the only pollen found on *D. cyanea* was that of *Palicourea aragmatophylla* K. Schum & Kraus, a member of the Rubiaceae whose androecium has very short filaments and hence anthers proximal to the insertion site of the *Diglossa*'s bill. Generally, ornithophilous plants have long filaments, and thus



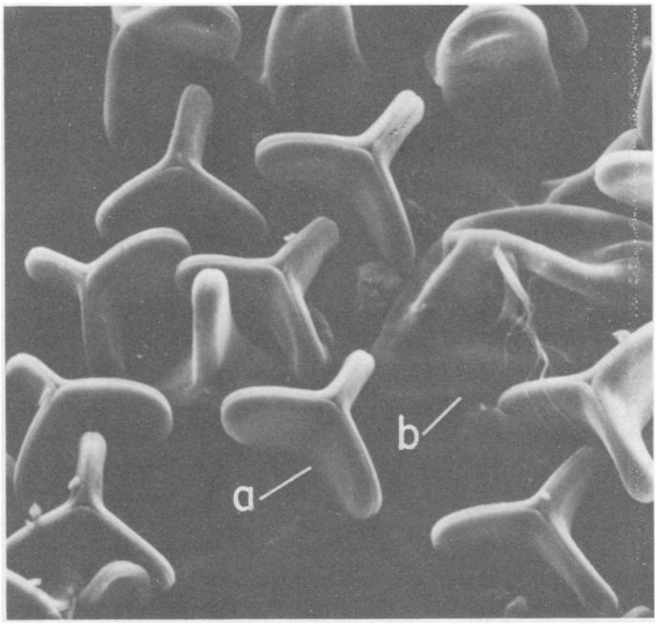


Fig. 1 (left). Pollen standard, *Phrygilanthus longebracteatus* (Desr.) Macbr. (Loranthaceae) (×1000). Fig. 2 (right). Pollen collected from head feathers of *Coeligena iris* (Trochilidae), showing pollen from (a) *Phrygilanthus longebracteatus* and (b) *Fuchsia* sp. (×500).