same material increases linearly with the applied field until saturation is reached at about 1.8×10^3 Oersteds. The presence of magnetite in three live bees was tested by freezing them to −196°C in liquid nitrogen, and then continually monitoring the remanence as they warmed up through the isotropic point of magnetite (−143°C). In each case, the remanence decreased slightly near this temperature, indicating the presence of magnetite (*19*). Regardless of what these attempts to characterize the magnets produce, only our behavioral experiments can establish whether or not bees actually use these magnetic crystals for orientation.

JAMES L. GOULD
Department of Biology, Princeton University, Princeton, New Jersey 08540
J. L. KIRSCHVINK, K. S. DEFFEYES
Department of Geological and Geophysical Sciences, Princeton University

References and Notes

1. W. T. Keeton, in *Animal Orientation and Navigation*, S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, R. E. Belleville, Eds. (Government Printing Office, Washington, D.C., 1972), pp. 579–594; C. Walcott and R. P. Green, *Science* **184**, 180 (1974).
2. W. Wiltschko and R. Wiltschko, *Science* **176**, 62 (1972).
3. M. Lindauer and H. Martin, *Z. Vgl. Physiol.* **60**, 219 (1968).
4. H. Martin and M. Lindauer, *J. Comp. Physiol.* **82**, 145 (1972); M. Lindauer and H. Martin, in *Animal Orientation and Navigation*, S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, R. E. Belleville, Eds. (Government Printing Office, Washington, D.C., 1972), pp. 559–567. Both R. Morse (personal communication) and I have been unable to replicate the comb-building experiment.
5. M. L. Brines, thesis, Rockefeller University (1978).
6. M. Lindauer, *Proc. Intern. Congr. Entomol. 15th* (1977), p. 450; the evidence is intriguing but indirect.
7. M. L. Kreithen and W. T. Keeton, *J. Comp. Physiol.* **91**, 355 (1974).
8. M. A. Bookman, *Nature (London)* **267**, 340 (1977).
9. J. Phillips, *J. Comp. Physiol.* **121**, 273 (1977).
10. H. A. Lowenstam, *Science* **156**, 1373 (1967); *Geol. Soc. Am. Bull.* **73**, 435 (1962).
11. R. Blakemore, *Science* **190**, 377 (1975); A. Kalmijn and R. Blakemore, in *Animal Migration, Navigation, and Homing*, K. Schmidt-Koenig, Ed. (Springer-Verlag, New York, 1978).
12. W. S. Goree and M. Fuller, *Rev. Geophys. Space Phys.* **14**, 591 (1967).
13. We have traced the induced remanence to small (200 μm) dark specks, which are widely distributed in the digestive tract of older bees. Under the scanning electron microscope, one class of these objects has been identified as inorganic. The other class is still being investigated.
14. We are reminded of D. Griffin's remark in a similar context that "if they do not use it, perhaps they ought to try."
15. K. M. Towe and H. A. Lowenstam, *J. Ultrastruct. Res.* **17**, 1 (1967).
16. R. F. Butler and S. K. Banerjee, *J. Geophys. Res.* **80**, 4049 (1975).
17. This is consistent with our measurements of increased induced remanence at very low temperatures, indicating that superparamagnetic domains have become stable. This is also consistent with the transverse field orientation data, since, in that orientation, only superparamagnetic crystals can easily be arranged to construct a hypothetical detector which could explain the dance misdirection data.
18. For example, the concentration of iron in nectar [M. Shabanov and N. Ibrishimov, *Acta Microbiol. Virol. Immunol.* **2**, 105 (1975)] and pollen [M. H. Hadak and M. C. Tanguary, *Tech. Bull. Minn. Agr. Exp. Sta. No. 160* (1943), p. 23] depends on the species of plants in bloom. The iron content of honey, for example, varies from 0 to 45 ppm. Without enough iron in the diet, bees could not synthesize the crystals. Alternatively, like first-flight pigeons which cannot use magnetic field information when raised in sunny areas [W. T. Keeton, *Sci. Am.* **231** (No. 6), 96 (1974)], perhaps bees do not build detectors when they do not need them. This is consistent with the observation that bees in horizontal hives do not begin orienting their dances to magnetic fields for several weeks. Since the average life-span of a forager is 3 weeks, these could easily be, and probably are, a new generation of bees.
19. M. Ozima, M. Ozima, S. Akimoto, *J. Geomagn. Geoelectr.* **16**, 165 (1964); S. Levi and R. T. Merrill, *J. Geophys. Res.* **83**, 309 (1978).
20. A preliminary survey of 18 species of invertebrates revealed natural remanences larger than 0.5×10^{-6} emu (against a background of 0.02×10^{-6} emu) in a Vespid wasp, housefly (*Musca domestica*), roach (*Periplaneta americana*), and staghorn beetle (*Passalus cornutus*), as well as a marginal remanence in a *Tenebrio* beetle. We thank T. C. Onstott and N. Dorety for making preliminary measurements, as well as the director (D. P. Elston) and staff (S. L. Bressler and M. E. Puruckner) at the U.S. Geological Survey Paleomagnetics Laboratory in Flagstaff, Ariz., for help and interdisciplinary enthusiasm. Supported by NSF grant BNS 76-01653A02 to J.L.G.

4 April 1978; revised 26 June 1978

Primate Infant's Effects on Mother's Future Reproduction

Abstract. *Female savanna baboons* (Papio cynocephalus) *had a longer postpartum amenorrhea and thereafter cycled longer before conceiving if their previous infant survived than if that infant died. Among mothers of surviving infants, differences in maternal care produced differences in age of weaning and age of independence but did not result in differences in interbirth intervals.*

Parental care expended on current offspring can reduce a parent's future reproductive success if such activities delay subsequent reproduction. Such activities are "parental investment," in that they increase one offspring's chances of surviving at the expense of the parent's ability to produce other offspring (*1*). The recent speculative and theoretical literature on parental investment (*2*) highlights the paucity of relevant data from natural populations. In this report we present evidence that, in savanna baboons (*Papio cynocephalus*), infants reduce their mothers' future reproduction success by effecting a delay in her subsequent reproduction through effects on two phases of her reproductive cycle.

Primate interbirth intervals consist of three main phases: (i) a period of postpartum amenorrhea or sterility; (ii) a period of cycling, itself consisting of one or more estrus (menstrual) periods, each of which usually includes ovulation; and (iii) a period of gestation. We now have sufficient longitudinal data from yellow baboons inhabiting Amboseli National Park, Kenya, to examine effects of infants on phases of their mothers' reproductive cycles. Of the three phases, only gestation length is subject to virtually no variability in Amboseli baboons (the mean was 177 days from onset of last deturgescence of the sexual skin, the standard error of the mean was 1 day, the standard deviation was 4 days, and N was 25). Thus gestation length can be assumed to be essentially unaffected either by a female's current infant or by other potentially important factors, such as maternal age or habitat quality. In contrast, both amenorrhea and length of time spent cycling prior to conception showed great variability. We shall consider each of these in turn.

Female baboons in Amboseli resume cycles approximately 3 weeks after infant death, regardless of the infant's age at death, a value in striking contrast with that for females with surviving infants, for whom the range of postpartum amenorrhea is 6 to 17 months with a mean of 12 to 12.5 months (*3*). In contrast, laboratory and zoo reports suggest that the comparable value in such confinement but without separation of mother and infant is about 5 to 6 months (*4*). These results suggest that some of the reported differences in populations may be accounted for not only by infant presence, but also by nutritional effects and differences in energy demands [see Jain *et al.* (*5*) for similar differences that correlate with socioeconomic class in humans]. Baboons in Amboseli appear to experience shorter periods of postpartum amenorrhea in years of good rainfall, but the patterns are not clear-cut nor are the data yet adequate for statistical testing.

From laboratory work on primate reproductive physiology (*6*), it has long been recognized that the presence of an infant can delay resumption of menstrual cycles, thereby delaying a female's next conception. More recently, several researchers (*7*, *8*) have reported that nonnursing females in two free-ranging, provisioned groups of rhesus monkeys (*Macaca mulatta*) produced infants approximately 1 month earlier in the birth season than did nursing females. In that population, earlier births are associated with higher infant survival and with greater probability of mothers giving birth in the following year (*8*). Kawai (*9*) and Tanaka *et al.* (*10*) reported that in

0036-8075/78/0915-1028$00.50/0 Copyright © 1978 AAAS

groups of provisioned Japanese macaques (*Macaca fuscata*), nonnursing females were more likely than were nursing females to have shorter (1-year) interbirth intervals (95 percent and 9 percent, respectively, in Tanaka's study). In none of these other field studies were effects on the different phases of the reproductive cycle identified, although several of the authors suggest that these effects resulted from changes in the length of postpartum amenorrhea. Gombe Stream chimpanzees may experience shorter postpartum amenorrhea if their most recent infant dies (*11, 12*). The role of lactation in extending the period of postpartum amenorrhea in humans has been well documented.

Infant survival also affected time spent cycling before conceiving. We now have 12 cases of infant death and 22 cases of infant survival for which data are available on the length of time the mother subsequently spent cycling before again becoming pregnant. For females whose previous infant had died before the female's next conception, both mean and median values for time subsequently spent cycling were 60 days or two estrus periods; the modal number of estrus periods for this group of females was one. In contrast, mothers with surviving infants cycled for a mean and median of 124 and 121 days, respectively, or four estrus periods, which was also the modal value. We used a sign test in which we asked whether the 12 values for time spent cycling in the case of infant death fell equally on the two sides of the median value (121) of the other group. We found that 10 of the 12 values fell below the median, an unlikely result ($P < .02$) under binomial assumptions. (A t-test comparison of mean cycle time of females with a surviving infant versus those without gave $P < .01$, but the assumptions of that test may not be adequately fulfilled.) In short, females with surviving infants cycled significantly longer before becoming pregnant (about twice as long on the average) than females whose previous infant had died. Further, for mothers of surviving infants, there was a nonsignificant tendency for those that resumed cycles early to take longer thereafter before becoming pregnant, a result produced primarily by the complete absence of conception in females with infants less than a year of age.

Perhaps the relation between infant age and maternal conception rate is spurious: infant age may not be the proximate variable. If the effect of surviving infants on maternal conception rate results from energy cost expended in carrying and suckling the infant, it would be a direct function of these variables, which are only imperfectly correlated with infant age. From the standpoint of parental investment, it is important to consider whether variability in some component of maternal care, such as the amount of time an infant is allowed in contact with its mother, affects the female's future reproductive success. For example, in a recent study of baboon mothers and infants (*13*), we found that infants of nonrestrictive mothers were 1 to 2 months ahead of their restricted peers when the time spent out of maternal contact and the age of weaning were measured. The nonrestrictive mothers experienced shorter postpartum amenorrhea than did the restrictive ones. As is consistent with the trend described above, however, these nonrestrictive mothers spent a longer time cycling before becoming pregnant, resulting in no difference in interbirth interval between the two groups, and thus negating the potential advantage of early cycling in reducing the interbirth interval. Perhaps that advantage is realized only in years of particularly good rainfall or food supply. If so, nonrestrictive mothers would then have shorter interbirth intervals. Additional longitudinal data will be required to clarify these interactions. In order to elucidate the nature and cost of maternal investment, we are analyzing data from a subset of infants for whom we have maternal contact and nursing data, in addition to reproductive data for their mothers.

One consequence of more rapid conception after loss of an infant is that it enables individuals and populations to recover rapidly from periods of high infant mortality. Infant loss will have a greater impact on shortening interbirth intervals in species with year-round breeding than in those with discrete breeding seasons. Furthermore, several authors have proposed that more rapid conception after loss of an infant might provide the opportunity for development of infanticide as an adaptive male reproductive strategy. For example, a male that takes over a one-male group from another male and then kills the infants in the group, as in some langur monkeys (*14*), might benefit doubly: by eliminating his predecessor's offspring and by increasing the number of his own infants if the females soon come into estrus and conceive (*15*). In general, the potential effectiveness of infanticide as a reproductive strategy will depend not only on its effectiveness in shortening the time to the infanticidal male's successful matings but also (i) on the length of time that a male is in a position of high reproductive status (*16*) and (ii) on some mechanism, social or otherwise, for ensuring that males do not kill their own offspring. In contrast, male infanticide generally will be selectively disadvantageous to females, because it reduces their reproductive success. Relatively promiscuous mating occurs in the multi-male, multifemale groups of many primate species, including the savannah baboons discussed here. The resulting uncertainty over paternity may be advantageous to females in that it reduces or precludes a selective advantage to male infanticide.

In summary, if an infant dies, its mother resumes cycling within 1 month and becomes pregnant again within 3 months of infant death. The presence of an infant under 1 year of age severely limits and perhaps eliminates the chance that a female baboon becomes pregnant during that time, that is, with both postpartum amenorrhea and cycling time lengthened compared to the values under the condition of infant death. In effect, the result is a period of complete sterility, which lasts approximately 12 months and is followed by several months of partial sterility or somewhat lower conception rate than that for females whose previous infant has died; young infants have the effect of a perfect contraceptive, older ones an effect more like a faulty contraceptive. However, available evidence does not support the idea that variability in mother-infant relationships, such as the rate of infant independence or the time of weaning, affects the mother's future reproduction success and could thus be considered variability in maternal investment.

JEANNE ALTMANN
STUART A. ALTMANN
University of Chicago, Allee Laboratory of Animal Behavior, Chicago, Illinois 60637
GLENN HAUSFATER
Cornell University, Section on Neurobiology and Behavior, Ithaca, New York 14853

References and Notes

1. R. L. Trivers, in *Sexual Selection and the Descent of Man, 1871–1971*, B. Campbell, Ed. (Aldine-Atherton, Chicago, 1972), p. 136.
2. R. Alexander, *Annu. Rev. Ecol. Syst.* **4**, 325 (1974); D. H. Boucher, *Am. Nat.* **111**, 786 (1977); R. Dawkins and T. R. Carlisle, *Nature (London)* **262**, 131 (1976); J. Maynard Smith, *Anim. Behav.* **25**, 1 (1977); R. L. Trivers, *Am. Zool.* **14**, 249 (1974).
3. J. Altmann, S. A. Altmann, G. Hausfater, S. A. McCuskey, *Primates* **18**, 315 (1977).
4. T. Rowell, *J. Zool.* **149**, 344 (1966).
5. A. K. Jain, T. C. Hsu, R. Freedman, M. C. Chang, *Demography* **7**, 255 (1970).
6. S. Zuckerman, *Proc. Zool. Soc. Lond.* (1931), p. 593; C. G. Hartman, *Carnegie Inst. Wash. Contrib. Embryol.* **23**, 1 (1932).
7. C. B. Koford, *Tulane Stud. Zool.* **13** (1), 1 (1966); J. G. Vandenbergh and S. H. Vessey, *J. Reprod. Fertil.* **15**, 71 (1968).

8. L. C. Drickamer, *Folia Primatol.* **21**, 61 (1974).
9. M. Kawai, *Nihonzaru no Seitai (Ecology of Japanese Monkeys)* (Kawade-shobo Shinsha, Tokyo, 1969), p. 300.
10. T. Tanaka, K. Tokuda, S. Kotera, *Primates* **11**, 113 (1970).
11. G. Teleki, E. E. Hunt, Jr., J. H. Pfifferling, *J. Hum. Evol.* **5**, 559 (1976).
12. C. B. Clark, in *Primate Bio-Social Development: Biological, Social and Ecological Determinants*, S. Chevalier-Skolnikoff and F. Poirier, Eds. (Garland, New York, 1977), p. 235.
13. J. Altmann, in *Ontogeny of Behavior*, G. Burghardt and M. Bekoff, Eds. (Garland, New York, 1978).
14. See for example the following, S. B. Hrdy, *Folia Primatol.* **22**, 19 (1974); S. M. Mohnot, *Mammalia* **35**, 175 (1971); M. B. Parthasarathy and H. Rahaman, in *Congr. 5th Int. Primatol. Soc., Nagoya* (1974), abstracts, p. 128; R. Rudran, *Folia Primatol.* **19**, 166 (1973); Y. Sugiyama, *Primates* **5**, 7 (1964); in *Social Communication Among Primates*, S. Altmann, Ed. (Univ. of Chicago Press, Chicago, 1967), p. 221.
15. W. Angst and D. Thommen. *Folia Primatol.* **27**, 198 (1977).
16. M. Chapman and G. Hausfater, in preparation.
17. This research was supported by PHS grant MH 19617 and NSF grant BNS-76-06259. We gratefully acknowledge the cooperation of the government of Kenya and especially that of Joseph Kioko, warden of Amboseli National Park.

21 February 1978; revised 27 June 1978

Competitive Interactions Between Neotropical Pollinators and Africanized Honey Bees

Abstract. *The Africanized honey bee, a hybrid of European and African honey bees, is thought to displace native pollinators. After experimental introduction of Africanized honey bee hives near flowers, stingless bees became less abundant or harvested less resource as visitation by Africanized honey bees increased. Shifts in resource use caused by colonizing Africanized honey bees may lead to population decline of Neotropical pollinators.*

If two species compete for a resource, it must be limiting in such a way that an increase in resource harvest by one species corresponds to diminished harvest by the other. Competition also occurs if resource harvest remains stable but harvest cost increases. The evidence of interspecies competition for food is usually circumstantial, and, despite extensive treatment of the subject, few field studies clearly demonstrate its importance (*1*). The Old World honey bee *Apis mellifera* is thought to displace native pollinators from both floral resources and geographic areas (*2*). During a study of competition between Africanized honey bees (feral hybrids of African and European *A. mellifera*) and native pollinators, I manipulated the number of Africanized honey bees foraging on certain flowering plants in French Guiana, South America. The experiments demonstrated that Africanized honey bees sometimes compete with native bees by diminishing their foraging success at flowers. Previous studies on the impact of introduced *A. mellifera* on the foraging activity of indigenous pollinators have not been made (*3*).

My study was conducted along a forest-savanna transition zone near Kourou, French Guiana, between November 1976 and June 1977. Introduced European honey bees were rare in French Guiana, and Africanized honey bees arrived in 1974 (*4*). The density of Africanized honey bee colonies was quite low at the time of the experiments. Feral Africanized honey bee swarms were captured and transferred to hives; each contained 6,000 to 15,000 bees when used in the experiments (*5*).

Hives of Africanized honey bees were introduced and later removed near patches of flowering plants visited by Africanized honey bees as well as stingless and other bees, wasps, and flies (Table 1). During periods when Africanized honey bee hives were present and absent, numbers of floral visitors were recorded in plots of *Mimosa pudica* (Fabaceae), *Melochia villosa* (Sterculiaceae), *Rhynchospora globosa* (Cyperaceae), and *Borreria* species (Rubiaceae) (*6*). I used different sizes and numbers of plots within patches of each plant species, and this permitted sufficiently large but accurate counts of foragers on flowers differing in spatial distribution (*6*). Foraging bees collected only pollen from *Rhynchospora* and *Mimosa*, but collected both nectar and pollen from the other flowers. Africanized honey bees from feral colonies foraged on all flowers except *Rhynchospora* when the experiments began, but had been in the area less than 2 years.

I began to take a census of foragers in the morning as flowers opened or first presented pollen and nectar. Bees depleted *Rhynchospora* and *Mimosa* pollen by midmorning, and few bees collected pollen on *Melochia* and *Borreria* after this time. However, the *Borreria* continued providing nectar and were visited in the early afternoon. During each day, forager counts were made at regular intervals for 80 to 180 minutes. Thus, five to ten separate counts were obtained on a daily basis of foragers in each plot within a larger patch of each plant species. Plots of *Mimosa* varied greatly in floral density over time, and flower counts in each were made daily. Floral densities remained stable in other species patches. Estimated mean total flowers in combined plots ranged from 843 in *Mimosa* to 27,000 in *Borreria*.

Additional measurements of pollen harvest were taken for stingless bees visiting *Mimosa* and Africanized honey bees foraging on *Rhynchospora*. I hypothesized that duration of floral visits varied with pollen abundance on *Mimosa* and measured the time spent visiting five flowers for 50 bees of the *Melipona* species with Africanized honey bees present and absent. Measurements were made during the first hour of foraging on 16 days when Africanized honey bees foraged and 4 days during their absence. Pollen harvest by two Africanized honey bee colonies visiting *Rhynchospora* was quantified by counting the number of foragers returning to each with pollen of this species for two 1-minute periods every 20 minutes.

Stingless bees became less abundant when Africanized honey bees increased in numbers on *Melochia villosa* (Table 1 and Fig. 1). Removal of Africanized honey bee hives led to reversal in abundance trends among Africanized and stingless bees ($P < .05$ in a nested analysis of variance; nested groups were comprised of days when Africanized honey bee hives were present or absent). The mean daily number of foraging Africanized honey bees dropped from 111.3 to 72.0 and that of stingless bees increased from 23.3 to 61.0 after Africanized honey bee removal. Figure 1 illustrates the relationship between Africanized and stingless bee abundance on *Melochia* (*7*). At low densities of each forager class, usually occurring at the first observations made at recently opened flowers, there was no negative numerical interaction. But at high densities of Africanized honey bees, their numbers increased as stingless bees became less abundant.

Africanized honey bee numbers changed significantly on *Rhynchospora* and *Mimosa* during the experiments (Table 1), but no significant change in numbers occurred within patches of *Borreria*, and competitive effects could not be assessed at this resource. The daily mean number of bees returning to Africanized honey bee hives with *Rhynchospora* pollen was 5187 ± 423 (S.D.). These were the only Africanized honey bees foraging on *Rhynchospora*, and their removal should have affected pollen availability, but no significant regres-

0036-8075/78/0915-1030$00.50/0 Copyright © 1978 AAAS