REPRODUCTIVE SUCCESS OF HAND-REARED VS. PARENT-REARED COCKATIELS (NYMPHICUS HOLLANDICUS)

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Abstract.—We studied the influence of early rearing experience on the reproductive success of Cockatiels (*Nymphicus hollandicus*) by force-pairing somatically mature birds that had been either hand-reared (H) or parent-reared (P) from hatch to 6 weeks of age. Pairs of H-males and H-females, H-males and P-females, P-males and P-females, or P-males and H-females were encouraged to breed by providing nest-boxes and exposing pairs to a sexually stimulatory environment. Hand-rearing produced gender-specific effects that greatly affected reproductive success. Pairs containing H-females were more likely to lay eggs and laid more eggs than pairs with P-females but often laid them on the cage floor rather than in nest-boxes, reducing hatching success. Pairs containing H-males were less likely than pairs with P-males to produce fertile eggs, inspect nest-boxes, or lay eggs in nest-boxes. Fledging occurred only in pairs containing P-males. Early rearing experience is important for males to learn characteristics of the opposite sex, and for males and females to learn characteristics of nest-sites. *Received 2 November 1987, accepted 25 March 1988.*

Cockatiels (*Nymphicus hollandicus*) are monogamous, cavity-nesting birds distributed throughout the interior of Australia in riparian woodland and open country dotted with scrub vegetation (Dawson 1965). They are considered opportunistic breeders in the wild, although southern populations migrate and breed seasonally (Forshaw 1981). Reproductive activity in captivity is promoted by providing nest-boxes and exposing birds to an environment that includes a daylength of 15 h (Millam et al. 1988). A mate is normally required for full gonadal development. Although the gonadotropic response to photostimulation is not learned, early behavioral experience may be critical in determining whether Cockatiels recognize conspecifics as potential mates, or nest-boxes as nest-sites.

Sexual imprinting is common in birds (see Immelmann 1972, 1985 for reviews). Among Psittaciformes, Rowley and Chapman (1986) found evidence of imprinting in Galahs (*Cacatua roseicapilla*) naturally cross-fostered to the sympatric *Cacatua leadbeateri*. As adults the cross-fostered Galahs associated solely with *C. leadbeateri*. Klinghammer (1967) reported anecdotal evidence for sexual imprinting in other Psittaciformes such as the Budgerigar (*Melopsittacus undulatus*) and Senegal Parrot (*Poicephalus senegalus senegalus*).

Birds may imprint on the habitat in which they were reared (Klopfer and Hailman 1965, Klopfer and Ganzhorn 1985). Zebra Finches (*Poephila guttata*) offered a choice of nest-sites tended to select the same habitat in which they were reared over the same nest-substrate upon which they were reared (Sargent 1965). The fledgling period appeared more important than the nestling period for the birds to acquire information about the habitat of the nest. Baptista and Petrinovich (1986) suggest that habitat imprinting may be responsible for the impaired reproductive success in captivity of wild-caught White-crowned Sparrows (*Zonotrichia leucophrys*). These observations suggest that learning during sensitive phases of development may be important in determining how Cockatiels identify nest-sites as adults.

We assessed the potential influence of early learning on reproductive success by investigating the influence of hand- vs. parent-rearing on adult males and females. Recently, Scott and Carpenter (1987) stressed the importance of quantitative studies on the role played by different rearing techniques in captive breeding. We found that hand-rearing of either sex Cockatiel produces gender-specific effects that greatly affect reproductive success. Early behavioral experience appears important for male Cockatiels to learn characteristics of the opposite sex,

and for males and females to learn character-
istics of nest-sites.

MATERIALS AND METHODS

Animals.—Cockatiel breeding stock was imported
from Belgium in 1979. Experimental subjects were the
F_1 or F_2 offspring of the imported stock.

Rearing conditions.—Hand-reared (H) birds were
hatched from artificially incubated eggs and trans-
ferred within several hours of hatching to brooders
where birds were kept individually in No. 2 paper
bags (initially $8 \times 12 \times 25$ cm) containing pine shav-
ings to a depth of about 6 cm. The tops of the bags
were then cut-off a few cm above head height to ease
handling while still restricting movement of the chick
to the inside of the bag. As chicks grew taller, new,
higher bags replaced shorter ones. About 63 chicks
were housed in each brooder (21 in each of 3 trays,
each about 0.34 m² in area) where they were visually
but not acoustically isolated from one another until
about 17 days of age. Birds were hand-fed by the
method of Roudybush and Grau (1986). Chicks were
fed about each 2 h for the first 2 days of life from
about 0600–2200 h, then each 4 h from about 0600–
2200 h until 7–10 d of age. Feeding intervals were
increased further as dictated by crop-emptying times.
Birds were handled for 5–10 s at each feeding, but
were in intermittent visual contact for about an ad-
ditional 10 min during each feeding time. Eyes open
at about 7–10 days of age and chicks over 17 days of
age occasionally peered over the tops of the bags.
Likewise chicks of this age occasionally escaped from
their bags. Brooders were intermittently lit by a 15-
watt incandescent lamp wired in series with the heat-
ing coil so the opportunity to see other birds was
present from 17 days of age onwards. H-birds were
moved to wire cages ($0.2 \times 0.2 \times 0.3$ m), 2 birds/cage,
at 3 weeks of age. After independence, birds were
moved to a semi-enclosed aviary and held in flights
($3 \times 2 \times 3.5$ m) of 30 birds. They were fed a crumbled
stock diet *ad libitum* (Roudybush and Grau, 1986). Males
and females were separated into same-sex groups at
approximately 6 months of age when males molt into
adult plumage. Flights were visually, but not acous-
tically, isolated from one another.

Parent-reared (P) birds were naturally incubated
and hatched in stainless steel nest-boxes ($0.2 \times 0.3 \times
0.3$ m) attached to wire cages ($0.3 \times 0.3 \times 0.6$ m).
Crumbled stock diet was available *ad libitum*. Nest-
boxes contained pine shavings to a depth of about 6
cm and had an entrance hole 6.5 cm in diameter. After
weaning at 6 weeks of age, birds were moved to the
same aviary as H-birds, but kept separate in flights
of about 30 birds each. Analogous to H-birds, sexes
were separated and held in same sex flocks from 6 to
18 months of age. The only potential for parent-reared
birds to see humans was during a brief 1–5 s period

each day when the lid of the nest-box was slightly
raised to observe the condition of nest material and
count the number of eggs or chicks.

Experimental design.—At 18 months of age, during
October 1985, H- and P-males and females were ran-
domly force-paired and assigned to one of 4 groups
of 9 pairs each. Group 1 pairs contained H-males ×
H-females (H × H); group 2, H-males × P-females
(H × P); group 3, P-males × P-females (P × P); and
group 4, P-males × H-females (P × H). Each pair was
held in a separate cage as described above and trans-
ferred to an environmentally controlled room. Cages
were held in a rack 3 cages high by 12 cages long.
Pairs were randomly assigned to cage locations.

Pairs were encouraged to breed in 2 studies, Trials
1 and 2, using a modification of the method of Millam
et al. (1988). Pairs were initially maintained under
nonstimulatory conditions (9L:15D photoperiod with
light onset at 0900 h, 50–250 lux light intensity, room
temperature 17°C, nest-boxes absent) for 3 weeks in
Trial 1 and 6 weeks in Trial 2; followed by stimulatory
conditions (15L:9D with light onset at 0500 h, 500–
1200 lux, room temperature 26°C, nest-boxes present)
for 12 weeks in both trials. Stimulatory conditions
were introduced gradually over a period of 1 week,
followed by nest-box presentation. Two males in group
2 died of unknown causes during the nonstimulatory
period of Trial 2.

Cages and nest-boxes were checked daily for eggs
and evidence of nest-box inspection. Eggs laid on cage
floors were removed and artificially incubated for 5
to 10 days to permit determination of fertility by can-
dling. Clear eggs were broken and examined for evi-
dence of earlier embryonic death. Eggs laid in nest-
boxes were date-marked and returned to the nest-box.
Nest-box inspection by Cockatiels was determined by
observing whether handmounded shavings had been
disrupted. If inspection occurred, shavings were re-
formed into a mound. If eggs were present, however,
shavings were not disturbed. If an egg was found in
a nest-box without previous disruption of the mound,
the nest-box was not counted as having been inspect-
ed.

Because Cockatiels usually lay every second day
(Millam et al. 1988), a clutch was operationally de-
fined as complete if a pause of 5 or more days occurred
without an egg being laid.

Hatching success (number of chicks hatched/num-
ber of eggs laid), fledging success (number of chicks
surviving to leave the nest-box/number of eggs
hatched) and breeding success (number of chicks
fledged/number of eggs laid) were measured for first
clutches only.

Approximately 0.8 ml of blood was collected by
venipuncture from the jugular vein for analysis of
hormone concentrations (Myers et al. unpubl.). Blood
samples were collected from all birds during nonstim-
ulatory conditions and 3 to 4 days after nest-box pre-
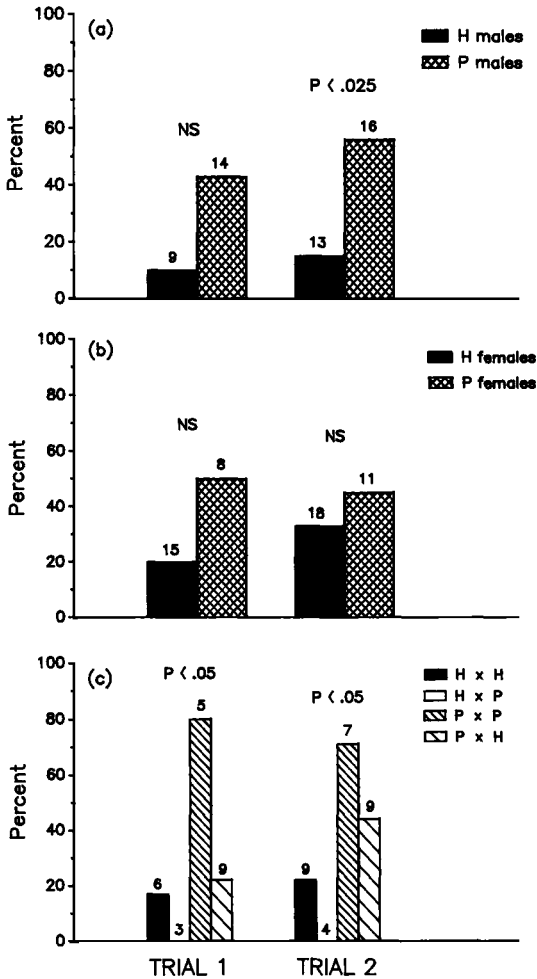sentation. Thereafter a blood sample was taken from

Fig. 1. Incidence of nest-box use by pairs by (a) male rearing condition, (b) female rearing condition, and (c) group. Number of pairs is indicated above bars.

each member of the pair after the first egg was laid, midway through incubation, during the nestling period and during the fledgling stage, and after removal of the nest-box.

Statistics.—Chi-square tests were used to compare frequency data. In comparison of groups (Figs. 1c, 2c, and 3c), P values refer only to the probability of rejecting the null hypothesis that no group effect was detected; group sample sizes were generally not large enough to permit between group comparisons. Student's *t*-test and one-way analysis of variance were used to compare means (Snedecor and Cochran 1967).

Results

In both trials pairs with P-males (groups 3, 4) were more likely to inspect nest-boxes than

pairs with H-males (groups 1, 2). In Trial 1, 8 pairs in groups 3 and 4 inspected nest-boxes vs. 0 pairs in groups 1 and 2 ($P < 0.01$). In Trial 2, 10 pairs in groups 3 and 4 inspected vs. 2 pairs in groups 1 and 2 ($P < 0.025$). In Trial 1, 3 pairs inspected nest-boxes for approximately 2 days each and subsequently laid on cage-floors while 2 pairs laid in nest-boxes without prior inspection. In Trial 2 all pairs that laid in nest-boxes ($n = 11$) first inspected them, 1 pair inspected but continued to lay on the cage-floor, and 1 pair inspected but never laid anywhere.

Male rearing condition influenced whether pairs laid eggs in nest-boxes (Fig. 1a). Of pairs laying, groups 3 and 4 were about 3 times more likely to lay in nest-boxes than groups 1 and 2 (Trial 1, NS; Trial 2, $P < 0.025$). Female rearing condition exerted no significant influence (Fig. 1b). The interaction of these effects is reflected in incidence of nest-box use by group (Fig. 1c). Incidence of laying pairs using nest-boxes was greatest in group 3, followed in descending order, in both trials, by groups 4, 1, and 2 (Trials 1 and 2, $P < 0.05$).

In both trials, group 3 and 4 laying pairs were far more likely than group 1 and 2 laying pairs to produce fertile eggs (Fig. 2a; Trial 1, $P < 0.001$; Trial 2, $P < 0.01$). In contrast, female rearing condition did not significantly influence pairs fertility (Fig. 2b). The interaction of these effects (Fig. 2c) was that in both trials, 100% of groups 3 and 4 laying pairs produced at least one fertile egg. We observed a similar pattern of pair fertility in both trials, although in Trial 2 fertility increased in groups 1 and 2. The pattern of percent-eggs-fertile was the same in both trials (Table 1). Egg fertility was significantly higher in groups 3 and 4 pairs than groups 1 and 2 pairs (Trial 1, $P < 0.005$; Trial 2, $P < 0.005$). Male rearing condition had no significant effect on incidence of pairs laying (Fig. 3a). In contrast, H-female pairs (groups 1 and 4) were more likely than P-female pairs (groups 2 and 3) to lay (Fig. 3b; Trials 1 and 2, $P < 0.025$). As with other measures of reproductive performance, number of laying pairs increased slightly in all groups in Trial 2 (Fig. 3c).

Data on number of eggs in first clutches for pairs laying in nest-boxes were combined for Trials 1 and 2. Clutch size by group was, in decreasing order: group 4 (7.0 ± 0.8 eggs [mean ± SE], $n = 7$); group 4 (5.8 ± 0.8, $n = 9$); group 1 (5.0, $n = 2$); and group 2 ($n = 0$). Combining all 4 groups, the size of first clutches of nest-

TABLE 1. Percent eggs fertile.

Groups	Percent eggs fertile[a]
Trial 1	
(1) H × H	35.6
(2) H × P	0
(3) P × P	76.5
(4) P × H	54.1
Trial 2	
(1) H × H	58.4
(2) H × P	19.0
(3) P × P	89.5
(4) P × H	64.5

[a] Groups 3 and 4 vs. Groups 1 and 2 sig. $P < 0.005$ in both trials.

box layers increased nonsignificantly from 5.1 ± 0.6 eggs ($n = 7$) in Trial 1 to 6.5 ± 0.8 ($n = 10$) in Trial 2. Many pairs, however, failed to use nest-boxes.

For the number of eggs laid by oviposition site (Table 2), groups 1 and 4 pairs laying on cage-floors laid significantly more eggs than groups 2 and 3 pairs laying on cage-floors ($P < 0.05$). We combined data on incubation times from both trials. Incubation bouts ranged from 16–23 days, mean of 17.9 ± 0.4 days ($n = 12$). Incubation times for individual eggs were related to position within the clutch; first eggs were incubated the longest. The correlation coefficient of incubation times in days (y-axis) vs. position of egg within the clutch (x-axis) was -0.39 ($P < 0.01$). The linear regression equation had an intercept of 19.8 days and a slope of -0.40 days per clutch position. Hatching was highly asynchronous, with up to 5 days elapsing between the hatching of first and last chicks of a clutch.

Successful hatching and fledging occurred only in groups 3 and 4 (Table 3). In Trial 1,

TABLE 2. Number of eggs laid by oviposition site (nest-box vs. cage-floors) of hand- vs. parent-reared female pairs.

	Number of eggs[a]	
Groups	Nest-box	Cage-floor
Trial 1		
H-females	8.3 ± 3.2 (3)	14.1 ± 2.5 (13)[b]
P-females	4.5 ± 0.6 (4)	5.4 ± 2.6 (5)[c]
Trial 2		
H-females	12.5 ± 3.3 (6)	14.4 ± 2.0 (14)[b]
P-females	11.2 ± 2.6 (5)	7.0 ± 2.2 (6)[c]

[a] Mean ± SE (n).
[b,c] Significantly different ($P < 0.05$) within trials.

TABLE 3. Hatching, fledging and breeding success of Cockatiel pairs.

Groups	n	Hatching success[a]	Fledging success[a]	Breeding success[a]
Trial 1				
(1) H × H	1	0	0	0
(2) H × P	0	0	0	0
(3) P × P	3	78.6	100	78.6
(4) P × H	1	100	100	100
Trial 2				
(1) H × H	2	0	0	0
(2) H × P	0	0	0	0
(3) P × P	5	85.3	86.4	73.5
(4) P × H	4	39.3	100	39.3

[a] Groups 3 and 4 vs. Groups 1 and 2 sig. $P < 0.005$ in both trials.

group 4 pairs had greater breeding success than group 3 pairs but, in Trial 2, group 3 pairs had significantly greater breeding success ($P < 0.005$) than group 4 pairs. Groups 3 and 4 pairs were significantly more successful than groups 1 and 2 pairs in hatching, fledging, and breeding success ($P < 0.005$). For 20 pairs that laid in both trials, the mean number of days from nest-box presentation until laying of the first egg decreased by more than 2 weeks in Trial 2. The mean number of days from nest-box presentation to laying was 33.85 ± 3.41 days in Trial 1 and 16.70 ± 2.35 days in Trial 2 ($P < 0.001$).

DISCUSSION

Hand-rearing of either male or female Cockatiels produced gender-specific effects that greatly altered reproductive success. Fertility of H-male pairs was severely impaired suggesting that hand-rearing prevented normal sexual imprinting in males. Little experimental evidence exists from which to predict whether sexual imprinting occurs in other psittacine species although Galahs (*Cacatua roseicapilla*) naturally cross-fostered to sympatric *Cacatua leadbeateri* continued to associate solely with the cross-fostered species as adults, and shunned approaches from conspecifics (Rowley and Chapman 1986). In contrast, fertility of H-female pairs was not lower than P-female pairs. This supports the observations of Warriner et al. (1963) on Pigeons, Schutz (cited in Ten Cate 1985) on Mallards (*Anas platyrhynchos*), and Immelmann (1972) on Zebra Finches that sexual imprinting more often occurs in males than females. However, sex differences in mate choice may occur
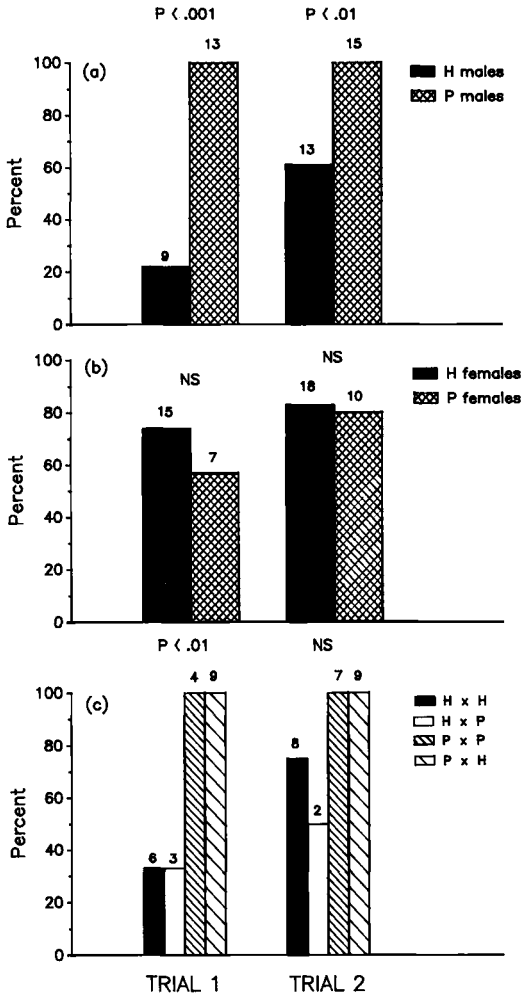
Fig. 2. Incidence of laying pairs fertile by (a) male rearing condition, (b) female rearing condition, and (c) group. Number of pairs is indicated above bars.
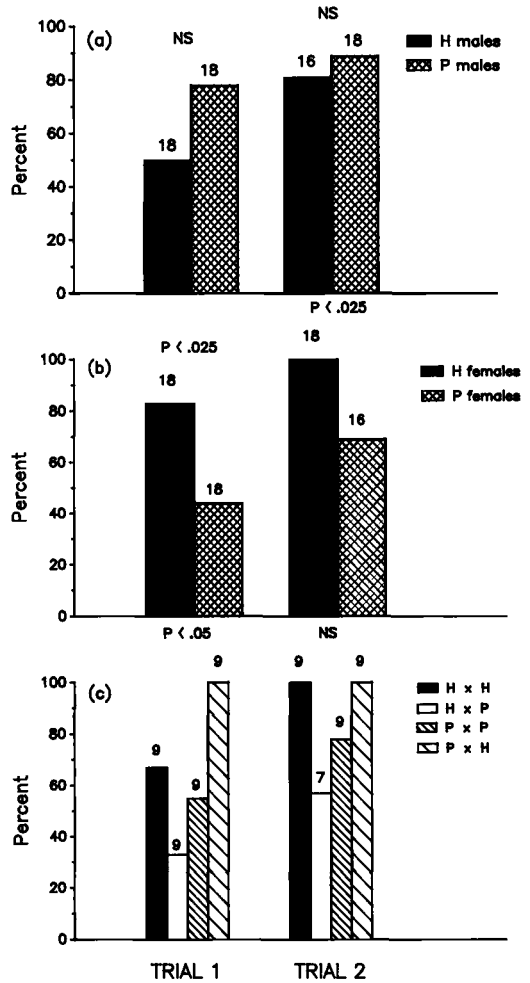

Fig. 3. Incidence of pairs laying by (a) male rearing condition, (b) female rearing condition, and (c) group. Number of pairs is indicated above bars.

but do not necessarily result from differences in imprintability (Ten Cate 1985). Alternatively, the observed sex differences may occur because male and female chicks imprint on different cues, only one of which may be plumage characteristics, the factor most typically studied in testing situations. Thus, we cannot conclude that sexual imprinting did not occur in female Cockatiels, as potential behavioral deficits may not have been reflected in our measures of reproductive success.

H-females were far more likely to produce eggs. Why this occurred is not clear. One possibility is that H-females may have imprinted on humans and as a result experienced less stress

in response to handling or the presence of animal caretakers and experimenters during the breeding trials. Baptista and Petrinovich (1986) also found that H-female White-crowned Sparrows were far more likely to produce eggs than wild-caught sparrows. They attributed this to a difference in habitat imprinting. It is also possible that if H-females failed to imprint sexually, the requirement for social interaction with a mate would be inconsequential and therefore would not constrain photo-induced sexual activity. Klinghammer (1967) found that hand-reared Mourning Doves (*Zenaida macroura*) removed before 8 days after hatch remained tame to humans but still mated with conspecifics.

Hand-rearing also impaired reproductive

success by increasing the likelihood of eggs being laid outside of the nest-box. This is compatible with the hypothesis that early behavioral experiences normally confer stimulus properties of a nest-site on the nest-box but that H-birds of both sexes were deprived of these experiences.

Habitat imprinting occurs in several species (Klopfer and Hailman 1965, Immelmann 1975, and Klopfer and Ganzhorn 1985). Habitat imprinting encompasses the acquisition of behaviors that range from preferences for general features of locality such as shrubs vs. trees (e.g. Chipping Sparrows [*Spizella passerina*] [Klopfer 1963]) to habitat and nest-site selection (e.g. Zebra Finch [Sargent 1965], Lesser Snow Geese [*Chen c. caerulescens*] [Cooke and Abraham 1978], Linnets [*Acanthis cannabina*] [Gluck 1984]). In cavity-nesting birds such as Cockatiels, habitat imprinting may have additional significance because nest-sites serve both as a nest for eggs and as a stimulus for reproductive activity. Learning the attributes of a nest-site may aid in selecting an appropriate nest-site and in conferring on a nest-site stimulus properties that may later elicit sexual activity.

Hand-rearing clearly affected both male and female Cockatiels, but in different ways. H-males failed to inspect nest-boxes, an event which generally occurs several days in advance of oviposition (Millam et al. 1988). Although the incidence of nest-box use by females was not significantly different in either trial, H-females laid significantly more eggs. This result may not reflect increased reproductive potential because H-females tended to lay eggs on the cage-floor. Because cage-floor eggs were removed, a normal clutch size was never attained; so egg removal probably encouraged laying. Preventing clutch formation by removing eggs from nest-boxes greatly increased egg production in Cockatiels (Millam et al. 1988).

The design of this experiment required force-pairing. The success of force-pairing varies widely among species. In Canvasback Ducks (*Aythya valisineria*), force-pairing generates an increase in male-directed aggression by females (Bluhm 1985) whereas in Ring Doves (*Streptopelia risoria*) force-pairing is a routine husbandry technique of captive management. Force-pairing in Cockatiels produced intermediate results and reflected both the importance of self-selection of mates and their relatively high degree of sociality (Brereton 1963). Judged in terms of

number of eggs, reproductive success was greatest in H-female groups, but in terms of number of fertile eggs, reproductive success was greatest in the P-male groups which were the only two groups to fledge young. Therefore, the efficacy of force-pairing must be assessed differently for different end-points.

Overall, there was a pronounced improvement in reproductive performance in Trial 2, resulting partly from an accelaration in the rate of progression of the sexual cycle. Perhaps more importantly, there was a tendency for the behavioral deficits of hand-rearing to be attenuated by breeding experience. For example, some pairs that laid on cage-floors in Trial 1 used nest-boxes in Trial 2. Likewise, some H-male pairs that were infertile in Trial 1 produced fertile eggs in Trial 2. There appears to be an innate tendency both to nest in a cavity and to mate with a conspecific. The behavioral deficits of hand-rearing were reversible to some degree.

These results may have implications for the captive propagation of cavity-nesting species when birds are to be released into the wild. If natural habitat is supplemented with artificial nest-boxes, for example, reproductive success of released birds may be improved if artificial nest-boxes are of the same design as used during the rearing period. Follow-up studies to assure that released birds have a repertoire of adult sexual behaviors that includes the ability to identify cavities as potential nest-sites are important.

These results demonstrate that rearing conditions from hatch until 7 weeks of age influence adult habitat selection, but a discrete "sensitive" phase has not yet been determined. It is possible that the behavioral deficits in hand-reared birds could be prevented by exposing chicks to nest-boxes and conspecifics at critical times.

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