REPRODUCTIVE ACTIVITY OF FORCE-PAIRED COCKATIELS (*NYMPHICUS HOLLANDICUS*)

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ABSTRACT.—In some monogamous birds random force-pairing of mates results in successful reproduction. In addition, prior social experience with a mate may enhance subsequent reproductive success. We investigated the influence of force-pairing and prior pair association on reproductive activity in Cockatiels stimulated to breed by long daylengths and nest-box access. Birds force-paired at the onset of long days had reduced reproductive activity compared to birds force-paired prior to long days. Both groups of force-paired birds displayed less activity than established control pairs. Birds force-paired prior to long days but then reunited with former mates at the onset of long days did not show impaired reproductive activity compared with controls. We show that force-pairing can lead to some breeding activity in this species and that mate familiarity improves the reproductive activity resulting from force-pairing. Furthermore, pairs with histories of breeding do not require continuous mate access to maintain pair bonds. *Received 1 February 1988, accepted 23 August 1988.*

COCKATIELS (*Nymphicus hollandicus*) are small (ca. 100 g), granivorous, sexually dimorphic cavity-nesting parrots that inhabit arid areas throughout much of Australia (Cayley 1938, Blakers et al. 1984). They are colonial and monogamous; as in other Cacatuini species, both sexes incubate and care for the young (Brereton 1963). It is generally accepted that pair bonds in the wild are quite stable and may be lifelong, although this is not well documented (Smith 1978). In the wild, Cockatiels are nomadic, opportunistic breeders although migratory movements occur in the south of Australia (Forshaw and Cooper 1981). In captivity, photostimulation (sexual stimulation via exposure to long daylengths) dramatically enhances the amount of sexual activity elicited by nest-box presentation (Millam et al. 1988, Myers et al. 1989).

Particularly in species with biparental care, mate selection for parental and other qualities is a strategy by which reproductive success may be increased (Trivers 1972, Burley 1981). The degree of selectivity of an individual should be proportional to the amount of parental investment it contributes relative to its mate (Trivers 1972). Hence, mechanisms for assuring selection of high-quality mates would be expected in individuals with considerable parental investment. Free mate choice is important for successful breeding in species such as domestic pigeons (*Columbia livia;* Klint and Enquist 1981) and Canvasback Ducks (*Aythya valisineria*). Force-pairing in the latter species (i.e. placing males and females together in pairs such that there is no opportunity for free mate choice) may result in extreme female aggression toward the male (Bluhm and Phillips 1981, Bluhm 1985). In other monogamous species, however, force-pairing is used quite successfully to induce breeding, e.g. California Quail (*Lophortyx californicus;* Leopold 1977) and Ringed Turtle-Dove (*Streptopelia risoria;* Lehrman and Wortis 1967).

Mate familiarity, established through social contact or pair formation, may also influence reproductive success in some monogamous species. Among male Zebra Finches (*Poephila guttata;* Caryl 1976) and Ringed Turtle-Doves (Erickson 1973), exposure to familiar potential mates rather than novel partners increased the likelihood of the performance of nest-soliciting behaviors (as opposed to initial courtship behaviors). Erickson and Morris (1972) proposed that mate familiarity may decrease aggression between mates and increase male sexual behavior towards the female, thereby stimulating female ovarian development. In addition they suggested that mate familiarity may enhance reproductive success by improving pair coordination in some breeding activities, such as incubation. It is unknown whether mate familiarity enhances the performance of reproductive activities in new Cockatiel pairs or whether reproductive activity is independent of prior mate exposure and dependent exclusively on sexual stimulation elicited by environmental factors.

The reproductive advantages of mate familiarity may explain, in part, the long-term stability of the pair bond in many monogamous species. In captive Zebra Finches, although repairing (with a new mate) occurs readily after separation from the original mate, this second pair attachment does not destroy the original pair bond (Silcox and Evans 1982). In addition, auditory contact alone can maintain established pair bonds in Zebra Finches (Silcox and Evans 1982) and possibly in Ringed Turtle-Doves (Morris and Erickson 1971), even when pair members are given access to new potential mates. Evidence of a strong tendency for pairs to reunite (after nonbreeding season separation) has also been found among Black-legged Kittiwakes (*Rissa tridactyla*) and Red-billed Gulls (*Larus novaehollandiae scopulinus*), Common Oystercatchers (*Haematopus ostralegus*), Great Tits (*Parus major*), Northern Fulmars (*Fulmaris glacialis*), and Buller's Albatross (*Diomedea bulleri*) (Richdale and Warham 1973, Mills 1973, Dunnet and Ollason 1978, Coulson and Thomas 1983, Perrins and McCleery 1985, Harris et al. 1987). In these species, mate retention (from previous breeding seasons) is associated with greater reproductive success than mate replacement.

We compared the degree of reproductive activity of unfamiliar force-paired Cockatiels with that of established Cockatiel pairs when all birds were given environmental conditions stimulatory to breeding (long daylengths and access to nest boxes). We also tested whether social interactions that increase familiarity between birds force-paired during nonbreeding conditions facilitate reproductive activity when birds were subsequently exposed to stimulatory breeding conditions. Finally, we assessed the reproductive activity of established mates that were separated, exposed to novel partners, and then reunited under breeding conditions. Our findings suggest that previous mates and individuals with whom some social contact has been shared enhance reproductive response to breeding conditions in Cockatiels and so are likely to be preferred over novel mates in successive breeding attempts.

METHODS

Animals.—Seventy-two pairs of normal gray (wild type) Cockatiels were obtained from an experimental flock bred and maintained on the University of California-Davis campus since 1979. These pairs were originally formed in free choice situations, in which 10-40 individuals were placed in large flights and permitted to choose mates. Pair formation was identified by co-occupancy of a nest box by a male and female. The number of reproductive attempts made by any bird prior to the study covaried with age (generally birds in this flock were given the opportunity to breed once annually beginning in their second year). The birds ranged in age from 3 yr to at least 7 yr and were classified into 4 categories according to their level of reproductive activity in previous breeding trials. In these trials, they had been held 1 pair/cage during long daylengths and presented with nest boxes to encourage breeding. Birds in the first category ($n = 35$ pairs) were known to have laid in nest boxes and incubated fertile eggs. The second category ($n = 20$ pairs) consisted of pairs that had laid fertile eggs but had been denied the opportunity to incubate them. The third category ($n = 9$ pairs) contained pairs that had laid infertile eggs. Birds in the fourth category ($n = 8$ pairs) had shown evidence of pair formation (i.e. clumping or perching in close proximity; see Butterfield 1970), but had failed to produce eggs.

Treatments and procedure.—We randomly assigned approximately equal numbers of pairs from each category to 1 of 5 treatment groups. The birds were held in cages (60 cm long × 30 cm wide × 30 cm high) in batteries (3 tiers/battery with 12 cages/tier) in 2 experimental rooms (1 battery/room). Equal numbers of pairs from each treatment group were in each room. Across treatment groups, male age ranged from 4.36 (±0.59) to 4.86 (±0.50) yr and average female age ranged from 3.43 (±0.43) to 4.42 (±0.54) yr.

Treatment groups were numbered 1-5. In Group 1, birds ($n = 14$ pairs) remained with their mates continuously but were moved to a new location within the battery at the start of nonbreeding conditions to control for the movement of pairs in other groups. Birds in Group 2 ($n = 12$ pairs) remained with their mates continuously but were moved to a new location within the battery at the start of both nonbreeding and breeding conditions to control for the movement of pairs in other groups. Group-3 birds ($n = 14$ pairs) were randomly re-paired and moved to a new location at the beginning of nonbreeding conditions then reunited with their former mates and moved to a new location at the beginning of breeding conditions. Birds in Group 4 ($n = 13$ pairs) were randomly re-paired with new mates at the beginning of nonbreeding conditions and placed in a new location within the battery (birds were visually, but not acoustically, isolated from their previous mates). Finally, Group-5 birds ($n = 13$ pairs) remained with their mates during the nonbreeding condition but were randomly re-paired and moved at the beginning of the breeding condition.

All birds were held under nonbreeding conditions for 12 weeks, then, under breeding conditions for 7 weeks. Birds were provided free access to water and nutritionally balanced crumbled diet throughout the study (Roudybush et al. 1984). During the nonbreeding condition nest boxes were absent, photoperiod was 9:15 LD and ambient temperature was about 20°C. Light phase light intensity during the nonbreeding condition (measured at head height in the middle of the cage) ranged from 1-10 lux in room 1, and from 50-200 lux in room 2. For all treatment groups, we found no effect of light intensity during the nonbreeding condition on any of the measured variables. Both rooms were between 50 and 200 lux during the breeding condition. During the breeding condition photoperiod was 15:9 LD, ambient temperature was about 22°C, and nest boxes were attached to cage ends. Nest boxes (20.3 cm × 30.5 cm × 30.5 cm) were constructed of stainless steel and filled to a depth of about 10 cm with pine shavings. We formed shavings into a mound when boxes were introduced. Following nest-box presentation, we inspected them daily to observe whether birds had inspected the nest box, formed a nest bowl, laid eggs, or incubated. A bird conspicuously flattened out the mound of shavings thereby revealing nest inspection. We identified nest-bowl formation by the appearance of an obvious cup-shaped depression in the shavings, and established incubation by observance of birds sitting on or (due to being disturbed by the observer) standing above eggs.

Eggs incubated in nest boxes between 5 and 10 days were candled to determine fertility. Eggs appearing infertile were later opened to inspect for undetected early embryonic death. Eggs laid on the cage floor were incubated artificially and checked for fertility. Artificially incubated fertile eggs were occasionally exchanged for infertile eggs of incubating pairs to increase chick production for other experimental purposes. Exchanging eggs did not influence incubation in Cockatiels.

During the course of the study, 2 pairs in Group 2 were deleted from the analysis because of the deaths of 2 females, aged 7 yr and 4 yr. One pair was deleted from Group 4 due to the death of a 6-yr-old female, and one pair was deleted because of the misidentification of a male as a female. Two pairs were deleted from Group 5 because of the death of a 6-yr-old male: the pair of which the male was part during the nonbreeding condition and the pair this male would have formed during the breeding condition.

Behavioral scoring and analysis.—Reproductive activity of each pair was scored daily. For each activity we assigned an arbitrary value: nest box inspected (1), nest bowl formed (2), infertile egg laid on cage floor (3), fertile egg laid on cage floor or infertile egg laid in nest box (4), fertile egg laid in nest box or incubation of infertile eggs (5), and incubation of fertile clutch (6). We averaged pair scores within each group first for each day, then for each week of the breeding condition. Weekly reproductive activity scores were averaged by treatment group; then we compared the scores using the SAS-GLM program for repeated measures (SAS Institute Inc. 1985). Comparison among groups for days to first nest inspection, nest-bowl construction, and first oviposition were performed with the SAS-LIFETEST program (SAS Institute Inc. 1985). Clutch sizes were compared via one-way ANOVA.

Incidence in each group of nest inspection, nest-bowl formation, egg production, incubation, and fertility were compared via linear stepwise regression using the BMDP LR program (Dixon 1983). Unless otherwise indicated, significant differences reported may be assumed to have P-values of 0.05 or less.

RESULTS

Likelihood of nest inspection, bowl formation, egg laying, incubation, and fertility.—There were no differences between treatment groups in the likelihood of nest inspection; most pairs in each group inspected nest boxes. However, birds force-paired at the onset of breeding conditions (Group 5) had a significantly reduced likelihood of completing bowl formation compared to control (Groups 1 and 2) or reunited (Group 3) pairs ($P < 0.003$) (Fig. 1). In addition, Group 5 birds had a significantly lower likelihood of completing bowl formation than birds force-paired at onset of nonbreeding conditions (Group 4) ($P < 0.005$). There were no significant differences in the likelihood of bowl formation between control groups and reunited pairs. Across all groups, male age was positively correlated with the likelihood of nest inspection ($P < 0.023$) and bowl formation ($P < 0.10$). Male age was not a determinant of differences between treatment groups.

In addition to being less likely to form nest bowls, pairs force-paired at the onset of breeding conditions were significantly less likely than control or reunited pairs to lay eggs, incubate, or be fertile (Fig. 1). Those birds force-paired at the onset of breeding conditions had significantly lower likelihood of completing these activities than birds force-paired at the onset of nonbreeding conditions (laying, $P < 0.010$; incubating, $P < 0.008$; fertility, $P < 0.020$). Pairs force-paired at the onset of nonbreeding conditions were less fertile than control or reunited pairs. There were no differences in these measures across control and reunited groups. Across treatment groups, female age correlated positively with the likelihood of laying ($P < 0.031$) and incubation ($P < 0.014$), but not fertility. As with male age, group differences were not attributed to female age.

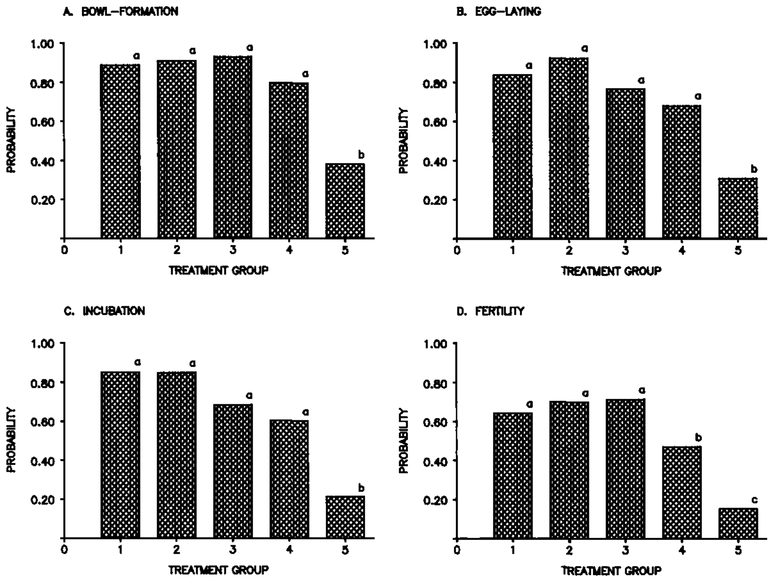

Fig. 1 (A-D). Likelihood of completing bowl-formation (A), laying eggs (B), incubating eggs (C), and being fertile (D) after onset of stimulatory breeding conditions (nest boxes presented on day 0). Significant differences ($P < 0.05$) are indicated by unlike superscripts.

Time to nest inspection, bowl formation, and onset of egg laying.—Groups differed in the numbers of pairs inspecting nest boxes (Fig. 2A), forming nest bowls (Fig. 2B), and laying eggs (Fig. 2C), and in the times it took these pairs to complete these activities after nest-box presentation. There were no differences in times between control pairs (Groups 1 and 2) and reunited pairs (Group 3). Compared to control pairs, Cockatiels force-paired at the beginning of breeding conditions (Group 5) took longer to inspect nest boxes (by approximately 2 weeks), form bowls (by 9.5 days), and commence egg laying. There were no differences between groups in average time lapsed between bowl formation and commencement of egg laying; thus, force-paired birds took longer to lay due to delays prior to, but not after, completion of bowl formation. Cockatiels force-paired at the onset of nonbreeding conditions (Group 4) had a significantly longer delay to egg laying than control pairs.

Across treatment groups, the mean size of first clutches of laying pairs ranged from 5.13 to 7.00 eggs. No differences were significant (Table 1).

Reproductive Activity Scores.—Force-paired groups had reduced reproductive activity scores (Fig. 3), particularly those (Group 5) force-paired just at the onset of the breeding condition. This group's scores remained significantly lower than all other groups during weeks 1 to 3. By week 4 and thereafter, however, the scores were not different from those of the group force-paired at the onset of nonbreeding conditions. The scores of Group 5 were not significantly lower than control and reunited groups' scores until after week 4. There was no effect of moving pairs at the onset of breeding conditions, nor of moving at the onset of either nonbreeding and breeding conditions. Birds which resided with new mates during nonbreeding conditions did not show reduced activity when they were reunited with former mates at the onset of photostimulation. Activity scores of control and reunited groups were virtually indistinguishable over time.

DISCUSSION

Free mate choice is important for successful initial establishment of the pair bond. Mate familiarity also has a powerful influence on pair formation and reproductive activity, as well as on maintenance of the pair bond in Cockatiels.

Among monogamous long-lived species with biparental care, reproduction is a complex, precisely timed process that requires the close cooperation of both members of a pair (Erickson 1978). Reproductive success in these species depends on successful pair formation where in-

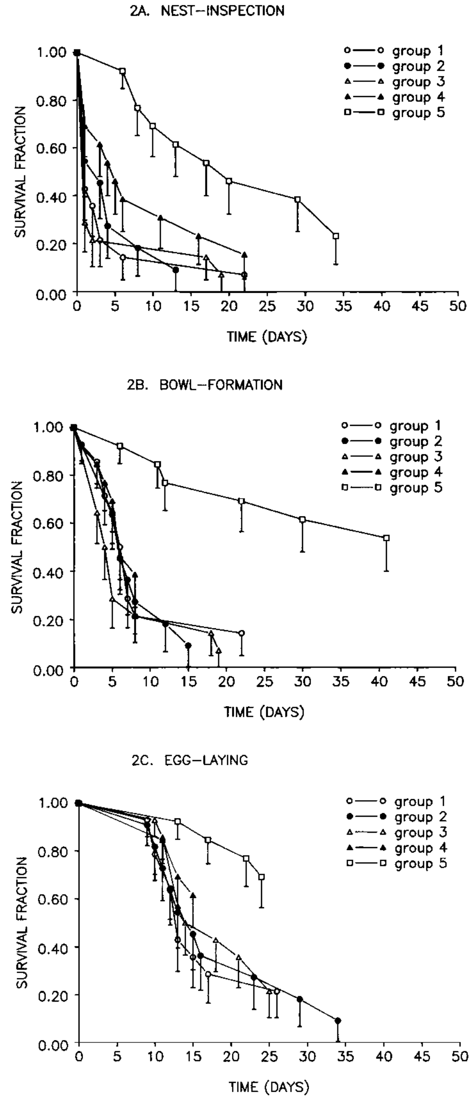

Fig. 2 (A-C). Survival estimates for nest-inspection occurrence (A), bowl-formation completion (B), and commencement of egg laying (C) during stimulatory breeding conditions (nest boxes presented on day 0). The survival fraction indicates the number of remaining pairs in a group that have not completed a given activity at the corresponding x-axis time.

dividuals of a pair coordinate their activities and are well matched in their parental or reproductive abilities (Coulson 1966, 1972; Trivers 1972; Mills 1973; Bluhm and Phillips 1981). Given these conditions, and depending on individual variance in potential mate quality, it is likely that selection of compatible mates with high reproductive potential will be a primary means by which individuals can maximize reproductive fitness (Parker 1983). It follows that, without opportunity for selection, pair formation might not occur, and the complementarity and compatibility necessary to coordinate reproductive activities might not be established. Our findings in force-paired Cockatiels support this postulate. Compared to established pairs, force-paired birds had lower incidences of, and took longer to complete, certain reproductive activities. Presumably this reflects lack of synchronization between pair members and deficits in the quality of pair formation.

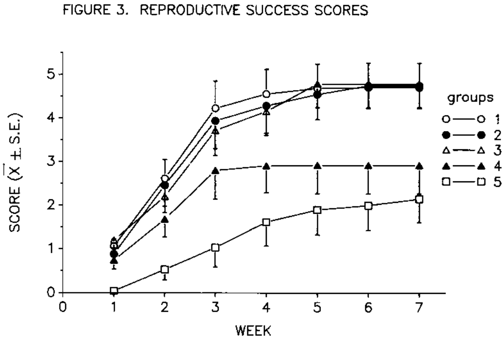

Fig. 3. Mean weekly reproductive activity scores of groups during stimulatory breeding conditions.

Mate familiarity is a possible contributing factor in achieving reproductive synchrony between mates. Familiarity may also influence pair formation and subsequent reproductive success (Caryl 1976; Erickson 1973). In studies of captive Common Black-headed Gulls (*Larus ridibundus*), prior social experience with the mate was a significant predictive factor of pair formation (Van Rhijn and Groothuis 1987). Thus familiarity seems to be an important component of successful pair formation and may function to promote coordination of reproductive behavior of mates. Enhanced synchrony may accelerate reproductive activities during the breeding season and, as a result, increase reproductive suc-

Table 1. Mean clutch sizes by treatment group.

Group No.	*n*	No. of pairs laying	Eggs/pair ($\bar{x}$ ± SE)
1	14	10	7.00 ± 0.91
2	12	8	5.23 ± 1.02
3	14	10	5.60 ± 0.91
4	13	5	5.60 ± 1.29
5	13	2	6.00 ± 2.04

cess (Rowley 1983). We observed precisely this effect in force-paired Cockatiels although denial of mate choice proved to be a reproductive handicap. If birds were permitted a period prior to the breeding condition during which they could become familiar with each other, overall reproductive success was greater than if they were paired at the onset of breeding conditions.

It is likely that mate familiarity and enhanced coordination of mates were also important factors in the high degree of reproductive activity of reunited pairs. In the Lesser Snow Goose (*Anser c. caerulescens*), a precocial monogamous species, experienced pairs tend to be more attentive and coordinated in their nest defense than new pairs, and they rarely separate (Cooke et al. 1981). Similarly, in monogamous species with extended chick care, mate retention throughout successive breeding seasons was correlated with greater reproductive success. Females that retain rather than replace mates tended to lay earlier, lay larger clutches, and have greater hatching success (Coulson 1966, Mills 1973, Perrins and McCleery 1985). In addition, while mates may not maintain physical contact during the nonbreeding season, if the pair had a successful reproductive history, there was a strong tendency to reunite at the onset of the breeding season (Coulson and Thomas 1983, Rowley 1983, Van Rhijn and Groothuis 1987). Likewise, in species with continuous, long-term pair bonds, experimental mate separation leads to successful reuniting (Butterfield 1970, Morris and Erickson 1971, Silcox and Evans 1982). Therefore, it is not surprising that captive Cockatiel mates that were reunited after 12 weeks of physical and visual isolation had reproductive scores that were not different from control pairs that remained together throughout the study. It should be recalled that separated mates were not isolated acoustically from one another. Thus, acoustic recognition may be one mechanism by which mutual attachment of mates is maintained in Cockatiels. Miller (1979) demonstrated such a mechanism in Zebra Finches.

In addition to treatment effects, we found significant effects of male and female age on reproductive activity. Generally, in other studies, older birds have been reported to have greater reproductive success than younger birds (Coulson and White 1958, Coulson and Horobin 1976, Dunnet and Ollason 1978). We found that the incidence of several reproductive activities were positively correlated with parental age in Cockatiels. Enhanced reproductive success of older age groups may be ascribable to superior breeding or survival skills due to experience, to higher survivability among birds of high quality or fitness, or both (Ryder 1980, Harvey et al. 1985, Nol and Smith 1987). Breeding experience may be a strong determinant of reproductive potential, because breeding success in sexually naive Cockatiels is known to improve significantly after completion of the first breeding cycle (Myers et al. 1988). Another hypothesis explaining the greater reproductive success in older individuals is that "Residual Reproductive Value" decreases with age (due to decreasing number of future breeding seasons), while reproductive effort per clutch, and therefore success, should increase with age (Williams 1966, Curio 1983). Pugesek (1981) supported this hypothesis in California Gulls (*Larus californicus*). Breeding studies have also revealed differential influences of male and female age on reproductive activities and success (Coulson and White 1958, Lehrman and Wortis 1960, Mills 1973, Perrins and Moss 1974, Perrins and McCleery 1985). The distinct effects observed between the sexes probably reflect the different roles males and females have in various reproductive activities, but further studies are necessary for more thorough assessment of age factors of reproduction in Cockatiels.

Beyond ecological interpretation, our study has possible applications to the captive breeding of endangered avian species. For many endangered species it is conceivable that successful captive propagation will be a crucial factor in the effectiveness of programs to reestablish wild populations. In spite of the potential significance of captive breeding to conservation efforts, there is presently a critical lack of information concerning captive rearing techniques for exotic birds (Scott and Carpenter 1987). Because of its availability, hardiness, and willingness to breed in captivity, the Cockatiel is a good model species for investigations of the environmental and social requirements for successful reproduction in captivity.

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