antigenic structure in ependymal cells (*9*). We have found the presence of histocompatibility antigens on ependymal cells and are also developing a panel of monoclonal antibodies against these cells. We have not found Fc receptors or Thy 1.2 on the ependymal cell surface. A better understanding of the surface antigens on ependymal cells will facilitate the study of viral receptors as determinants of the affinity of viruses for the central nervous system (CNS).

Other cells from the CNS, such as oligodendrocytes, astrocytes, or neurons, could also be used to define the various classes of viruses to which they bind specifically. Thus our data suggest a new approach to the study of viral affinity for the CNS, the role of viral receptors in the age-dependent susceptibility of the CNS to viruses, and the possibility that viral affinity for cell surface antigens may determine immune-mediated damage to specific cell types.

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26 August 1981; revised 20 October 1981

Helpers: Effects of Experimental Removal on Reproductive Success

Abstract. *Experimental removal of helpers from a communal bird population decreased the reproductive success of the reduced units. By controlling for variables that are potentially correlated with both reproductive success and unit size, this experiment establishes that helpers contribute significantly to their indirect fitness.*

Helping behavior may be defined as the performance of parent-like behavior toward young that are not offspring of the helper (*1*), usually a nonbreeder. Thus helpers offer the closest parallel among vertebrates to the "sterile" workers of the social insects. Consequently, helping is useful in field tests of inclusive fitness theory (*2*) in vertebrates because of its potential contribution to indirect fitness (*3*), an effect often invoked in theories of the evolution of helping behavior (*4*). Previous studies of this contribution in populations of communal birds and mammals have relied on the positive correlation of reproductive success with numbers of helpers in situations where the helpers and recipient are usually closely related (*5*).

It has seemed likely that helpers caused increased reproductive success in their social units, since their help was often conspicuously visible. Nevertheless, competing hypotheses have not been rejected. A positive correlation between reproductive success and unit size in singular breeding species (*6*) could also arise from positive correlations of reproductive success and unit size with other variables. A factor not adequately controlled in previous studies is the quality of the territory. Since helpers in many species are the offspring of the same parents in a previous breeding season, if certain territories usually enable greater reproductive success than others, then a positive correlation between reproductive success and unit size could arise from this relation alone, with no contribution from the helpers (*7*). Similar results could arise if older parents were consistently more successful than younger ones.

Another objection to the interpretation that helpers increase reproductive success was raised by Zahavi (*8*) after observing agonistic behavior within social units of babblers. He claimed that "nonbreeding birds may do more harm than help to the reproduction of the breeding pair." Zahavi did not find a positive correlation between reproductive success and unit size in his data, although on reexamination it was found by others (*9*). In this and other studies in which the anticipated positive correlation was not significant, the small sample sizes made it difficult to show a significant relation of any kind (*10*).

To determine whether the correlation between reproductive success and unit size was caused by the number of helpers or by other variables correlated with both reproductive success and unit size, we removed helpers, in an experiment performed in the field under natural conditions. Twenty social units of the gray-crowned babbler (*Pomatostomus temporalis*) of approximately the same original size (six, seven, or eight birds) were separated into groups of nine experimental units and 11 control units, matched as nearly as possible for original size. Experimental units were reduced to three birds, the original breeding pair and one yearling helper chosen at random; the other group of units served as controls (*11*). Because the removals were performed after the first brood of young, the dependent variable used as an index of reproductive success was the total number of young that were reared to the point of leaving the nest from second and subsequent broods—that is, fledglings from all broods after the first (F2). In this design, other variables that might be correlated with the original size of the unit, such as vegetation, other components of territorial quality, and age or ability of parents, would not be affected by the removals and should average the same in the two groups (*12*).

Comparison of experimental units with natural control units of the same original size, by controlling for variables correlated with original size, allows an independent estimate of the effect of helpers on reproductive success. Control units had an average of 2.4 fledglings from the second and subsequent broods, more than twice as many as the experimental units, which had an average of 0.8 (*13*). This result allows us to reject the hypothesis that the difference in reproductive success between control and experimental groups is the result of factors correlated with the original size.

Comparison of experimental units with natural units of two and three members, by controlling number of helpers, allows an estimate of the effects of other factors correlated with the original size. The reproductive success of experimental units was very close to that of natural

0036-8075/82/0122-0421$01.00/0

units of the reduced size (*14*). We conclude that factors correlated with the original size, such as territorial qualities and parental age, had no statistically significant influence on the difference between natural units of two or three members and units of six, seven, and eight members.

In this study, both unit size and reproductive success were correlated with vegetation on the territory and with parental age (*15*). Comparison of these and other variables revealed no significant differences between experimental and control groups of the same original size.

In summary, the positive correlation between reproductive success and the number of helpers is not the result of other variables that are correlated with unit size and reproductive success. It is caused mainly by the helpers or by an interaction of the helpers with another variable. We reject the hypothesis that helpers do more harm than good. Because helpers in this species are typically offspring of the breeder in their units (*16*), we have demonstrated, without the reservations expressed in (*7*), that helpers significantly improved the reproductive success of their parents, thereby increasing their own indirect fitness (*17*).

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11. Control and experimental units were treated equally. Both were lured into mist nets with tape-recorded calls; all birds were color-banded for individual recognition, weighed, measured, and released where caught. Removed birds were killed. These procedures did not cause units to leave; all units remained on their territories for at least several months.
12. This study was performed at Meandarra, Queensland, Australia, from August 1976 to August 1977. For further details on the study, see J. L. Brown, D. D. Dow, E. R. Brown, S. D. Brown, *Behav. Ecol. Sociobiol.* **4**, 43 (1978); M. S. Johnson, J. L. Brown, *ibid.* 7, 93 (1980); J. L. Brown, *Emu* **79**, 1 (1979).
13. These groups differed in a Mann-Whitney U test ($U = 76$, $P < .05$, two-tailed). Observed values of F2 for control units were 0, 0, 1, 2, 2, 2, 2, 3, 3, 5, and 6 and for experimental units were 0, 0, 0, 0, 0, 1, 1, 2, and 3. Most control units had a second brood; most experimental units did not. A few control units had three successful broods; no experimental units did. Statistics were calculated by using *BMDP-77*, W. J. Dixon and M. B. Brown, Eds. (Univ. of California Press, Berkeley, 1977).
14. These two groups did not differ in a Mann-Whitney U test ($U = 40$, two-tailed). Observed values of F2 for natural units of two and three were 0,0,0,0,0,0,0,1, and 2.
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16. In August 1977, all banded young of banded parents reared in the 1976 breeding season ($N = 45$) were still with their parents in their natal territories. The 1975 year class showed similar, but less impressive, site fidelity.
17. We limit our conclusion to the variables considered here. We intend no implications about the mechanisms of the effect of helpers on reproductive success. Specifically we do not want to imply that the increment to reproductive success arises only from the feeding of young by helpers. Helpers may also allow savings to the energy budgets of breeders by means of aid in territorial defense and antipredator behavior. For further discussions of relevant mechanisms, see J. L. Brown, *Annu. Rev. Ecol. Syst.* **9**, 123 (1978).
18. We thank R. Jamieson, E. Perry, and their families. Supported by the authors, by Public Health Service grant MH 16345, by the Australian Research Grants Committee, and by the University of Queensland.

28 September 1981

Reputed Band Attractiveness and Sex Manipulation in Zebra Finches

Burley's conclusions (*1*) that zebra finches (*Poephila guttata*) choose mates by their leg-band colors, that birds wearing certain colors produce more offspring than others, and that the sex ratio of the offspring depends upon the parental band colors are all unsupported by the evidence. We summarize selected objections.

(i) The study (*1*) depends upon the interpretation of unpublished (*2*) data. (ii) Band colors used were not identical with those of the unpublished study. (iii) It is unclear whether the same birds were used as in the unpublished study; zebra finches are known (*3*) to have individual preferences in mating. (iv) In either case, no history of prior nesting and mating experiences are provided, although the past experience also affects mating preferences in this species (*3*). (v) The approach criterion for sexual preference has already been established (*4*) as invalid for this species. (vi) The birds were grossly overcrowded: 60 individuals were released into an 80-m^3 aviary and at least some parents reared at least four clutches (*5*) during the study, so that density probably increased continuously. (vii) It is not reported whether renesting birds (*5*) retained the same mates. (viii) Data are not broken down by individual pairs, so individual differences in productivity of offspring are confounded with band color effects, and a direct test of mating preferences was thus ignored. (ix) At least 11 offspring were omitted because they could not be sexed by plumage (*5*) and no standard laparotomies were performed. (x) Four clutches were omitted because they were tended by a female-female pair (*5*), thus eliminating about 24 additional offspring. (xi) The very occurrence of female-female pairs (*5*) suggests behavioral pathology, and the implied infidelity casts doubt on the assignment of parentage for all offspring. (xii) The complex multivariate design with four independent variables (individual, sex, band color, and successive renesting of parent) and two dependent variables (number of male and female offspring) was invalidly analyzed with chi-square statistics. (xiii) A conservative estimate suggests that the design has more than 280 data cells, filled by only 125 data points. (xiv) Even using the χ^2 analysis, conclusions do not follow from the data. The analysis is too complicated to present here in summary, but a Xerox copy of our detailed comments may be obtained by writing J.P.H.

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5. Reference 7 of (*1*): "Data on 11 'white' birds are excluded because birds with this plumage mutation cannot be accurately sexed on the basis of external appearance. Data are also excluded for one homosexual female couple (orange-blue) that raised four clutches with no apparent male assistance."
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6 April 1981; 23 June 1981

0036-8075/82/0122-0422S01.00/0