and Reed did not and could not have addressed all potential group effects or combinations of group effects that may have resulted in the patterns that they observed. Indeed, they indicate that non-red-banded males tended to have more helpers than red-banded males. The difference was not significant ($P = 0.12$), but fewer helpers could be symptomatic of general group features that could have decreased the reproductive output of red-banded males.

Because of the widespread use of colored leg bands in field ornithology and the likelihood that in some cases colored bands have an undesired effect on the birds under study, there is a serious need for field studies to test the effects of leg bands on wild birds. At the same time, because of the potential implications for many studies that are founded on the assumption that colored leg bands have no effect on birds, investigations of the effects of color bands must be carefully designed and data must be analyzed and interpreted conservatively. We believe that the study by Hagan and Reed is sufficiently flawed in both the design of the experiment and the interpretation of results that it should be discounted as evidence for an effect of colored leg bands.

We thank Robert Payne for his comments on an earlier draft of this manuscript.

LITERATURE CITED

BRODSKY, L. M. 1988. Ornament size influences mat-ing success in male Rock Ptarmigan. Anim. Behav. 36: 662–667.

BURLEY, N. 1981. Sex-ratio manipulation and selection for attractiveness. Science 211: 721–722.

———. 1985. Leg band color and mortality patterns of captive breeding populations of Zebra Finches. Auk 102: 647–651.

———. 1986. Sex-ratio manipulation in color banded populations of Zebra Finches. Evolution 40: 1191–1206.

———, G. KRANTZBERG, & P. RADMAN. 1982. Influences of color banding on the conspecific preferences of Zebra Finches. Anim. Behav. 30: 444–455.

HAGAN, J. M., & J. M. REED. 1988. Red color bands reduce fledgling success in Red-cockaded Woodpeckers. Auk 105: 498–503.

SOKAL, R. R., & F. J. ROHLF. 1981. Biometry. New York, W. H. Freeman and Co.

STEEL, R. G. D., & J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. New York, McGraw-Hill Book Co., Inc.

WATT, D. J. 1982. Do birds use color bands in recognition of individuals? J. Field Ornithol. 53: 177–179.

Response to Hill and Carr

JOHN M. HAGAN[1] AND J. MICHAEL REED[2]

Hill and Carr (1989) present three criticisms of our analyses of color-band effects on Red-cockaded Woodpeckers (*Picoides borealis*; Hagan and Reed 1988): (1) that, by failing to adjust the experimentwise error rate as a result of performing multiple tests, our conclusions concerning effects of red bands are invalid, (2) that we have two problems with independence of observations (the sample observations of reproductive success appeared in >1 treatment, and observations of a single individual bird made in different years were treated as independent samples), and (3) that color bands were not assigned randomly to the individuals in our study.

The first criticism, that the error rate was not prop-erly adjusted, is based on a fallacious interpretation of our analytical approach. In fact, the error rate needs no adjustment for the analysis of the color red. We clearly stated in the introduction that our a priori hypotheses concerned only red bands. These hypotheses were constructed in advance of analysis, and based on biological reality and conclusions reached by Burley in research on Zebra Finches (*Poephila guttata*) (1981; 1985a, b; 1986a, b, c; Burley et al. 1982). Plumage of the Red-cockaded Woodpecker is entirely black and white, with the interesting exception that males have a small tuft of red feathers above and behind the eye that is revealed during intense agonistic encounters. Our a priori hypotheses were based on plumage color of this particular species. Thus, for each population parameter, we had only a single hypothesis, regarding a single color, red. The Type I error rate for these a priori hypotheses is 0.05, for $\alpha = 0.05$.

We analyzed the effects of other band colors subsequent to our tests of "red hypotheses" as a result

[1] Manomet Bird Observatory, P.O. Box 936, Manomet, Massachusetts 02345 USA.

[2] Department of Zoology, Campus Box 7617, North Carolina State University, Raleigh, North Carolina 27695 USA.

of the suggestion of an anonymous reviewer who proposed that effects of other colors should be examined as well. The original submitted manuscript incorporated only analyses of red bands. These multiple analyses of the eight other colors, with no a priori hypotheses, do require the Type I adjustment alluded to by Hill and Carr (1989). The adjustment is moot, however, as none of the tests approached even the unadjusted Type I error rate. The adjustment, applied properly, suggests that effects of colors other than red were nonexistent, which strengthened our contention that red color bands affect Red-cockaded Woodpeckers.

The first of Hill and Carr's criticisms on sample independence is also incorrect with respect to our analyses of red bands, for reasons stated above. There was no lack of independence for our a priori hypotheses (i.e. a bird could not both wear a red band, and not wear a red band). Red-banded birds did wear other band colors, however. We point out, that from a practical standpoint, few studies that involve the application of color bands as a tool will have the luxury of assigning only a single color to an individual. The usefulness of color banding necessitates the application of multiple colors. Thus, assessment of the effect of any single color will always be confounded by possible effects of other colors present. To accomplish a field experiment actually designed to test the effects of specific band colors, without these confounding effects, would represent a considerable undertaking, and yield no information on specific individuals, at least from a distance (i.e. all birds could wear only a single color). For this reason, it is necessary to use existing data, and to construct logical a priori hypotheses concerning colors naturally occurring on the species of interest.

The second criticism of sample independence, that we treated separate reproductive attempts of the same individual in different years as separate observations, could be a potential problem, as we noted (Hagan and Reed 1988: 502). If there is a correlation between an individual's reproductive success in one year relative to another, then observations are not independent. Four pairwise correlations of reproductive success of individuals in consecutive years (with proper Type I adjustment) showed that two were positively significant (at $P = 0.05$) and two were not. These results are fairly inconclusive, but suggest that observations were not entirely independent, and thus some adjustment should be made. We circumvented this problem condensing the one to six observations of reproductive success on each individual into a single long-term mean value. This value was then used as the dependent variable in an ANOVA, but it was weighted, using the GLM WEIGHT statement in SAS (SAS 1985), by the number of observations used for calculating that point (i. e. 1 to 6). In this manner, the proper degrees of freedom were used in the analysis, and proper weight was given to estimates of repro-

ductive success for an individual. This model was significant at $P = 0.019$, again indicating that red-banded birds produced significantly fewer fledglings than birds without red color bands.

Hill and Carr's third criticism, that bands were not assigned randomly, is a valid one, and again one which we acknowledged. We stated "both individual color bands and group colors were assigned in a haphazard rather than random fashion" (Hagan and Reed 1988: 502). We did not, however, let this observation stand, but instead we examined all likely biases (age, habitat, numbers of helpers) that might be present in the distribution of red bands. No indication of biases was found. We will not recount what exists in print. We will present additional evidence in support of a nonbiased distribution of bands. We conducted a Monte Carlo simulation by taking the actual numbers of the various color bands that were used in the field, and then randomly assigning these bands to 400 imaginary Red-cockaded Woodpeckers, on 100 independent trials. The random distribution of color bands produced by this simulation was indistinguishable from the actual pattern observed in the field. A random distribution, in the pure sense, can never be attained for our data set, but we are convinced that all reasonable precautions for assessing a systematic bias were accommodated. Hill and Carr do not present any suggestions regarding sources of bias in band distribution that we did not address in Hagan and Reed (1988).

Our original conclusions remain unaltered. There is substantial evidence implicating red color bands as affecting certain life-history parameters of Red-cockaded Woodpeckers. That this species is endangered warrants erring on the conservative side if color bands are to be used on them. That is, red bands should not be applied. Our work generated testable hypotheses which could definitively address the function that red color bands might have. Of equal or greater significance is that color bands, under field conditions, can have potential effects on avian behavior, and that those using color banding as a tool should strive to apply colors randomly.

LITERATURE CITED

BURLEY, N. 1981. Sex-ratio manipulation and selection for attractiveness. Science 211: 721–722.

———. 1985a. Leg band color and mortality patterns of captive breeding populations of Zebra Finches. Auk 102: 647–651.

———. 1985b. The organization of behavior and the evolution of sexually selected traits. Pp. 22–44 *in* Avian monogamy (P. W. Gowaty and D. W. Mock, Eds.). Ornithol. Monogr. 37.

————. 1986a. Comparison of the band color preferences of two species of estrilid finches. Anim. Behav. 34: 1732–1741.

————. 1986b. Sexual selection for aesthetic traits in species with biparental care. Am. Nat. 127: 415–445.

————. 1986c. Sex-ratio manipulation in color banded populations of Zebra Finches. Evolution 40: 1191–1206.

————, G. KRANTZBERG, & P. RADMAN. 1982. Influence of color banding on the conspecific pref

erences of Zebra Finches. Anim. Behav. 30: 444–455.

HAGAN, J. M., & J. M. REED. Red color bands reduce fledgling success in Red-cockaded Woodpeckers. Auk 105: 498–503.

HILL, G. E., & D. E. CARR. 1989. Statistical inference from color banding data. Auk 106: 517–518.

SAS INSTITUTE INC. 1985. SAS user's guide: statistics, 1985 ed. Cary, North Carolina SAS Institute Inc.

Sex Ratios of Fledgling Golden Eagles

GARY R. BORTOLOTTI[1]

Edwards et al. (1988) examined sex ratios of fledgling Golden Eagles (*Aquila chrysaetos*) over a 15-yr period in Idaho. Their analysis addressed potential deviations from a 1:1 sex ratio each year and for all years combined, and the potential relationship between prey abundance and eagle sex ratios. The rationale was that in times of food shortage brood reduction commonly occurs; large siblings restrict access to food of small siblings. The relative size of nestling eagles, and hence the probability of siblicide, depends in part on each bird's sex (females are larger than males [Bortolotti 1984, Edwards and Kochert 1986]) and order in the hatching sequence (Bortolotti 1986a). Edwards and Collopy's (1983) measurements of nestlings, and Bortolotti's (1986b) more theoretical argument, both suggest that brood reduction in two-chick broods of Golden Eagles is most likely to occur when a female hatches before a male (F-M). There is less of a size difference between siblings for other combinations of sex and hatching sequence (M-F, F-F, M-M) (Bortolotti 1986).

Edwards et al. (1988) stated correctly that the "tendency for the occurrence of siblicide in F-M broods should be manifest in population-level fledgling sex ratios." However, some statistical considerations cast doubt as to whether Edwards et al.'s analyses can test effectively sex ratios at the population level.

In the original analysis, sample size was a major problem. The number of fledglings ranged from 4 to 48 per year, and the number of broods varied between 3 and 28 per year. Analysis of the sex ratio of each year's cohort was tested against a 1:1 ratio using nestlings from broods of all sizes (Edwards et al. 1988: table 1). The hypothesis that brood reduction results

in an excess of females might have been better tested by examining broods with only a single fledgling. The sex ratio of one-chick broods should be biased, but that of two-chick broods should not. Limited sample size may have been a problem for such an analysis; however, inclusion of broods in which no mortality from brood reduction has occurred makes matters worse.

Consider the following possible, although extreme, example. All broods initially contain two offspring, and sex and hatching sequence are independent. All F-M broods experience brood reduction but mortality of nestlings in other broods is independent of sex. If such were the case, the population's true sex ratio would be 0.75 (male/female). In an analysis that lumps one- and two-chick broods, 0.75 is the most strongly female-biased sex ratio possible (excluding stochastic events), and is the easiest to test statistically. The minimum sample size required to find a significant difference between a ratio of 1 and 0.75 would be about 193 birds (i.e. 4–28 times larger than the sample sizes tested by Edwards et al.). If single-chick broods resulting from the hatching of only one egg or from random sources of mortality unrelated to siblicide are included, as was presumably done by Edwards et al., the sex ratio increases and the analysis requires even larger samples. Therefore, a test of the sex-biased siblicide hypothesis using sex ratios of cohorts requires a reanalysis, larger sample sizes, or both.

Edwards et al. also tested the sex ratio of all years combined (*n* = 320 birds). This is a poor test of the hypothesis of sex-biased siblicide because mortality in F-M broods would be expected only in times of poor food resources (9 of the 15 years in their study). The sex ratio of the combined sample would be some unknown degree greater, presumably much greater, than 0.75. It may have been more profitable to examine the distribution of the sexes in two-chick broods

[1] Department of Biology, University of Saskatchewan, Saskatoon, Saskatchewan S7N 0W0, Canada.