effort to optimize their inclusive fitnesses. Workers do not lay while the original queen is on the nest, so they should be strongly selected to bias their parental investment in favor of females.

KATHARINE M. NOONAN
Museum of Zoology, University of Michigan, Ann Arbor 48109

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5. M. J. West Eberhard, *Misc. Publ. Mus. Zool. Univ. Mich. 140* (1969).
6. Wide variation in the relative wet weight per individual of each sex produced on nests would undermine my estimates of the sex ratio of parental investment. Relative weights for a large sample of nests, needed to estimate the variance, were not obtained. Relative wing length data collected for 15 nests in 1974 suggest that inter-nest variation in this respect is not great. Wing length correlated significantly with body length in both sexes [males: $r^2 = .86$; females: $r^2 = .76$ (*5*)]. Wing length ratios ranged from 93 percent to 106 percent (males divided by females) averaging 98 ± 3 percent.
7. Estimating the population investment ratio by counting progeny of a random sample of nests departs from the χ^2 test's assumption of independent observations (here, individuals) when nests differ significantly from one another in their investment ratios. Sex differences in mortality and visibility, however, are likely to introduce errors in estimation after the termination of parental care. Thus, sex ratio data reported in the literature are often based on sampling by brood [for example (*2*); H. Howe, *Ecology* **57**, 1195 (1976); M. F. Willson, *Ecol. Monogr.* **36**, 51 (1966)]. The higher the proportion of all broods sampled, the smaller the effect of nonindependent sampling on the estimate. In view of the high proportion of known nests sampled in my study (0.85), the error introduced into the analysis by this departure from the assumptions is probably slight.

   Significant heterogeneity in investment patterns occurred in the pooled sample of nests (χ^2, $P < .001$). The proximate mechanisms by which differences in the sex ratio of parental investment are effected were not apparent in this study. I would expect them to be environmental cues at the time of egg-laying, which would influence queens to fertilize varying proportions of their eggs. It is possible, for example, that certain investment skews are associated with early or late production of reproductive offspring, the size of the worker force at a critical time, or the number of laying subordinate foundresses present. The precise control over the sex ratio afforded queens by haplodiploidy might allow them to track variations in the optimal sex ratio for their broods more closely than diplo-diploid parents. The long hazardous period of parental investment, with varying degrees of help from subordinate foundresses, and the production of sterile workers before any reproductive offspring undoubtedly increases the variety in circumstances to which egg-laying queens might respond.

   Whatever its proximal causes, heterogeneity in investment ratios among parents is predictable from sex-ratio theory. Fisher (*8*) argued that selection favors a particular ratio of investment in the population as a whole. Heterogeneity in the contributions of individual parents will not be selected against so long as the population investment ratio stays at its optimal value [(J. F. Crow and M. Kimura, *An Introduction to Population Genetics Theory* (Harper & Row, Evanston, 1970)].
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11. On four occasions, males from two different parental nests were seen together in the vicinity of mating aggregations. On one occasion, progeny of at least four nests were seen together in a crevice where courtship and mating occurred.
12. J. Owen, thesis, University of Michigan (1962).
13. If the queen dies on a multiple-queen nest and is replaced by a sister, the workers must rear cousins instead of brothers and sisters. Their relatedness to the brood falls from 1/2 (assuming monogamy and a 1:1 sex ratio) to 3/16. If the queen dies on a single-queen nest and is replaced by a worker daughter, leaving the rest of the workers to rear nieces and nephews, the relatedness of the workers to the brood falls only half as much, from 1/2 to 3/8. Although such a nest would produce only males (because workers are uninseminated), it would have to flood the local breeding population with offspring to the point that male reproductive value was halved for the workers to suffer the same reproductive loss as the workers on the multiple-queen nest.
14. R. D. Alexander, *Am. Zool.* **12**, 648 (1972); *Annu. Rev. Ecol. Syst.* **5**, 325 (1974); in preparation.
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17. Mechanisms by which workers could forcibly affect the investment ratio are (i) by physically excluding the queen from cells after she has laid in them so she cannot eat or replace eggs or even assess the sex ratio of a brood and (ii) by keeping the queen from distributing food unequally to larvae, perhaps by preventing her from feeding them at all.
18. Colonies of *Polistes metricus* also produce males earlier than reproductive females [Metcalf and Whitt (*19*); Metcalf (*20*)]. Metcalf notes that this increases the expense to workers of discriminating against the queen's sons. Queens in *P. metricus* populations mate at least twice, using sperm from the two inseminations in a ratio of 9:1 (*19*). The sex ratio of investment in populations near Urbana, Ill., is approximately 1:1 (*20*).
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Frequency Discrimination Following the Selective Destruction of Cochlear Inner and Outer Hair Cells

Abstract. *Frequency discrimination was measured behaviorally before and after drug-induced lesions of cochlear hair cells in the cat. Discrimination was unaffected by complete loss of outer hair cells provided that at least 50 percent of inner hair cells were intact. Thus, inner hair cells are important for frequency discrimination, and they can function normally in this regard without the influence of outer hair cells.*

The role of the inner and outer hair cells of the cochlea in frequency discrimination is not clearly understood. There is evidence, however, for a difference in their roles in auditory behavioral threshold determination (*1*) and in cochlear frequency selectivity (*2*). As frequency discrimination or the detection of frequencies separated in time is a different task from frequency selectivity or the ability to separate the individual components of a complex signal, it is of interest to determine the relative roles of the inner and outer hair cells in frequency discrimination.

Our behavioral study was carried out on three monauralized cats trained to respond by a conditioned suppression technique (*3*), as this retains the advantages of classical reward-and-avoidance conditioning without the disadvantages. With this technique a steady baseline of responding (lick rate) was first established. A test stimulus, which termi-

Table 1. Behavioral thresholds, outer and inner hair-cell loss, and frequency discrimination after kanamycin administration.

Frequency (kHz)	Cat	Hair-cell loss (%)		Behavioral threshold changes (dB)	Frequency discrimination changes (*F*)
		Inner	Outer		
1	6	0	0	−8	4.04*
	8	0	0	−5	0.96
	10	0	0	7	0.80
4	6	0	0	0	0.79
	8	35	0	0	0.60
	10	25	0	−2	0.48
8	6	65	0	23	1.46
	8	100	0	22	0.65
	10	95	0	21	1.73
10	6	100	0	28	1.22
	8	100	5	26	0.86
	10	100	15	36	1.06
12	6	100	75	40	6.47*
	8	100	50	51	4.30*
	10	100	<100	49	2.57*

*For $F(9, 24) > 2.36$, $P < .05$.

nated in a brief unavoidable shock, was then presented. This led to a reduction in the lick rate from which the suppression ratio could be calculated. Behavioral auditory thresholds were determined by plotting suppression ratios for frequencies of 1, 4, 8, 10, 12, and 16 kHz. This procedure was carried out in a specially designed conditioning box (*4*) placed in a sound-attenuated room; the acoustic field in the conditioning box was measured for the test frequencies at 60 dB (with reference to 0.0002 dyne/cm^2). Frequency discrimination was also determined by plotting suppression ratios for various changes in frequency ($\Delta f/f$) at 1, 4, 8, 10, 12, and 16 kHz, at an intensity of 60 dB.

In presenting the stimuli, the intensity was randomized by the computer over a 10-dB range to prevent the intensity maxima and minima in the auditory field being used as false clues. The cats were then given a series of intramuscular injections of kanamycin (200 mg per kilogram of body weight per day) for 10 days to selectively destroy the outer hair cells, and behavioral thresholds were determined shortly afterward to assess the extent of the hearing loss. Frequency discrimination at 60 dB was then measured, at least 14 days after the cessation of the ototoxic drug, at all the previous frequencies except 16 kHz, where the auditory behavioral threshold was too high. Behavioral thresholds were again determined to ensure that no progressive deterioration in thresholds had occurred. Immediately afterward, the animals were anesthetized, first with pentobarbital sodium (40 mg/kg, injected intraperitoneally) and then with supplementary injections to maintain a satisfactory anesthetic level. The animals were perfused, the cochleas were prepared for surface-preparation histology (*5*), and the inner and outer hair cells were photographed and counted along the length of the cochleas through the use of a differential interference phase contrast microscope. As a result, cochleograms showing the inner and outer hair-cell losses for different frequencies were constructed on the basis of the frequency-to-distance relationship determined from the studies of Schuknecht (*6*) and Kiang *et al.* (*7*).

Table 1 shows the changes in hearing thresholds in decibels following the administration of kanamycin and the percentage of inner and outer hair-cell losses for the test frequencies. Changes in frequency discrimination were evaluated with a two-way analysis of variance. The interaction of the $\Delta f/f$ effect and the predrug and postdrug effect was considered appropriate for assessing changes in frequency discrimination, and their *F* values are shown (Table 1). The hearing thresholds were increased by from 21 to 51 dB at 8, 10, and 12 kHz. Examination of the surface preparations showed the outer hair-cell loss was complete at the cochlear locations corresponding to 10 and 12 kHz, complete in one animal and partial for two at 8 kHz, and partial for two animals at 4 kHz. On the other hand, inner hair-cell loss was considerably less. Furthermore, at frequencies of 8 and 10 kHz where there was a marked loss of outer but not inner hair cells, there was no significant difference between the frequency discrimination result before and after the ototoxic antibiotic. A significant difference occurred only with the loss of inner hair cells in excess of 50 percent, at a frequency of 12 kHz. The significant result for cat 6 at 1 kHz can be explained from the raw data, which showed an improvement in frequency discrimination after the drug rather than a decrease; this was thought to be a practice effect.

The evidence indicates that frequency discrimination is not affected by the loss of outer hair cells. It is, however, reduced when the loss of inner hair cells is greater than 50 percent. Thus, the inner hair cells are important for frequency discrimination, and they can function normally without needing intact outer hair cells.

TERRY G. W. NIENHUYS
GRAEME M. CLARK
Departments of Otolaryngology and Psychology, University of Melbourne, Parkville 3052, Victoria, Australia

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Dieldrin-Induced Mortality in an Endangered Species, the Gray Bat (*Myotis grisescens*)

Abstract. *Brains of juvenile gray bats,* Myotis grisescens, *found dead beneath maternity roosts in two Missouri caves contained lethal concentrations of dieldrin. One colony appeared to be abnormally small, and more dead bats were found a year after the juvenile bats had been collected. This is the first report to link the field mortality of bats directly to insecticide residues acquired through the food chain.*

Insecticides have long been blamed for the decline of bat populations (*1*), but compelling data were lacking. Recently, strong, although indirect, data showed that DDE in the food chain probably has been an important cause of the decline of free-tailed bats (*Tadarida brasiliensis*) at Carlsbad Caverns, New Mexico (*2*). Our study documents mortality and probable population decline in the gray bat (*Myotis grisescens*) resulting from routine insecticide usage.

In August 1973 the U.S. Army Corps of Engineers completed its Environmental Impact Statement for the proposed Meramec Park Lake (MPL), Missouri. Because this statement predicted that the lake would have adverse effects on the habitat of the endangered Indiana bat (*Myotis sodalis*), a survey of all *Myotis* species in the park area was undertaken, sponsored jointly by the Corps of Engineers, the U.S. Fish and Wildlife Service (USFWS), and the Missouri Department of Conservation. This 18-month study began in July 1975. The gray bat, which is abundant in the MPL area, was added to the USFWS's list of endangered species in 1976. Dead gray bats found in three caves during the survey were sent to the Patuxent Wildlife Research Center (PWRC) in an effort to determine whether organochlorine pollutants were the cause of death (*3*).

The precise locations of the caves are confidential; therefore, we will refer to them by numbers assigned by the USFWS. Two of the three caves, caves 048 and 054, are in Franklin County; the third, cave 036, is in Dent County (*4*). These three caves contain the known maternity roosts of the gray bat in the MPL area. All bats found dead were juveniles. Data from another population

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