

## EFFECTS OF BAND COLOR ON SURVIVORSHIP, BODY CONDITION AND REPRODUCTIVE EFFORT OF FREE-LIVING AUSTRALIAN ZEBRA FINCHES

RICHARD ZANN

*Department of Zoology, La Trobe University, Bundoora, Victoria, 3083 Australia*

**ABSTRACT.**—In domesticated laboratory Zebra Finches (*Taeniopygia guttata*), leg bands of certain colors affect mate selection, parental effort, reproductive success, sex ratio of offspring, and survivorship. I tested the effects of these same colors on survivorship, body condition and reproductive effort of free-living Zebra Finches over several breeding seasons at two colonies in northern Victoria, Australia. At the "Cloverlea" colony, adults of each sex received either "attractive" or "unattractive" color bands. Nevertheless, survivorship to 12 months was not affected by band color nor was there compelling evidence (mass, bill color and molt) for deteriorating body condition due to reproductive costs; there were no sex differences in survivorship. Reproductive effort each breeding season in these free-living birds may not be as great as that in some laboratory populations because in nature the season is shorter and the interval for recovery correspondingly longer. In contrast, at the "Danaher" colony, where birds had unique color combinations of three bands (plus one metal band), a retrospective analysis of four years of data showed that there were significant effects of band color on reproductive effort of females; they laid more eggs if mated to males having a single red band (attractive color) in their combination than if mated to males having a single light-green band (unattractive color) or bands of other colors (neutral attractiveness). They laid an extra clutch, but this did not result in significantly more fledglings and independent young being raised by the pair. There were no band-color or sex effects on survivorship of adults at this colony. There were no obvious biases in the allocation of band colors or identification of breeding pairs that might explain the extra-clutch effect. The finding on red-banded males is largely consistent with that described for domesticated Zebra Finches, where females make a differential reproductive allocation in response to their partner's band color. No similar effects were found for female band color where, contrary to expectation, females with black (attractive) bands had significantly fewer fledglings than did females with color bands of neutral attractiveness. The overall conclusion is that color bands do not significantly affect the behavior of wild Zebra Finches, but it would be wise to omit red bands on males where possible. Received 18 August 1992, accepted 8 December 1992.

COLORLED LEG BANDS affect mate selection (Burley 1981, 1986a, Burley et al. 1982), parental investment (Burley 1988a), reproductive success (Burley 1986b), sex ratio of offspring (Burley 1986c) and longevity (Burley 1985) in laboratory stocks of domesticated Australian Zebra Finches (*Taeniopygia guttata castanotis*). The fact that wild-caught female Zebra Finches have the same band-color preferences as domesticated ones (Burley 1988b) strengthens Burley's (1985) warning about possible artifacts and biases created by color marking of individuals in wild populations of Zebra Finches and, by implication, other avian species. Conversely, Ratcliffe and Boag (1987) found that, under experimental conditions promoting intermale competition, leg-band colors of their domesticated laboratory Zebra Finches did not affect a male's ability to compete for nest sites and females; they con-

cluded that the potential of leg-band colors to create biases in behavioral studies of natural bird populations may be overestimated due to many confounding effects.

A number of studies have investigated the effects of leg band color on behavior of wild birds. Some *a posteriori* analyses of long-term banding data have demonstrated negative effects of band color on reproductive success (Hagan and Reed 1988), whereas others have found no effect (Beletsky and Orians 1991, Weatherhead et al. 1991). Similarly, findings are mixed with *a priori* designs: Metz and Weatherhead (1991, 1993) found negative effects, whereas Cristol et al. (1992) found no effect. The influence of leg-band colors on behavior appears to vary according to species, in particular whether the color matches one found on the bird's plumage or soft parts; if so, it may modify visual

communication processes with other members of the species.

To investigate effects of band color on behavior of wild Australian Zebra Finches, I studied the effects of leg-band colors in two adjacent breeding colonies ("Cloverlea" and "Danaher") in the southeastern part of the Australianwide distribution of the species. In the color-band experiment at Cloverlea I tested specifically the effect of band colors on body condition and survivorship. All males received either red bands or light-green bands, and all females were given black or light-blue bands. The bands (supplied by A. C. Hughes, Middlesex, England) were the same size, shade and material (celluloid plastic) as those used by Burley (1981, 1985, 1986a, b, c, 1988a) in her studies of domesticated populations, where she found that red bands (attractive to females relative to unbanded males) conferred significantly greater survivorship (89 vs. 40%) on male wearers than did light-green bands (unattractive to females); similarly, females with black bands (attractive to males) lived significantly longer than females with light-blue bands (unattractive to males). Birds with bands of other colors were indistinguishable in attractiveness from unbanded birds. Consequently, these colors were assumed to be neutral in effect. In order to test this finding in a natural population I predicted that, all things being equal, the red-banded males and black-banded female Zebra Finches would have a higher survivorship at the Cloverlea colony than their counterparts with light-green and light-blue bands. Survivorship was estimated from the number of birds recaptured 12 months or more after banding.

Burley (1985) postulated that an asymmetry in reproductive effort and its associated costs between the partners of the breeding pair accounts for the differential effects of band color on survivorship of domesticated Zebra Finches. Differential parental expenditure arises when the parent with the attractive band color has a lower per-offspring investment than its less attractive partner (the differential-allocation hypothesis; Burley 1986b); the different costs directly affect their respective life spans. If free-living Zebra Finches also incur reproductive costs during breeding, these may be reflected in mass loss and slow feather replacement over this period. Zebra Finches at a neighboring colony ("Padgett"; 3 km east of Cloverlea) replaced remiges in a slow, continuous manner through-

out the year, and continued to do so during the breeding season (Zann 1985). Consequently, if birds undergo reproductive stress resulting from reproductive effort it is feasible that feather replacement may be slowed or suspended during the period of stress. Reproductive stress might also affect bill color, which becomes less red over the breeding season in wild Zebra Finches (Burley et al. 1992); in domesticated Zebra Finches bill color declines during a single breeding cycle, and there is an overall decline with prolonged breeding (Burley 1985, Burley et al. 1992). Therefore, to detect changes in body condition due to reproductive stress, I measured differences in mass, molt and bill color before and after breeding in birds of each color-band type trapped at Cloverlea.

The second colony in which the effects of leg-band colors were investigated was the Danaher colony. The study was not designed with this specific purpose in mind. Rather, it was designed to investigate general aspects of behavior and population dynamics; here birds were given unique combinations of color bands for recognition of individuals. Survivorship and reproductive performance of many pairs was monitored each breeding season. These data were analyzed, *a posteriori*, according to whether the partners had attractive bands (red and black), unattractive bands (light-green), or neutral color bands; however, no unattractive light-blue bands were placed on females in this colony.

#### METHODS

*Color-band experiment.*—Members of this colony nested and roosted in a tall windbreak on a wheat/sheep property (Cloverlea; 36°09'S, 145°18'E) in the northern portion of the state of Victoria and had occupied the site since at least 1981 when I first discovered it. Zebra Finches were present each visit and breeding normally ran for eight months, from September (austral spring) to April (austral autumn; Zann and Straw 1984). The banding experiment ran from January 1987 through September 1989, and covered two and one-half breeding seasons—the second half of the 1986/1987 season, and the whole of the 1987/1988 and 1988/1989 seasons.

Birds were captured one day each month (except for the months of May and August 1989 when no birds were trapped) at a walk-in trap baited with a weekly ration of commercial seed. The assignment of band colors was random. Unbanded birds were grabbed "blind" from the holding box and allocated red or light-green bands if they were males, but black or light-blue bands if they were females. A few im-

males were banded if their sex could be positively determined; otherwise, they were released with a metal band only. The allocation of band colors alternated between successive birds of the same sex so that equal numbers of the color treatments were made. Three bands of the same color were placed on each bird together with a fourth, uniquely numbered metal (alloy) band; two bands were placed on each leg with the metal band always uppermost in order to expose the colored bands as much as possible. Red bands, which fade faster than other colors, were frequently replaced with new ones.

Each bird was aged and sexed by its external morphology (Zann 1985, Burley et al. 1989) and weighed to the nearest 0.1 g. The color of the dorsal surface of the upper mandible was scored with Munsell chips in the manner described by Burley and Coopersmith (1987), and transformed into a single score using the weighted method devised by Burley et al. (1992), where the redder, brighter and darker bills have a higher score than less red, paler bills. Molt of primaries of the right wing was scored in the numerical manner devised by Miller (1961) and Ashmole (1962). My research assistant, who took 90% of all measurements, was unaware of the hypotheses being tested on bill color, mass and molt. Survivorship of adults was measured at 12 months after initial capture and banding, a time interval sufficient at least for one or more breeding attempts. No attempt was made to monitor breeding performance of pairs at this colony because of problems in recognizing individuals and observing nests.

The effects of reproductive effort on bill color, mass, and primary molt in the Cloverlea birds were assessed by comparing these measures before and after an interval of at least two months (range 2–8 months, median 3 months) of the breeding season. The interval depended on when individuals were recaptured. As breeding was not monitored at this colony, there is no direct evidence that breeding was actually attempted by the banded subjects, but previous work at this and neighboring colonies (Zann and Straw 1984) suggests that most birds would be breeding and at least several clutches would be laid in this interval. If the bird was first banded as an adult during the breeding season, the first scores (time 1) for bill color, mass and molt were taken from that point and compared to those taken at least two months later or those at the end of the breeding season (early April) if the bird continued to reside in the colony (time 2). If banded in the nonbreeding season, the first score was taken from late August, just a few weeks before the breeding season began. In this way the effects of non-reproductive episodes over the interval of measurement could be minimized. If birds bred in more than one season, only the first data were included in the analysis.

*Four-year population study.*—The second colony, was located on another wheat/sheep property ("Dana-

her"; 36°09'S, 145°26'E) 6.7 km east of Cloverlea. All birds were given unique combinations of three color bands in addition to the uniquely numbered metal band. Birds were trapped at two baited (*ad libitum*) walk-in traps every two weeks during the breeding season and monthly otherwise. The project began in March 1984 and concluded in June 1989, although trapping and banding continue on an irregular basis.

Only seven band colors were approved by the Australian Bird and Bat Banding Scheme: red, light-green, black, dark-blue, white, orange and mauve. This gave 1,372 unique combinations with the metal band at different positions. Combinations with three reds, three greens, three blacks and three dark-blues were omitted at the outset to avoid the possibility of undesirable effects on survival and fecundity described by Burley (1985) for domesticated Zebra Finches. Light-blue bands, which are unattractive to domesticated males when placed on females, fade too fast in the wild and were not approved by the Banding Scheme.

Random numbers were not used to allocate band combinations, but triplets of bands were chosen "blind" from a list of combinations prepared before the study began, and the fourth band of the combination was added before a banding session commenced. This meant that only seven birds banded in succession had the same combination on one leg. Trapped birds were grabbed "blind" from the holding box and combinations applied irrespective of season, trap site, age, sex or kinship. The metal band, which served as a "first master," was located on the top left leg at the start of the study, then bottom left, then top right, and then bottom right as the unique triplets of the seven colored bands were used.

Over the four breeding seasons, 303 breeding attempts resulted in completed clutches that reached the incubation stage and, in 150 cases, it was possible to determine from observations at the nest the color bands of both parents making the attempt. The reproductive performance of these parents was studied; nests where one or both parents were unbanded were ignored. Where the clutch did not suffer predation it was possible to estimate how many young reached fledging age (18–20 days posthatching); in practice, this was taken as the number of young banded at 12 to 14 days of age because handling after this age results in forced fledging. The number of independent young (older than 35 days) was estimated by recapture at the walk-in traps. Breeding was attempted by 144 unique pairs (27 involved male re-pairing and 23 female re-pairing) formed by 122 males and 123 females. For the majority of pairs the number of eggs, fledglings and independent young were determined for the "lifetime" of each parent in the colony. In some cases these values will be less than those for the true lifetime of each parent because some birds may have bred elsewhere, either before arrival at the colony, having immigrated as adults, or after they disappeared from the study site.

TABLE 1. Survivorship of adult male and female Zebra Finches by band color expressed as number recaptured 12 months or more after banding.

Sex	Number of bands and color	Twelve months after banding		G-test <sup>a</sup>
		Recaptured	Not recaptured	
<b>Cloverlea<sup>b</sup></b>				
Female	3 black	13	32	1.15
Female	3 light-blue	10	44	
Male	3 red	11	35	0.06
Male	3 light-green	10	36	
<b>Danaher<sup>c</sup></b>				
Female	1-2 black	5	55	0.04
Female	3 nonblack	9	111	
Male	1-2 red	13	50	1.98
Male	1-2 light-green	4	35	

<sup>a</sup>  $df = 1$ . Two-tailed test. None significant ( $P > 0.5$ ).

<sup>b</sup> Color-banding experiment at Cloverlea, where each bird also had uniquely numbered metal band.

<sup>c</sup> Four-year population study at Danaher, where each bird had unique color-band combination and uniquely numbered metal band.

Males had a mean of  $2.19 \pm SD$  of 1.85 breeding attempts (range 1-6) and females  $1.96 \pm 1.45$  attempts (range 1-11). However, the number of unbanded young trapped suggests some successful attempts went undetected; consequently, these are minimum lifetime values. We found that 90% of birds bred in one season only then disappeared, 9% bred in two seasons, and 1% in three. Therefore, mean attempts per lifetime are only slightly greater than attempts/season. Mean clutch size was based on the number of eggs in a completed clutch that reached the incubation stage.

High levels of brood parasitism (11% of offspring in February 1988) and low levels (2.4%) of extrapair copulation at this colony (Birkhead et al. 1990) meant that the parents identified at the nest may not necessarily have been the genetic parents of the young they were tending. The evidence for a pair bond was based on joint nesting activity. The date the bond began was arbitrarily taken as the date the first egg of the first attempt was laid, and the date the bond was terminated was taken as the date the young fledged from the last breeding attempt the pair made in the colony. Alternatively, if the pair were seen at the walk-in trap after the last breeding attempt, the last date they were observed together was taken as the termination date. None of 50 re-pairings occurred while the first partner was still found in the colony, so I assume that all pairings were serially monogamous. Where a bird had more than one partner, the mean duration of the bonds was used.

Parametric statistics have been used where possible, but only if data could be successfully normalized and significant differences in variances removed.

Otherwise, nonparametric methods were employed. All statistics were computed by JMP (SAS Institute 1991) or SAS (ver. 6.06; SAS Institute 1990), and all probabilities were two-tailed.

## RESULTS

*Survivorship.*—At Cloverlea there was no significant difference in the recapture rate 12 months or more after initial banding of adults for either sex or band color (Table 1), nor did recapture rate differ significantly between the sexes ( $G = 0.004$ ,  $df = 1$ ,  $P = 0.95$ ). The number of birds recaptured was the outcome of two indistinguishable effects, emigration and mortality; however, there is no reason to believe that band color would affect the former.

At the Danaher colony there was no significant difference in the recapture rate of males 12 months or more after first banding as adults among those that had one or two red bands in their unique combination or those with one or two light-green bands (Table 1). There were no black/blue contrasts made with females at this colony because the blue-band allocated here was dark-blue rather than light-blue. Apparently, these are neutral in attractive effect with respect to unbanded females, in contrast to the unattractive light-blue bands used at Cloverlea (N. Burley pers. comm.). When black-banded females were compared with females banded with colors other than black, there was no significant difference in survivorship to 12 months (Table 1). There were no significant differences in recapture rate between the sexes of all color-band types over 6.5 years of the banding study at Danaher (31/277 females vs. 47/337 males;  $G = 1.14$ ,  $df = 1$ ,  $P = 0.29$ ). Thus, there were no detectable differences in survivorship due to sex or color band. However, recapture rate was significantly higher at Cloverlea (44/191 recaptured vs. 78/614 recaptured at Danaher;  $G = 11.02$ ,  $df = 1$ ,  $P = 0.0009$ ), possibly because of a lower predation rate or less frequent human interference.

*Bill color, mass and molt.*—Bill-color scores fell (i.e. became less red) significantly over the breeding interval in females; changes in males with light-green or red bands were not significant (Table 2). There were no significant color-band effects on bill color before or after breeding for either males or females. As expected, male bill-color scores were significantly greater than those of females before (Wilcoxon two-

TABLE 2. Effects of leg-band color on changes in bill color, mass and molt of adult Zebra Finches over a breeding interval beginning at t1 and ending at t2. Medians with interquartile ranges in parentheses. Bill-color scores are transformed totals of weighted Munsell measures of hue, chroma and value (Burley et al. 1992). Molt scores are in ordinal units where: (0) an old feather; (1) a missing feather or new pin; (2) new feather one-third grown; (3) new feather two-thirds grown; (4) new feather nearly fully grown; (5) a new feather fully developed.

	Males			Females		
	Red-banded	Green-banded	Test <sup>a</sup>	Black-banded	Blue-banded	Test <sup>a</sup>
<b>Bill color</b>						
t1	21.8 (19.8-21.8)	21.8 (21.2-21.8)	0.70	17.3 (16.5-17.8)	17.3 (16.5-17.3)	0.01
t2	21.4 (20.9-21.8)	21.5 (21.0-21.8)	0.009	16.5 (15.9-17.2)	16.5 (16.5-17.3)	0.45
n	30	24		28	35	
S-value <sup>b</sup>	-3.0	-13.5		65.0*	95.0**	
<b>Mass</b>						
t1	12.4 (11.7-12.7)	12.3 (11.7-12.9)	0.24	12.6 (12.1-13.1)	12.8 (12.3-13.3)	1.06
t2	12.3 (11.8-12.9)	12.7 (12.0-13.2)	1.21	13.3 (11.9-13.7)	13.0 (12.5-13.2)	0.17
n	30	24		26	34	
t-value <sup>c</sup>	-0.47	-1.90		1.58	1.06	
<b>Molt</b>						
(t2 - t1)	7.0 (5.7-9.3)	6.2 (3.6-7.9)	1.50	5.7 (4.0-6.9)	5.8 (4.2-8.3)	1.09
n	27	20		24	32	

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; other values not significant ( $P > 0.05$ ).

<sup>a</sup> Wilcoxon two-sample test ( $z$ ) for bill color, and Student  $t$ -test ( $t$ ) for mass and molt.

<sup>b</sup> Wilcoxon signed-rank matched pairs test.

<sup>c</sup> Paired  $t$ -test.

sample test,  $z = 8.88$ ,  $P = 0.001$ ,  $n = 54$  and 63) and after breeding ( $z = 9.30$ ,  $P = 0.001$ ). There were no significant changes in mass over the breeding interval for either sex, nor were there any significant within-sex band effects (Table 2). Females were significantly heavier than males before ( $t$ -test,  $t = 2.82$ ,  $df = 112$ ,  $P = 0.006$ ) and after ( $t = 3.32$ ,  $df = 112$ ,  $P = 0.001$ ) the breeding interval.

Birds continued to grow primaries throughout the breeding period at a rate of about one primary per month, but there was no significant difference among the band-color types within each sex (Table 2); females, however, molted at a slower rate than did males, but this does not reach 5% significance ( $t = 1.898$ ,  $df = 101$ ,  $P = 0.060$ ). Thus, over a breeding episode three measures of condition that might reflect reproductive costs showed no differential effects due to band color, but fading of bill color and slower primary replacement suggest that females may lose body condition more than males; this is probably due to their greater reproductive effort which, nevertheless, failed to lead to any significant loss of mass.

*Reproductive performance by males.*—To assess the effect of band color on reproductive performance, the uniquely banded males at the

Danaher colony (for which data on lifetime reproductive success were available) were allocated to three groups: those with at least one red band in their combination; those with at least one light-green band; and those with colors other than red or light green. Nine males had both red and light-green bands in their combinations and were excluded from the analysis on the assumption that the predicted antagonistic effects may not necessarily cancel each other out. By chance no male in the data set had two red bands or two light-green bands in its color combination.

There was no significant heterogeneity among the three classes of male band colors for the number of young fledged and the number raised to independence, but there was highly significant heterogeneity in the number of eggs laid by their females (Table 3). Mates of red-banded males laid significantly more eggs than did the mates of males with a light-green band (Wilcoxon two-sample test with continuity correction of 0.5,  $z = 3.11$ ,  $df = 1$ ,  $P = 0.002$ ) and mates of males with neither red nor light green ( $z = 2.88$ ,  $df = 1$ ,  $P = 0.004$ ). There were no significant differences in egg numbers laid by females mated to males with bands in the last two categories ( $z = 0.40$ ,  $df = 1$ ,  $P = 0.69$ ).

TABLE 3. "Lifetime" reproductive performance of male Zebra Finches by leg-band color (*n* in parentheses). Medians with interquartile ranges in parentheses.

	Male bands included			Test <sup>d</sup>
	Red <sup>a</sup> (35)	Green <sup>b</sup> (35)	Neither <sup>c</sup> (34)	
Independent young	1 (0-3)	0 (0-0)	0 (0-3)	1.43
Fledglings	4.5 (2-9)	4 (0-5)	3 (0-6)	2.57
Eggs	11 (6-15)	6 (5-10)	5 (4-11)	11.86**
Clutch size <sup>e</sup>	5 (4.6-6)	5 (4.5-5.2)	5 (4-5)	5.20
Number of clutches	2 (1-4)	1 (1-2)	1 (1-2)	10.12**
Pair-bond duration	81 (55-135)	51 (28-108.5)	54.5 (25-104)	5.08

<sup>a</sup> One metal band, one red band, and two other colors excluding light green.

<sup>b</sup> One metal band, one light-green band and two other colors excluding red.

<sup>c</sup> One metal band and three of following color bands: orange, white, black, dark blue or mauve.

<sup>d</sup> Kruskal-Wallis test for ANOVA by ranks (chi-square approximation; SAS ver. 6.06 1990), *df* = 2. \*\*, *P* < 0.01; others not significant (*P* > 0.05).

<sup>e</sup> Number of eggs laid/number of nonpredated clutches that reached incubation stage.

Although females of red-banded males tended to lay larger clutches this failed to reach significance (Kruskal-Wallis  $X^2 = 5.2$ , *df* = 2, *P* = 0.074; Table 3); however, there was significant heterogeneity among the three groups in the number of clutches laid by their mates ( $X^2 = 10.12$ , *df* = 2, *P* = 0.006; Table 3). Females of red-banded males laid a median of two clutches whereas females of light-green-banded males and males with neither red nor light green laid a median of only one clutch; these differences were highly significant ( $z = 2.93$ , *df* = 1, *P* = 0.003, and  $z = 2.49$ , *df* = 1, *P* = 0.013, respectively). There was no significant difference in clutch number between females of light-green-banded males and those of males with neither red nor light-green bands ( $z = 0.26$ , *df* = 1, *P* = 0.78).

Even though males with red bands did not survive longer in the colony than those with light-green bands (Table 1), there was a suggestion that they remained paired for longer; however, this did not reach significance (Kruskal-Wallis,  $X^2 = 5.84$ , *df* = 2, *P* = 0.08; Table 3).

It is possible that the extra clutch laid by females of red-banded males may not be a consequence of band color per se, but arises from artifact(s) associated with banding, or with identification of breeding pairs. For example, by chance, more red bands may have been placed on males during good seasons than bad seasons, and these males would have gone on to father more eggs that season. Indeed, there were significant differences in the overall reproductive performance over the four breeding seasons. The proportions of clutches (*n* = 303) of different sizes (3-7) differed significantly among seasons ( $G = 30.76$ , *df* = 12, *P* = 0.002), principally

because there were more smaller clutches in the 1986/1987 season and more larger clutches in the 1988/1989 season. Correspondingly, there were also significant differences in the proportion of nesting attempts (at least one egg laid) made over the four seasons, with fewer in the 1986/1987 season and more in the 1988/1989 season ( $G = 33.67$ , *df* = 3, *n* = 476, *P* = 0.0001). The mean number of breeding attempts per pair for the first two breeding seasons was 1.5 attempts, whereas 2.0 attempts were made for the last two seasons of the study.

Over the four years of the study there were no significant differences in the proportion of the three color-band categories (red, green, neither) allocated to males that constituted the data set ( $G = 11.24$ , *df* = 6, *n* = 115, *P* = 0.081; Table 4) although a disproportionate number of green bands were allocated in the 1988/1989 season (11 green, 4 red and, 3 others). This did not lead to any significant differences in the proportions of males in the color categories that provided breeding performance data in each of the four seasons ( $G = 2.32$ , *df* = 4, *n* = 112, *P* = 0.89; Table 4). Finally, there were no significant differences in proportion of the three band-color categories allocated by age ( $\leq 35$  days, 36-100, and >100 days) at banding ( $G = 7.11$ , *df* = 4, *n* = 112, *P* = 0.13). In sum, there were no obvious biases in the allocation of the band colors, nor in data collection that might have produced the significant differences in egg numbers by male band type.

*Reproductive performance by females.*—Forty-two of the uniquely banded females that bred during the study had one or two black bands in their combinations and 63 had no black bands. There was no significant difference in perfor-

TABLE 4. Number of males by color-band combination that contributed "lifetime" reproductive performance data during four years of study: (1) season males were first caught and allocated color bands; and (2) season males had their maximum breeding performance<sup>a</sup>.

Combination included	Year of banding <sup>b</sup>			
	1985-1986	1986-1987	1987-1988	1988-1989
Green	11	5	9	11
Red	8	9	17	4
Neither	13	9	16	3
Year of maximum breeding performance <sup>c</sup>				
Green	9	4	7	17
Red	8	2	9	15
Neither	9	6	7	19

<sup>a</sup> If males bred in two or more breeding seasons, they were allocated to that season in which most clutches were laid.

<sup>b</sup> H<sub>1</sub>: No significant difference in proportion of males allocated three types of combinations over four study seasons ( $G = 11.24$ ,  $P = 0.08$ ).

<sup>c</sup> H<sub>1</sub>: No significant difference in proportion of males with three types of combinations, and their season of maximum reproductive performance ( $G = 2.32$ ,  $P = 0.89$ ).

mance of the two band categories for number and size of clutches produced, number of eggs laid, number of young that reached independence, and duration of the pairbond (Table 5); however, contrary to expectation (Burley 1986b), the black-banded females fledged significantly fewer young than did females with no black (medians 3 and 4.5 respectively; Wilcoxon two-sample test,  $z = 1.97$ ,  $P = 0.048$ ).

*Re-pairings.*—I found 15% of males (18/123) had more than one female partner during the study, but there was no significant difference in the proportions across band-color categories (8/42 red-banded males re-paired, 3/36 light-green-banded males, and 6/36 males with nei-

ther red nor light-green bands;  $G = 2.04$ ,  $df = 2$ ,  $P = 0.36$ ; 1/9 males with both red and light green also re-paired). On re-pairing, red-banded males did not pair significantly more frequently with black-banded females than did other males (red males had 0/8 re-pairings with black-banded females vs. 3/9 for males without red; Fisher's exact test,  $P = 0.21$ ). This suggests that the most attractive males do not pair up with the most attractive females.

I found 15% of females (18/123) also re-paired, but there was no significant difference in the proportion that re-paired between black-banded females and those without black (4/42 black vs. 14/77 without black; Fisher's exact test,  $P = 0.19$ ). Of 18 that re-paired three did so with males that had both red and green in the combination, and of the remaining 15 there was no significant bias towards red males from chance expectation (8 red, 5 green and 3 neither red nor green; goodness-of-fit test,  $G = 2.03$ ,  $df = 2$ ,  $P = 0.36$ ).

## DISCUSSION

*Body condition and survivorship.*—But for slight fading of bill color in females, evidence of reproductive costs on body condition is not compelling in the Cloverlea experiment. There were no significant changes in mass over the breeding interval for either sex or band-color type; furthermore, birds continued to replace primaries during the breeding period, although at a slower rate in females than males. Previous investigations at a neighboring colony, Padgett, where there was no baited walk-in trap, showed that the rate of feather replacement was significantly faster during the breeding season than

TABLE 5. "Lifetime" reproductive performance of female Zebra Finches by leg-band color ( $n$  in parentheses). Medians with interquartile ranges in parentheses.

	Female bands included		Test <sup>c</sup>
	Black <sup>a</sup> (42)	No black <sup>b</sup> (63)	
Independent young	0 (0-1)	0 (0-3)	1.51
Fledglings	3 (0-5)	4.5 (1.5-8)	1.97*
Eggs	6.5 (5-11)	6 (4-14)	0.45
Clutch size <sup>d</sup>	5 (4.0-5.5)	5 (4.3-5.5)	0.48
Number of clutches	1.5 (1-2)	2 (1-3)	0.86
Pair-bond duration	52 (25-95)	57 (25-105)	0.23

<sup>a</sup> One metal band, one black band, and two other colors.

<sup>b</sup> One metal band and three other colors, excluding black.

<sup>c</sup> Wilcoxon two-sample test ( $z$ ; normal approximation with continuity correction of 0.50; SAS ver. 6.06 1990); \*,  $P < 0.05$ ; others not significant ( $P > 0.05$ ).

<sup>d</sup> Number of eggs laid/number of nonpredated clutches that reached incubation stage.

during the nonbreeding season, which implies that reproductive stress need not affect feather replacement; however, during the peak of nesting activity, fewer females were in molt than males (Zann 1985). Despite the biparental nature of brood care reproductive effort is greater in females than males: females (mean mass 13 g) lay five eggs (each about 1 g) and are responsible for all of the nocturnal incubation and one-half the diurnal incubation (Zann and Rossetto 1991). Overall, the evidence indicates that under the breeding conditions at the Cloverlea colony: (1) bill color and feather replacement are more sensitive indicators of stress than mass; and (2) reproductive stress appears to have only a slight effect on female condition and no detectable effect on that of males. Consequently, there were no significant differences in survivorship between the sexes over the course of the study.

It is feasible that the food ration at the walk-in trap supplemented the diet to an extent that it blunted the costs of reproduction so that early signs of reproductive stress were not evident; however, previous studies on the effect of supplemented seed at the Padgett colony showed that it did not have a strong effect on breeding and, even without supplementation, seed resources are not limited at Cloverlea except during very early spring (Zann and Straw 1984). It is also possible that a nonbreeding interval allowed birds at Cloverlea to recover from reproductive stress before I could recapture them. Indeed, Burley et al. (1992) found that under a high-quality aviary diet, recently caught Zebra Finches at Alice Springs that were prevented from breeding could significantly increase bill color in just three weeks. They also found that bill color of domesticated males, which gradually fades over a nesting cycle, can rebound rapidly between nesting cycles implying that factors other than reproductive effort may also affect bill color.

In contrast to the situation at Cloverlea, where there were no significant differences in survivorship between color-band types, Burley (1985, 1986b, 1988a) found that mortality rates of domesticated Zebra Finches were significantly affected by leg-band color when subjected to prolonged breeding episodes: red-banded males and black-banded females lived longer than light-green-banded males and light-blue-banded females. Birds were allowed to breed continuously for 22 months in Burley's banded-male experi-

ment and for 15 months in the banded-female experiment; however, continuous breeding in the wild is never this long because of the intervention of unfavorable conditions. The number of "equally good months for breeding" (EGM, a derivative of the Shannon-Wiener diversity index; MacArthur 1964), which is an index of the length of the breeding season in birds, can be calculated for the four, mostly southern sites in Australia where Zebra Finch breeding (number of nests with eggs) has been monitored each month for a year or more: (1) Griffith (35°20'S, 149°9'E), 8.6 EGM (Frith and Tilt 1959); (2) York (31°52'S, 116°47'E), 8.0 EGM (Davies 1979); (3) Armidale (30°30'S, 151°40'E), 8.9 EGM (Kikkawa 1980); (4) Danaher (36°09'S, 145°26'E), 7.6 EGM (this study). For most species of birds the breeding season is longer at lower latitudes (Wyndham 1986), but this is not so with Zebra Finches because breeding is inhibited in the wet-dry tropics of northwestern Australia (15°42'S, 128°36'E) by too much or too little monsoon rain, leaving only six months of the year suitable for breeding (Immelmann 1963, 1965a, b). Therefore, throughout much of the distribution, there is a nonbreeding period of at least three to four months every year that limits the extent of continuous breeding; this may prevent those levels of reproductive stress reached in the laboratory. Furthermore, the nonbreeding pause in the wild may allow some recovery from reproductive stress that is not possible under continuous breeding regimes in the laboratory.

In harsher, more arid environments, Zebra Finches may be more susceptible to reproductive stress. After a two-year drought in 1986, Zebra Finches at Alice Springs (a semi-arid zone) had bill colors (transformed Munsell scores) before breeding that were almost identical to those at Cloverlea ( $\bar{X} = 21.8$  and 17.6 for Alice Springs males and females, respectively [Burley et al. 1992] vs. 21.8 and 17.3 for males and females at Cloverlea [Table 2]). However, the scores after the breeding interval were lower at Alice Springs (19.59 and 14.67) than at Cloverlea (21.4 and 16.5) for males and females, respectively. Whereas the decline in color was significant for both sexes at Alice Springs, only the females at Cloverlea showed significant decline. Thus, despite similar bill colors at the onset of breeding and the fact that both colonies had *ad libitum* supplies of commercial seed at the baited walk-in traps, the birds at Alice Springs may have



been in poorer condition due to the drought and less able to withstand reproductive stress than birds at Cloverlea. Alternatively, they may have made a greater reproductive effort over the breeding interval and, thus, have been subjected to greater stress.

Under optimal aviary conditions Zebra Finches are renowned for prolific breeding; up to 23 successive broods have been raised by a single pair in a continuous "reproductive season" of three years (Serventy 1971). Consequently, aviculturists are advised to remove nesting sites in order that excessive breeding not "weaken the birds" (Immelmann 1965b). Data on continuous breeding throughout a season by free-living pairs are difficult to collect since not all nests and pairs can be found and monitored. Nevertheless, females from 22 pairs at the Danaher colony that were monitored fairly regularly throughout one breeding season fledged a mean of  $11.1 \pm 3.66$  young (range 8–19) over a mean period of  $4.0 \pm 1.46$  months (range 2–6). In order to make the data comparable to the captive situation, any pairs whose breeding attempts suffered predation were excluded and only pairs that produced at least two clutches were included. Thus, females making multiple breeding attempts without predation produced a mean of 2.75 fledglings per month of the breeding season. By comparison, the females in Burley's (1986b, c) banded-female experiment produced a maximum of 1.2 independent young per month of the much longer "breeding season." Assuming that most fledglings in the laboratory reach independence, it suggests that wild Zebra Finches may achieve a higher reproductive success per month of breeding activity than domesticated Zebra Finches, yet reduce reproductive stress with a shorter breeding season. Furthermore, wild Zebra Finches may be more resistant to reproductive stress than domesticated ones because human intervention in the latter has caused pronounced changes in selection pressures that affect reproduction (Sossinka 1970, 1982). The extent of reproductive stress in wild-caught Zebra Finches under conditions of continuous breeding should be investigated to verify this possibility.

*Reproductive performance.*—At the Danaher colony, mates of males with one red band in their color combination made a significantly greater reproductive effort than did mates of males with a light-green band, or mates with

neither a red nor light green in their combination. This is most strikingly manifested in the number of eggs laid, due principally to an extra clutch laid by mates of red-banded males, although there is a suggestion (nonsignificant statistically;  $P = 0.07$ ) that these females also lay larger clutches. There was no significant band-color effect for number of fledglings, nor number of independent young, although in both instances median values were greater for pairs with red males. Unfortunately, nest mortality was high (64% of all attempts reached the incubation stage and 41% of these produced at least one fledgling; however only 32% of fledglings were recaptured after 35 days, the age when nutritional independence is achieved) due mainly to predation, which reduced the sample size so that any small differences in production of fledglings and independent young across band-color types were not statistically detectable. The longer pair bond of males with a red band is probably an outcome of the extra clutch being laid by their mates, since I defined the start and end of the pair bond, in most instances, in terms of first and last breeding attempts.

In this retrospective analysis of the effects of band colors on reproductive performance of males, it is difficult to exclude artifacts due to improper sampling as explanations for the extra clutch laid by mates of red-banded males. Band combinations were not allocated in a statistically random way, but in a blind or haphazard procedure. However, over the four study seasons there was no significant departure from random in the proportion of the three color categories allocated to the subject males, nor in the reproductive data gathered from them. If birds with red bands were more conspicuous in the field, it is conceivable that nesting attempts by pairs where a male was red-banded would be easier to discover and to identify. This could lead to the situation where they would be observed for longer intervals and so allow the detection of an extra clutch that might go undetected in pairs with other color bands. This explanation is unlikely, first because the red bill makes all birds equally conspicuous to discover in the first place and, second, the red color band was the most difficult to identify of all band colors because it faded quite rapidly and was often hard to distinguished from orange; it also provided the least contrast with the reddish-orange leg.

It is also conceivable, but unlikely, that the

red band conferred an advantage to male Zebra Finches because it enhanced their aggressive display. Red bands are known to affect the aggressive display of Red-cockaded Woodpeckers (*Picoides borealis*; Hagan and Reed 1988) and Red-winged Blackbirds (*Agelaius phoeniceus*; Metz and Weatherhead 1991, 1993), both of which have patches of red plumage. Zebra Finches are not territorial and did not compete for nesting sites or food, which were both abundant at my study site. Moreover, Ratcliffe and Boag (1987) found that leg-band colors did not affect the ability of domesticated Zebra Finches to compete for nest sites and females. Thus, in the field situation it is hard to see how a red band could confer an advantage in male-male competition for limiting resources such that an extra clutch would be produced through earlier breeding, or through breeding in a more favorable location.

Differences in survivorship and reproductive success ascribed to band colors in domesticated Zebra Finches have been explained by two non-mutually-exclusive hypotheses: (1) the differential-access hypothesis (Burley 1986b); and (2) the differential-allocation hypothesis (Burley 1988a). In the former, attractive band colors permit the bird to pair with a superior member of the opposite sex so that the attractive individual produces more offspring of a superior quality than do birds that do not get superior mates. With the exception of extrapair copulations, this mechanism should operate only when the bird is given the attractive band color before pair formation. If given an attractive band after pair formation, the bird is stuck with the current partner. This partner can then respond to the sudden increase in attractiveness of the partner by increasing its allocation to the reproductive effort of the pair. Hence, if birds are given the color band before they reach the age of pairing, both hypotheses could operate, but if the bird is already paired when the band is acquired then only the differential-access hypothesis should operate. To evaluate this possible difference I compared the number of eggs laid by mates of red-banded males according to whether the males were banded before the age of pair formation or afterwards. Although some pairs form and lay eggs between 60 to 70 days, many do not lay until older so that in the analysis birds first banded at 90 days or earlier were assumed to be unpaired, whereas older ones were assumed to have been paired at the time of banding. There was no significant difference

in the number of eggs laid in the two groups (Wilcoxon two-sample test,  $z = 0.73$ ,  $n = 12$  and  $21$ ;  $P = 0.46$ ). This suggests that differential access to superior quality females provided by red bands did not produce a significant increase in the reproductive success beyond that which could be explained by the differential-allocation hypothesis.

Two important differences in design exist between Burley's studies (1981, 1986a, b, 1988a) and my own: (1) only one member of each pair of domesticated birds had colored leg bands in Burley's (1988a) study (males in banded-male experiment and females in the banded-female experiment), whereas both partners at my two colonies wore colored bands; (2) many wild birds were probably already paired and may have bred before banding, whereas the domesticated birds were all unpaired and had not previously bred. Therefore, differential access to mates (Burley 1986b, 1988a) due to band color may have been limited to some degree in the field studies except in cases of re-pairing (15%).

Despite these differences, males with red bands in both studies averaged a greater number of clutches than did males with light-green bands or males with bands of neutral attractiveness, as predicted by the differential-allocation hypothesis (Burley 1986b:427). In addition, in both studies there were no significant differences in mean number of clutches and reproductive success for light-green-banded and neutral-banded males. The hypothesis predicts that light-green-banded males would have less parental investment by their partners but make more investment themselves, thereby increasing their own reproductive costs, which subsequently reduce their life-span. The survivorship data from the wild Zebra Finches did not confirm this prediction. Red-banded males should have had a greater re-pairing rate than males with neutral colors as a consequence of their greater attractiveness to females and the fact that life-span of their mates should be shorter. This was not the case at Danaher but some red-banded males in Burley's (1986b:425) laboratory study became simultaneous polygamists.

Presumably, in the case of red-banded males at Danaher, their females detect the sudden increase in their partners' attractiveness and respond with increased reproductive effort by laying more eggs; however, this does not appear to be translated into more fledglings and in-

dependent young, perhaps because red-banded males do not increase their parental expenditure in response to that of their partner sufficient to raise the young to fledging and independence. A larger sample size might detect significant differences. Apparently, red-banded laboratory males perceive the change in their attractiveness and gradually decrease their parental expenditure over time, whereas light-green-banded males increase theirs (Burley 1988a:622). The tendency for mates of red-banded wild males to lay a larger clutch was not found in domesticated birds, leading Burley (1986b, c, 1988a) to conclude that clutch size cannot be adjusted facultatively.

DNA fingerprinting of parents and broods at Danaher early in 1988 indicated that 10 of 25 broods had one nestling from an egg laid by an intraspecific brood parasite (Birkhead et al. 1990). In one case the male nest owner, who had no red bands, was thought to be the father and the parasite the mother. It is possible that red-banded males in this study are attractive to other females who trade an extrapair copulation for the opportunity to "dump" their eggs in the males' nests. This is one possible explanation for larger clutches of red-banded males, but it cannot explain why an extra clutch was laid.

Whereas the effect of red-banded males on reproduction corresponds reasonably well between field and laboratory studies, the situation with banded females differed significantly. Black-banded females at Danaher had significantly fewer fledglings than did those banded with neutral colors, but there were no significant differences in Burley's (1986b:442) laboratory study; however, she did find that light-blue-banded females had only one-half as many offspring as females banded with black or neutral colors. In the laboratory the increased reproductive success of black-banded females was due to their greater survivorship, presumably an outcome of lower reproductive costs incurred on their part arising from the compensating increase in reproductive effort by their partner; however, survivorship of females at both Cloverlea and Danaher colonies was independent of band color and, consequently, lowered reproductive success of black-banded females is unlikely to be due to a reduced lifespan.

Taken together, the results of the two studies provide mixed, somewhat equivocal, support for Burley's (1981, 1985, 1986a, b, c, 1988a) ideas

on the effects of leg-band color on Zebra Finch behavior. The experimental study at Cloverlea found no evidence for band effects on survivorship or reproductive stress. The experimentally weaker retrospective analysis of band effects on reproductive performance at Danaher provided partial support for Burley's hypothesis, but only for red bands on males. There was no evidence that other band colors had any effect on behavior of males or females, except for black bands on females, which had an effect that went in the opposite direction to that predicted by Burley. Finally, the significant red-band effect on males did not alter their fitness because they did not have a significant increase in numbers of surviving offspring over males banded with other colors. In sum, it is reasonable to conclude that color bands do not create significant biases in most aspects of the behavior of wild Zebra Finches, but in future studies it would be wise to allocate color combinations in a statistically random way and to avoid where possible the use of red bands on males.

#### ACKNOWLEDGMENTS

I thank L. and M. Powney (Cloverlea) and B. and M. Danaher for generous access to their farms where the study sites were located. David Runciman and Bruce Male collected and entered most of the field data. The M. A. Ingram Trust, La Trobe University and the Australian Research Council funded the project. Permits were provided by the Victorian Department of Conservation and Environment and the Australian Bird and Bat Banding Scheme. Nancy Burley trained us in the correct use of Munsell chips for scoring colors. Mike Clarke, Ian Thornton, Aldo Poiani, David Runciman, and three anonymous reviewers made valuable comments on drafts of the manuscript.

#### LITERATURE CITED

- ASHMOLE, N. P. 1962. The Black Noddy *Anous tenuirostris* on Ascension Island. *Ibis* 103b:235-273.
- BELETSKY, L. D., AND G. H. ORIANS. 1991. Red bands and Red-winged Blackbirds. *Condor* 91:993-995.
- BIRKHEAD, T. R., T. BURKE, R. ZANN, F. M. HUNTER, AND A. P. KRUPA. 1990. Extra-pair paternity and intraspecific brood parasitism in wild Zebra Finches *Taeniopygia guttata*, revealed by DNA fingerprinting. *Behav. Ecol. Sociobiol.* 27:315-324.
- BURLEY, N. 1981. Sex-ratio manipulation and selection for attractiveness. *Science* 211:721-722.
- BURLEY, N. 1985. Leg-band color and mortality patterns of captive breeding populations of Zebra Finches. *Auk* 102:647-651.
- BURLEY, N. 1986a. Comparison of band color pref-

- erences of two species of estrildid finches. *Anim. Behav.* 34:1732-1741.
- BURLEY, N. 1986b. Sexual selection for aesthetic traits in species with biparental care. *Am. Nat.* 127:415-445.
- BURLEY, N. 1986c. Sex-ratio manipulation in color banded populations of Zebra Finches. *Evolution* 40:1191-1206.
- BURLEY, N. 1988a. The differential allocation hypothesis: An experimental test. *Am. Nat.* 132:611-628.
- BURLEY, N. 1988b. Wild Zebra Finches have band-color preferences. *Anim. Behav.* 36:1235-1237.
- BURLEY, N., G. KRANTZBERG, AND P. RADMAN. 1982. Influence of colour banding on the conspecific preferences of Zebra Finches. *Anim. Behav.* 30:444-455.
- BURLEY, N., AND C. COOPERSMITH. 1987. Bill colour preferences of Zebra Finches. *Ethology* 76:133-151.
- BURLEY, N., R. A. ZANN, S. J. TIDEMANN, AND E. B. MALE. 1989. Sex ratios of Zebra Finches. *Emu* 89:83-92.
- BURLEY, N., D. K. PRICE, AND R. A. ZANN. 1992. Bill color, reproduction and condition effects in wild and domesticated Zebra Finches. *Auk* 109:13-23.
- CRISTOL, D. A., C. S. CHIU, S. M. PECKHAM, AND J. F. STOLL. 1992. Color bands do not affect dominance status in captive flocks of wintering Dark-eyed Juncos. *Condor* 94:537-539.
- DAVIES, S. J. F. 1979. The breeding seasons of birds in south-western Australia. *J. R. Soc. West Aust.* 62:53-64.
- FRITH, H. J., AND R. A. TILT. 1959. Breeding of the Zebra Finch in the Murrumbidgee irrigation area. *Emu* 59:289-295.
- HAGAN, J. M., AND REED, J. M. 1988. Red color bands reduce fledging success in Red-cockaded Woodpeckers. *Auk* 105:98-503.
- IMMELMANN, K. 1963. Tierische Jahresperiodik in öologischer Sicht: ein Beitrag zum Zeitgeberproblem, unter besonder Berücksichtigung der Brut- und Mauserzeiten australischer Vögel. *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere* 91:91-200.
- IMMELMANN, K. 1965a. Versuch einer ökologischen Verbreitungsanalyse beim australischen Zebrafinken, *Taeniopygia guttata castanotis* (Gould). *J. Ornithol.* 106:415-430.
- IMMELMANN, K. 1965b. Australian finches in bush and aviary. Angus and Robertson, Sydney.
- KIKKAWA, J. 1980. Seasonality of nesting by Zebra Finches at Armidale, N.S.W. *Emu* 80:13-20.
- MACARTHUR, R. H. 1964. Environmental factors affecting species diversity. *Am. Nat.* 98:387-397.
- METZ, K. J., AND P. J. WEATHERHEAD. 1991. Color bands function as secondary sexual traits in male Red-winged Blackbirds. *Behav. Ecol. Sociobiol.* 28:23-27.
- METZ, K. J., AND P. J. WEATHERHEAD. 1993. An experimental test of the contrasting-color hypothesis of red-band effects in Red-winged Blackbirds. *Condor* 95:395-400.
- MILLER, A. H. 1961. Molt cycles in Andean sparrows. *Condor* 63:143-161.
- RATCLIFFE, L. M., AND P. T. BOAG. 1987. Effects of color bands on male competition and sexual attractiveness in Zebra Finches (*Poephila guttata*). *Can. J. Zool.* 65:333-338.
- SAS INSTITUTE. 1990. SAS user's guide: Statistics, version 6.0. SAS Institute, Inc., Cary, North Carolina.
- SAS INSTITUTE. 1991. JMP ver. 2.0. Software for statistical visualization. SAS Institute, Inc., Cary, North Carolina.
- SERVENTY, D. L. 1971. Biology of desert birds. Pages 287-339 in *Avian biology*, vol. 1 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.
- SOSSINKA, R. 1970. Domestikationserscheinungen beim Zebrafinken *Taeniopygia guttata castanotis*. *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere.* 97:455-521.
- SOSSINKA, R. 1982. Domestication in birds. Pages 373-403 in *Avian biology*, vol. 6 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.
- WEATHERHEAD, P. J., D. J. HOYSACK, K. J. METZ, AND C. G. ECKERT. 1991. A retrospective analysis of red-band effects on Red-winged Blackbirds. *Condor* 93:1013-1016.
- WYNDHAM, E. 1986. Length of birds' breeding seasons. *Am. Nat.* 128:155-164.
- ZANN, R. 1985. Slow continuous wing-moult of Zebra Finches *Poephila guttata* from southeast Australia. *Ibis* 127:184-196.
- ZANN, R., AND M. ROSSETTO. 1991. Zebra Finch incubation: Brood patch, egg temperature and thermal properties of the nest. *Emu* 91:107-120.
- ZANN, R., AND B. STRAW. 1984. Feeding ecology and breeding of Zebra Finches in farmland in northern Victoria. *Aust. Wildl. Res.* 11:533-552.