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LITERATURE CITED

ABRAHAM, K. F., C. D. ANKNEY, & H. BOYD. 1983. Assortative mating by Brant. Auk 100: 201–203.

BOYD, H., & L. S. MALTBY. 1979. The Brant of the western Queen Elizabeth Islands, N.W.T. Pp. 5–21 *in* Management and biology of Pacific Flyway geese (R. L. Jarvis and J. L. Bartonek, Eds.). Corvallis, Oregon, Oregon State Univ. Bookstores, Inc.

KIRBY, R. E., H. M. OBRECHT III, & M. C. PERRY. 1983. Body shot in Atlantic Brant. J. Wildl. Mgmt. 47: 527–530.

PENKALA, J. M. 1977. A technique for identifying yearling female Atlantic Brant. J. Wildl. Mgmt. 41: 585–587.

SMITH, L. M., L. D. VANGILDER, & R. A. KENNAMER. 1985. Foods of wintering Brant in eastern North America. J. Field Ornithol. in press.

Leg-band Color and Mortality Patterns in Captive Breeding Populations of Zebra Finches

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Color-banding is a research technique widely utilized to facilitate recognition of individuals and membership in "groups" such as age classes. Despite the fact that many species of birds routinely attire themselves in colorful plumes, the possibility that color-marking by humans may affect the social behavior of birds has hardly been considered (but see Bennett 1939, Goforth and Baskett 1965). Instead, it appears that researchers have proceeded largely on the tacit assumption that no such effects occur. Here I report that in long-term breeding experiments involving Zebra Finches (*Poephila guttata*), mortality patterns of birds varied with the color of the bands placed on them prior to the beginning of experiments.

The experiments reported here were conducted to investigate the significance of other results from my laboratory (Burley et al. 1982, Burley 1985), which indicated that Zebra Finches find certain colors of leg bands attractive when worn by opposite-sex individuals and find other colors unattractive. In those experiments, attractiveness was measured as the time test subjects spent associating with stimulus birds banded with one of several colors in relation to the time spent with unbanded birds. Attractive colors were those that test birds preferred, and unattractive colors were those test birds appeared to avoid, relative to their tendency to associate with birds wearing no color bands. The present experiments were designed primarily to explore the effects of altered attractiveness on reproduction.

Two experiments were performed. In one (the Banded Male Experiment), adult males were banded, prior to their release into the experimental aviary, with one of the following colors: bright red (previously determined to be attractive to females), light green (unattractive to females), or orange (neutral with respect to the unbanded condition—adult Zebra Finches have orange legs). In the reciprocal experiment (the Banded Female Experiment), females were banded with black (attractive to males), light blue (unattractive to males), or orange (neutral). Randomization procedures were employed in assigning band colors. Color-banded birds wore one color band on each leg. In addition, each bird wore one uniquely coded aluminum band. (All bands were supplied by A. C. Hughes, Middlesex, England.) In the Banded Male Experiment, females were not color-banded, and males were not color-banded in the Banded Female Experiment.

All individuals were adults (5–11 months of age at the beginning of experiments) that had been placed in unisexual groups prior to sexual maturation and that, as a result, had no previous reproductive experience. All birds had wild-type plumage characteristics and appeared in excellent physical condition at the beginning of experiments. The founding populations of the two experiments came from identical sources.

Experiments were initiated by releasing 24 adults of the color-banded sex into an aviary; 1 week later, 24 opposite-sex individuals were added. Approximately 1 week later, nest sites and other resources needed for reproduction were made available in

abundance. Birds were permitted to breed continuously until the end of the experiment. During the first 6 months of each experiment, individuals that died were replaced by birds randomly selected from a "substitute" pool created for this purpose. Offspring were removed from aviaries 2–5 weeks after fledging. Additional methodological details are reported elsewhere (Burley MS).

The Banded Male Experiment ran for 22 months. During this time, 1 of 8 red-banded males, 3 of 9 orange-banded males, and 6 of 10 green-banded males died. One red-banded male was excluded from this analysis for technical reasons. He was in good health at the time of his removal and survived past the end of the experiment. The difference in incidence of mortality among color classes was clearly significant (Fisher 2 × 3 Exact Test, $P = 0.017$).

Unlike the Banded Male Experiment, the Banded Female Experiment consisted of several discrete phases. After the first 10 months of the experiment, color bands were removed from females, but the birds were allowed to continue breeding for 5 additional months. At that time, breeding was suspended by the removal of nesting sites, but the surviving adults remained in the experimental aviary for an additional 5 months. Within several days after the initiation of this experiment, 1 bird (a black-banded female) caught a band in the aviary netting and 2 birds became unable to fly. As a result, I removed 6 birds from the experiment (1 female from each color class and 3 males) and replaced them with birds from the substitute pool. These birds were excluded from analyses below.

During the 10 months in which females were color-banded, 1 of 10 black-banded females died, as did 4 of 11 orange-banded females and 9 of 14 blue-banded females. Mortality patterns varied significantly among color classes (Fisher 2 × 3 Exact Test, $P = 0.022$). For the entire 20-month timespan, trends remained identical: 4 of 10 black-banded females, 6 of 11 orange-banded females, and 10 of 14 blue-banded females died. This difference was not significant (Fisher 2 × 3 Exact Test, $P > 0.35$). However, a comparison of the relative "lifespans" (the number of days between release into the experiment and death) of the color classes indicated a strong and significant trend. Black-banded females that died survived an average of 425.4 days in the experiment, orange-banded females an average of 286.8 days, and blue-banded females a mean of 190.9 days. This difference was significant (Kruskal-Wallis test for analysis of variance by ranks, $H = 6.33$, 2 df, $P < 0.05$).

In both experiments, then, the color of bands applied to individuals affected survivorship. In most cases the specific cause of death was not ascertained, although autopsies were performed on a number of birds by the Department of Veterinary Pathology of the University of Illinois. Many birds that died displayed premortum declines in physical condition, including deteriorating feather condition, weight loss, changes in beak color, loss of balance, and the adoption of postures typical of ill birds.

The birds that died displayed a variety of symptoms, and it is fairly certain that they died from a variety of specific causes. Of greater interest here are the "general" causes, such as the nature of stresses that impaired physical capacity and increased risk of death. These include intraspecific interference competition, senescence, predation, accidents, and reproductive effort. Disease is not mutually exclusive with any of the above categories except accidental death, but there was no direct or circumstantial evidence to suggest that mortality patterns resulted from contagious diseases.

Most general causes of mortality can be excluded as *major* contributors in these experiments. Interference competition can be ruled out for two reasons. Only one bird (a male in the Banded Female Experiment) sustained noticeable injuries inflicted by other finches. Also, Zebra Finches are naturally gregarious and nonterritorial (Immelmann 1962). In these experiments they were maintained in large aviaries [density was about 1 adult/m³—less than half the density suggested by Immelmann (1965) as the desired maximum], and competition for resources was deliberately minimized by supplying nesting sites, nesting materials, and food in abundance.

Senescence is not a relevant factor. The potential lifespan of Zebra Finches is at least 5–7 years under these lab conditions; all birds were less than 3 years old at the time of death. For founders, there were no differences in age composition among color classes. Birds that were added as substitutes tended to be slightly younger than founders, but more substitutes were added in those classes with higher mortality rates.

I attempted to eliminate the possibility of predation. However, the building in which these experiments were performed was inhabited by house mice (*Mus musculus*), and 1 (black-banded) female was decapitated by a house mouse while she incubated at night. The small light that usually was left on (primarily to protect the birds from wing damage should there be a nocturnal disturbance) burned out on the night she was killed. Zebra Finches usually do not attempt to fly in the dark, and I believe she was vulnerable for this reason.

At least two deaths probably were "accidental," i.e. unrelated to the bird's physical condition. One of these was the black-banded female that was decapitated, and the other was an orange-banded male that succumbed after he became entangled by a leg band. In two other cases, apparently "accidental" deaths involved birds that displayed declining condition prior to death. A male in poor condition in the Banded Female Experiment hanged himself by a strand of

human hair that he was using for nest building. Hair was not provided purposefully to finches, but many nests contained at least a few strands, implying that the finches sought out those inadvertently shed by lab personnel. No other bird became entangled by hair. A red-banded male that had difficulty maintaining his balance drowned in a water bowl.

The remaining possible cause of mortality is stress resulting from reproductive effort. The fact that Zebra Finches are opportunistic breeders suggests that this is an important cause. They begin to breed rapidly upon encountering permissive conditions and produce clutches continuously and in quick succession as conditions permit (Keast and Marshall 1954, Serventy and Marshall 1957, Immelmann 1963). In their native habitats, future reproductive opportunities are often difficult to predict, and they often may sustain high risk of mortality when conditions are not favorable for reproduction (Finlayson 1932, Frith and Tilt 1959, Keast 1959, Immelmann 1963). Hence, Zebra Finches may stress themselves reproductively even under seemingly "unstressful" conditions afforded in the laboratory. To maximize longevity, it commonly is advised that breeders limit reproductive opportunities by withholding nest sites. Immelmann (1965), for example, advocated permitting pairs to rear no more than 4 clutches per year, although he noted their potential is much greater.

Reproductive stress may account for differences in mortality rates of color classes. Elsewhere (Burley MS) I hypothesize that, in species with biparental care, individuals adjust the parental investment they are willing to commit to a particular mate's offspring to affect their own mate-getting abilities. That is, unattractive individuals may incur a larger than average share (for their sex) of parental duties to obtain a mate that is superior to what they otherwise could acquire (see also Burley 1981). Unusually attractive individuals, on the other hand, should have no trouble acquiring superior mates, and they may restrict their investment (at their mates' expense), thus reducing their risk of mortality. This hypothesis (the Differential Allocation Hypothesis) predicts that attractive individuals should have lower per-offspring parental investment than unattractive individuals of the same sex. Mortality trends reported here are consistent with this hypothesis. Time-budget estimates of parental investment obtained by focal nest sampling procedures also are consistent with the hypothesis (Burley in prep.).

Limited evidence also suggests that the color-banded sex, in aggregate, sustained an increased rate of mortality. In my populations of non-color-banded birds, adult females generally appear to have a somewhat higher mortality rate than do adult males. However, in only a few cases do I have data for males and females that were obtained from identical source populations and were matched for age and prior reproductive history. Moreover, mortality rate varies with housing conditions (especially density and diet provided) and whether or not birds are permitted to breed. To compare the incidence of mortality among nonbreeding birds, I selected matched cohorts of young adult males and females and housed them in separate but identical aviaries for 10 months. (Population density in these aviaries was about 10 times that of the Banded Male and Banded Female experiments.) During this interval, 2 of 52 males died, whereas 9 of 46 females died; this difference was significant ($\chi^2 = 5.373$, 1 df, $P < 0.025$).

A breeding population of non-color-banded birds was established and maintained for 10 months under conditions similar to those of the Banded Female and Banded Male experiments. Males and females in this population came from the same source, but from a different source than those used in the Banded Male and Banded Female experiments. Two of 26 males died during the experiment, whereas 7 of 28 females died. This difference was not statistically significant (Fisher 2×2 Exact Test, $P = 0.141$), but its trend is consistent with patterns obtained in other colonies. In the Banded Male Experiment, there was no evidence of a sex difference in rate of mortality: 10 of 28 males and 12 of 29 females died (Fisher 2×2 Exact Test, $P = 0.787$). Thus, it appears that banded males had a relatively higher than "typical" rate of mortality. In the Banded Female Experiment, females had a much higher rate of mortality: 20 of 35 females died, whereas 10 of 34 males died (Fisher 2×2 Exact Test, $P = 0.029$). Unfortunately, direct comparisons in mortality rates among the various breeding experiments involving banded and nonbanded birds cannot be made because birds came from different source populations and reproduced at different rates and for different lengths of time.

In sum, mortality rates of Zebra Finches in breeding populations are affected by leg-band color. Differential mortality of color types appears to result from differential parental investment by attractive and unattractive types. Results also suggest that the color-banded sex sustains an overall increased rate of mortality, but given the mortality patterns in my populations, a much larger sample would be required to demonstrate this conclusively.

The implications of these results for the technique of color-banding are disturbing. Color-banding has consistent, highly structured effects on the behavior (Burley et al. 1982, Burley 1985), reproductive patterns (Burley MS), and mortality patterns (this study) of one species of estrildid finch. How widespread such effects are is unknown and would be difficult to determine. I believe it would be very hard to clearly discern effects from data on uniquely marked birds, especially in field studies, where factors such as site fidelity and the identity of nonbreeding members of breeding populations often are poorly known and

where death typically is inferred from "disappearance" from or "nonreturn" to a study site. The situation is further complicated by lack of knowledge of which colors are "attractive" or "unattractive" in particular species under study and whether color-banding affects intrasexual or intersexual interactions.

I do not advocate that researchers abandon the use of color-banding. Some method of individual identification is necessary, or at least highly desirable, in studies on many topics of contemporary interest, and color-banding has many positive features. Also, using multiple colors on each bird may reduce the effects of color-banding. That is, if most birds wear a combination of attractive and unattractive colors, banding may constitute only an additional source of "noise" in a study rather than systematically affecting results.

The possibility of introducing systematic bias to results, however, can be minimized only if the process of assigning band colors is truly random. For this reason, I would caution against using particular colors to identify age class, study site or place of origin, parentage, or any other information. Both color and order of band combinations should be random, and colors that the phenotype of the species under study suggests may be particularly attractive to the opposite sex or very important in intrasexual interactions (e.g. Smith 1972) should be avoided altogether. I also would recommend avoiding particularly "stunning" band combinations [such as yellow-red-yellow or black-red-black on the legs of male Northern Cardinals (*Cardinalis cardinalis*)], despite their possible advantage of easy recognition. It would seem prudent to require multiple colors in each band combination (the number depending on colors available and the number of bands used per bird) to avoid creating extreme phenotypes. In this respect, I have found that female Zebra Finches are attracted to males that have had the entire exposed portion of their tarsometatarsi painted red even more than they are to males wearing only one red band on each leg (Burley 1985). Finally, the results of my research on Zebra Finches suggest that more detailed specification of the color-banding procedures employed in research may be warranted in scientific publications. The inconvenience involved in a thoughtfully designed banding scheme should be greatly outweighed by the reassurance that such a procedure minimizes the possibility of systematic bias caused by the birds' color sensitivity in general and their use of color for intraspecific communication in particular.

Color-banding is not the only method of identification that appears to have unanticipated and undesirable effects on bird survival and reproduction. Southern and Southern (1985), for example, recently have found that wing-tagged female Ring-billed Gulls (*Larus delawarensis*) experience considerable difficulty in obtaining mates at the beginning of the breeding season. Lensink (1968) reported that green neck bands inhibit the reproduction of female Black Brant (*Branta bernicla nigricans*); effects on males were not ascertained. Male Ring-necked Pheasants (*Phasianus colchicus*) that were neck-banded and tail-bobbed were found in association with females less often during the mating season than were males not so marked (Geis and Elbert 1956). Sayre et al. (1981) presented evidence indicating that radio-tracking devices have adverse short-term effects on courtship cooing in male Mourning Doves (*Zenaida macroura*). Longer-term effects of radio-tagging on behavior have been documented for male American Woodcock (*Scolopax minor*, Ramakka 1972). Collectively, these findings point to the need for systematic investigation of the possible effects of all marking procedures.

LITERATURE CITED

BENNETT, M. A. 1939. The social hierarchy of Ring Doves. Ecology 20: 337–357.

BURLEY, N. 1981. Mate choice by multiple criteria in a monogamous species. Amer. Natur. 117: 515–528.

———. 1985. The organization of behavior and the evolution of sexually selected traits. *In* Avian monogamy (P. A. Gowaty and D. W. Mock, Eds.). Ornithol. Monogr. in press.

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

FINLAYSON, H. H. 1932. Heat in the interior of South Australia. Holocaust of bird-life. South Australian Ornithol. 11: 158–163.

FRITH, H. J., & R. A. TILT. 1959. Breeding of the Zebra Finch in the Murrumbidgee irrigation area, N.S.W. Emu 59: 289–295.

GEIS, A. D., & L. H. ELBERT. 1956. Relation of the tail length of cock Ring-necked Pheasants to harem size. Auk 73: 289.

GOFORTH, W. R., & T. S. BASKETT. 1965. Effects of experimental color marking on pairing of captive Mourning Doves. J. Wildl. Mgmt. 29: 543–553.

IMMELMANN, K. 1962. Beitrage zu einer vergleichenden Biologie australischer Prachtfinken (Spermestidae). Zool. Jahrb. 90: 1–196.

———. 1963. Drought adaptations in desert birds. Proc. 13th Intern. Ornithol. Congr.: 649–657.

———. 1965. Australian finches in bush and aviary. Sydney, Halstead Press.

KEAST, A. 1959. Australian birds: their zoogeography and adaptations to an arid continent. Pp. 89–114 *in* Biogeography and ecology in Australia (A. Keast, R. L. Crocker, and C. B. Christian, Eds.). The Hague, Netherlands, W. Junk.

———, & A. J. MARSHALL. 1954. The influence of drought and rainfall on reproduction in Australian desert birds. Proc. Zool. Soc. London 124: 493–499.

LENSINK, C. J. 1968. Neckbands as an inhibitor of reproduction in Black Brant. J. Wildl. Mgmt. 32: 418–420.

RAMAKKA, J. M. 1972. Effects of radio-tagging on breeding behavior of male Woodcock. J. Wildl. Mgmt. 36: 1309–1312.

SAYRE, M. W., T. S. BASKETT, & P. B. BLENDEN. 1981. Effects of radio-tagging on breeding behavior of Mourning Doves. J. Wildl. Mgmt. 45: 428–434.

SERVENTY, D. L., & A. J. MARSHALL. 1957. Breeding periodicity in western Australian birds. Emu 57: 44–126.

SMITH, D. G. 1972. The role of epaulets in the Red-winged Blackbird (*Agelaius phoeniceus*) social system. Behaviour 41: 251–268.

SOUTHERN, L. K., & W. E. SOUTHERN. 1985. Some effects of wing tags on breeding Ring-billed Gulls. Auk 102: 38–42.

Floating Populations of Female Tree Swallows

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A floating population is a surplus of nonbreeding individuals during the breeding season that are able and willing to establish a territory and breed if the necessary resources become available (Brown 1969). Floaters often are excluded from breeding due to competition for limited breeding resources. Floating populations of males have been reported for many bird species (e.g. Hensley and Cope 1951, Stewart and Aldrich 1951, Delius 1965, Watson and Jenkins 1968, Power 1975, Smith 1978, Rutberg and Rohwer 1980, Weatherhead and Robertson 1980), but there are relatively few reports of female floating populations (Watson and Jenkins 1968, Harris 1970, Knapton and Krebs 1974, Smith 1978, Hannon and Zwickel 1979, Saether and Fonstad 1981, Hannon 1983). One reason for this bias is that intrasexual competition for breeding opportunities tends to be very intense among males relative to females (Selander 1972). Intense competition among females would be expected in hole-nesting species, where populations are limited by the availability of suitable nest sites (Holroyd 1975). If nest sites are limiting breeding opportunities, then females that are excluded from breeding may form a floating population. The purpose of this study was to estimate the extent and composition of female floating populations in a hole-nesting species, the Tree Swallow (*Tachycineta bicolor*). One-year-old female Tree Swallows have a distinct brown-blue subadult plumage, whereas older females have a blue adult plumage (Hussell 1983). This allows for a comparison of the proportion of one-year-old females in the breeding and floating populations.

The study was conducted during 1983 and 1984 at the Queen's University Biological Station, near Chaffey's Lock, approximately 50 km north of Kingston, Ontario. Two Tree Swallow populations were studied, both of which have been established for at least 5 yr. These appear to be 2 separate breeding populations, since only 2 out of 50 individuals that have been captured in the last 2 or 3 consecutive years are known to have moved between populations. One study site, the New Land (NL), was about 10 ha in size and consisted of several hay fields and two small ponds. The area was bordered by deciduous forest and was less than 1 km from open water. All nest sites were plywood nest boxes, and most were mounted on aluminum posts. The other study site, the Northeast Sanctuary (NES) of Lake Opinicon, was 10 km from the NL. Nest sites were distributed over approximately 5 ha of open, shallow water and consisted of both nest boxes and natural hollow stumps. The size of both populations increased between 1979 and 1981, but has remained stable since 1982. In May 1982, there were 54 breeding pairs in the NL and 30 pairs in the NES.

As an alternative to creating nesting opportunities by removing breeding females, we provided a surplus of nest boxes late in the season to attract females that had been excluded from breeding during May. Most females with nest sites had laid eggs by this time, so these females were not expected to be attracted to the new nest sites and prevent surplus females from settling. An attempt was made to band and individually color-mark all breeding females before erecting new boxes. Between 29 May and 16 June in 1983, 53 additional nest boxes were erected throughout the NL and NES (Table 1). In 1984, 45 new boxes were erected between 5 and 14 June. All new boxes were more than 15 m from existing nest sites, and were erected a few at a time to permit general observation of the activity around newly provided nest sites. The boxes were checked every 3–4 days