OPTIMAL OUTBREEDING:
MATE CHOICE OF MALLARDS (*ANAS PLATYRHYNCHOS*)
AND CONSEQUENCES TO BREEDING SUCCESS

by

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ABSTRACT

This study was undertaken to determine if mallards (*Anas platyrhynchos*) use kin recognition during mate choice as a means to achieve optimal outbreeding and to examine the consequences of inbreeding on breeding success. Mallards hatched from eggs collected in the wild were raised and bred to produce ducklings that were either inbred (parents were sibs) or outbred (parents not sibs). Ducklings were raised in isolated subfamily groups so that when sexually mature, they could be tested for mate preference among 4 choices: 1) a sib that was a brood mate, 2) a sib that the subject had not seen before, 3) a first cousin not previously seen, 4) an unrelated individual not previously seen. The initial preference test was inconclusive. In the second mate choice test when the subject and the four choice objects were allowed to interact for 22 hours, neither inbred, outbred females, nor outbred males showed any consistent preference. Inbred males, however, significantly avoided the familiar sister. The results provided no strong support for mallards using kin recognition to achieve optimal outbreeding, but rather suggested kin recognition as a mechanism for severe inbreeding avoidance. Optimal outbreeding in mallards may be achieved via other mechanisms such as female natal site fidelity. Comparison of mate compatibility between pairs of siblings (inbred matings) and pairs of unrelated individuals (outbred matings) indicated that males paired with a sister performed significantly less pre-copulatory head-pumping and were significantly more aggressive to their mates than males paired with an unrelated female. Breeding success was examined by comparing the laying characteristics and fertility of these pairs and comparing the morphological measurements of the resulting ducklings. While fertility was not affected, there

was a 50% reduction in hatchability of eggs from inbred matings. Inbred ducklings also had significantly lighter body mass and shorter extremities at days 15, 30 and 45 post-hatch compared to outbred ducklings. Although inbreeding depression was clearly evident after only one generation of full-sib mating, an occasional brother-sister mating may not seriously reduce the fitness of the population as a whole.

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ACKNOWLEDGEMENT

For my parents ~

CHAPTER 1

GENERAL INTRODUCTION

Inbreeding has been shown to adversely affect breeding success in domestic species (e.g. Cheng *et al.* 1985; Sato *et al.*, 1983, 1984) and juvenile dispersal in natural populations has generally been attributed to the avoidance of inbreeding (e.g. Greenwood *et al.* 1978; Moore & Ali, 1984). In mate choice experiments, domestic Japanese quail (*Coturnix japonica*), when given a choice, preferred first cousins over full-sibs or unrelated individuals as mates (Bateson, 1982). These experiments led to the subsequent interest in kin recognition and the resulting implications on the balance between inbreeding and outbreeding in natural populations (Sherman & Holmes, 1984). In ground squirrels (*Spermophilus tridecemlineatus*), sibling recognition seemed to be mainly due to the fact that they were raised together (Holmes, 1984). Studies of kin recognition in birds have mainly examined song birds and, not surprisingly, kin recognition seems to be through song or dialect (Payne *et al.* 1988).

With the recent proposal by the North American Wildlife Foundation to re-examine the use of hand-reared mallards as a means to replenish wild populations (Ward & Bluhm, 1991; Bluhm & Ward, 1991), the optimal outbreeding issue is again brought to attention. Critics of such a proposal are worried that the released birds, even though hatched from eggs laid by wild stock in captivity, may not have the same genetic variability as naturally occurring wild populations. Repeated releases may result in the disruption of the balance between inbreeding and outbreeding in the wild population (e.g. see Barnard & Fitzsimons, 1989). The study of mate choice with

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reference to genetic relatedness in mallards is therefore relevant to this issue of hand-rearing and release.

Mate choice tests of domestic Japanese quail showed they were more likely to approach a member of the opposite sex which they had not seen before, than one with which they grew up (Bateson, 1980). This observation seems to support the notion that animals generally avoid inbreeding. On the other hand, sibling voles (*Microtus ochrogaster*) raised apart bred more successfully than unrelated voles raised together (Gavish *et al.*, 1984). A study of splendid fairy wrens (*Malurus splendens*), found no evidence that decreased fitness resulted from inbreeding, nor any active avoidance of inbreeding based on kin recognition (Payne *et al.*, 1988) although studies of white-fronted bee-eaters (*Merops bullockoides*) suggest these birds utilize a fairly sophisticated system of kin recognition (Emlen, 1990). The existence of a captive breeding flock of wild mallards at the Delta Waterfowl and Wetlands Research Station near Portage la Prairie, Manitoba provided an excellent opportunity to test Bateson's (1980) hypothesis that kin recognition during mate choice is used to achieve optimal outbreeding in a genetically wild population. At the same time, a mate choice study will provide information needed to address the issue of gene flow between released birds and their wild conspecifics.

If there are ten million wild mallards, and one million hand-reared birds are released each year, it is estimated that by the 7th year, 75% of all mallards will be carrying some genes from the released birds even if only 10% of the released birds survived to enter the breeding population (Merrell, 1973). This calculation, however, is based on the assumption of totally random mating among the wild, released, and "hybrid" mallards. This assumption may not be realistic for two

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reasons: (1) the mallard population in North America may not have a panmictic mating system, and (2) the occurrence of mate choice in mallards.

Several authors (Hochbaum, 1960; Mayr, 1963; Johnsgard, 1968) considered most migratory waterfowl to have a panmictic mating system so there should not be regional variations in the population. However, differences were reported in reproductive parameters measured on mallards from Michigan compared to those from Manitoba, even when the two groups were reared in the same environment and under the same conditions (Batt and Prince, 1978). Although a study of snow geese (*Chen caerulescens*) concluded that a gene flow of close to 50% between geese nesting in different regions would prevent the development of regional differences (Cooke *et al.*, 1975), Endler (1973) listed conditions under which local differentiation could evolve even with considerable gene flow. These results indicated that regional differentiation of gene frequency in the North American mallard population is possible (Rhymer, 1982).

Mate choice studies of game farm and wild mallards indicated that drakes only courted and paired successfully with the type of females (game farm or wild) that they had been reared with (i.e. imprinted on; Cheng *et al.*, 1978, 1979). In a competitive situation, dominant drakes were able to court and stay with the females while the subordinate drakes spent most of their time avoiding the dominant drakes. Females, however, seemed to respond to males that courted them most vigorously, regardless of what type of males they were raised with. That female choice is affected by male courtship and male dominance was confirmed in a subsequent study involving mallards and black ducks (*Anas rubripes*; Brodsky *et al.*, 1988). The results of another study found that female mallards based their mate choice on the male's plumage condition and body size as well as on his courtship activities (Holmberg *et al.*, 1989).

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Despite the many studies of mate choice in mallards (see above), none to date have been conducted in the context of optimal outbreeding. If mallards adjust their mate preferences according to their own degree of inbreeding (i.e. general prediction by Bateson, 1983), then releasing hand-reared birds may not disrupt the balance between inbreeding and outbreeding.

It is, therefore, of interest to address several questions related to mate choice and optimal outbreeding, using captive-reared wild mallards as a model: (1) Do mallards choose their mates based on the degree of genetic relatedness between them and/or on their own degree of inbreeding? (2) Do they distinguish between familiar and novel kin during mate choice? And, (3) if they do mate with close kin, will this immediately lead to inbreeding depression? In Chapter 2, I report and discuss the findings from my study of mate choice in inbred and outbred mallards. In Chapter 3, I report on the consequences of inbreeding in this particular population of mallards.

CHAPTER 2

MATE PREFERENCE AND COMPATIBILITY IN CAPTIVE-REARED WILD MALLARDS

INTRODUCTION

The term *outbreeding* is used to describe matings between unrelated or distantly related individuals (e.g. Russell, 1996). In domestic animal breeding, outbreeding is practiced to take advantage of heterosis (or hybrid vigour) to maximize the animal's performance. In natural selection, "...a certain amount of crossbreeding is favourable but not too much" (Wright, 1933). Bateson (1983) listed the hypothetical costs of inbreeding and outbreeding and discussed them in detail. One genetic cost of outbreeding is that locally adapted genotypes (individual genes as well as linked groups) are lost or suppressed. In addition, there are also other costs such as the longer distance travelled by an individual to acquire a mate, and the possible incompatibility of the partners. The term *optimal outbreeding* is used to describe the optimal balance between inbreeding and outbreeding. Wright's (1933) idea was first explored by Bischof (1972) and Alexander (1977), and was expanded further by Bateson (1978). Natural selection is presumed to have operated on mechanisms involved in mate choice to minimize both sets of costs, so that the outcome is a preference for a mate that is neither too closely related nor too distantly related. Under this principle, Bateson (1982) further predicted that the degree of relatedness of most preferred mate would likely depend on the degree of inbreeding in the population.

Two mechanisms may lead to choice of a mate that is neither a close relative nor totally unrelated. The first is that members of one sex disperse from their natal area prior to breeding, but only so far that their mates are still likely to be distant relatives. The second is that animals are able to recognize close kin by heritable traits (appearance, voice, odour) and using these as measures of genotypic similarity, choose a mate that differs somewhat but not too much from close kin. These two mechanisms are not mutually exclusive; both could operate within a single species (Bateson, 1983).

There is certainly evidence of dispersal in many species (e.g. Greenwood and Harvey, 1982). Although sex differences in dispersal may be explained as a mechanism of inbreeding avoidance, other explanations cannot be excluded (Greenwood, 1980). Bateson (1983) also questioned whether such a system alone would be sufficiently fine-tuned to preserve the balance between outbreeding and inbreeding. Kin recognition, the other potential mechanism for optimal outbreeding, may be more promising (Bateson, 1978). While there have been cases where kin recognition seemed to be an innate process (e.g. Yamazaki *et al.*, 1978), Bateson (1983) argued that kin recognition in most species would be achieved through both filial and sexual imprinting. The ability of an individual to recognize novel kin from other novel individuals must depend on stimulus generalization from a standard acquired during imprinting.

This chapter examines mate choice of male and female mallards to address whether (1) mallards achieve optimal outbreeding by choosing mates with a certain degree of genetic relatedness, (2) inbred mallards make different choices than outbred mallards, and (3) mallards can distinguish familiar kin from their rearing group from novel kin they have never seen before during mate choice. Lastly, assuming they at least occasionally choose kin as mates, are

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breeding pairs consisting of related mates just as compatible as those consisting of unrelated mates?

With these questions in mind, I developed the following working hypotheses:

H_0 1. There is no difference in mate choice whether:

(a) the subject is inbred or outbred

(b) the subject is male or female

H_0 2. Mate choice is not affected by the degree of relatedness between the subject and the choices.

H_0 3. Mate choice is not affected by the degree of familiarity between the subject and the choices.

H_0 4. There is no difference in the reproductive compatibility of mates in inbred matings versus mates in outbred matings.

METHODS

EXPERIMENTAL BIRDS

Two separate experiments were conducted to test mate preference and mate compatibility. The mallards used in the mate compatibility experiment were collected as eggs from the wild in the summer of 1992, and reared in the Gaylord Avicultural Laboratory of the Delta Waterfowl Research Station near Portage la Prairie, Manitoba. After hatching, ducklings were individually identified by numbered web-tags (#5 fingerling tags, National Band and Tag

Co., Kentucky). Birds of the same brood were reared together but in visual isolation from other broods until "fledging" (45 days, Bellrose, 1980). The fledglings were fitted with coloured nasal disks (Doty & Greenwood, 1974) for easy identification, and assigned to one of four large mixed-sex groups of approximately 60 birds each such that brothers and sisters would not be over-wintered in the same group. In April 1993, to obtain the mating pairs required by the compatibility experiment, the four groups were rearranged such that male and female siblings were reunited and opposite sex birds that had been over-wintered together were separated to break up any pair bonds that may have already formed.

The mallards used in the mate preference tests conducted at the University of British Columbia San Rafael Research Aviary in Surrey, British Columbia, were the first generation offspring of the above mallards.

COMPATIBILITY BETWEEN MATES

Observations were conducted twice daily (dawn & dusk) for 7 days to document pair formation (Lebret, 1961) in the recently rearranged groups. Sixteen self-chosen breeding pairs were assigned to the experiment (Table 2.1). Another 16 males and 16 females were "force-paired" by placing two birds in a compartment. These forced pairs consisted of birds which had been observed performing courtship displays (i.e. appeared sexually active) but not toward their assigned partner.

Table 2.1   Experimental design of the compatibility experiment.

pair type	self-chosen	forced
sibling male and female	8 pairs (SS)	8 pairs (FS)
unrelated male and female	8 pairs (SU)	8 pairs (FU)

All 32 pairs were randomly assigned to visually isolated breeding compartments (approx. 1.5 x 2 m), each equipped with a swimming trough (with running water) and a nest box. Twenty-five minute observations were conducted each morning for the next 14 days until all pairs had been observed three times. The following courtship and agonistic behaviours were recorded during the observation period:

(i)   Male (MHP) or female (FHP) performing "pre-copulatory head-pumps" (Weidmann, 1956) alone.

(ii)   Male and female performing pre-copulatory head-pumps together (BHP).

(iii)   Female "inciting" (INC) (Lorenz, 1941; McKinney, 1975).

(iv)   Mounting attempt (MAT) - male grasps female by the nape, with one or both feet on female's back.

(v)   Copulation (COP) - male with both feet on female's back (treading), tail-bends, and subsequently performs post-copulatory display (Johnsgard, 1965).

(vi)   Male pecking female (MPF).

(vii)   Overall male aggression (MAG) - male either pecking (i.e. MPF), chasing, or grasping female by the wing or by the tail.

Approximate distance between the two birds (30 cm apart or less, 30 to 60 cm, 60 to 90 cm, and more than 90 cm apart) was recorded every 5 minutes during the observation period. Nest boxes were checked daily for eggs. When a full clutch was laid (no new eggs for 5 consecutive days), the clutch was removed, artificially incubated, and hatched. Gaylord Avicultural Laboratory protocol was followed for incubating eggs and rearing ducklings (Bluhm *et al.*, 1993). Ducklings hatched were used in the mate preference experiment. At the end of the season, the percentage of females that laid eggs was determined.

For all pairs, the following variables were also recorded: date of first egg; clutch size; and renesting attempt. Eggs set in the incubator were individually identified by pair number, clutch number, and date laid. Eggs were candled and those with no visible development after 1 week of incubation were removed and cracked open to verify infertility (Fant, 1957). The percent fertile eggs of total eggs set and date of first fertile egg were determined.

MATE PREFERENCE

Ducklings of known parentage (from the pairs described in the previous section, as well as others set up for a concurrent experiment, see Chap. 3) were hatched in individual compartments. Before being transferred to the brooder, each duckling within a brood was vent-sexed, web-tagged and randomly assigned to one of two sub-family groups (Fig. 2.1.). Broods were divided in half such that both groups derived from a single brood had approximately the same number of each sex. The two groups of ducklings from each brood were then reared in visual isolation from each other. This arrangement provided siblings which

had been reared together (familiar sibs) and apart (novel sibs) for the preference trials. To provide first cousins, only those broods that had a parent whose sibling was the parent of another brood were used. For cases where the brood was too small to be divided into two groups, the brood was not separated and instead a second brood of ducklings from the same parents was used to provide the test subject with novel siblings. In total, 96 sub-family groups were established using 303 ducklings. Of these groups, 34 had parents who were siblings (inbred matings) and 62 had parents who were unrelated (outbred matings). The sub-family groups were reared without visual contact with other duckling groups until fledging.
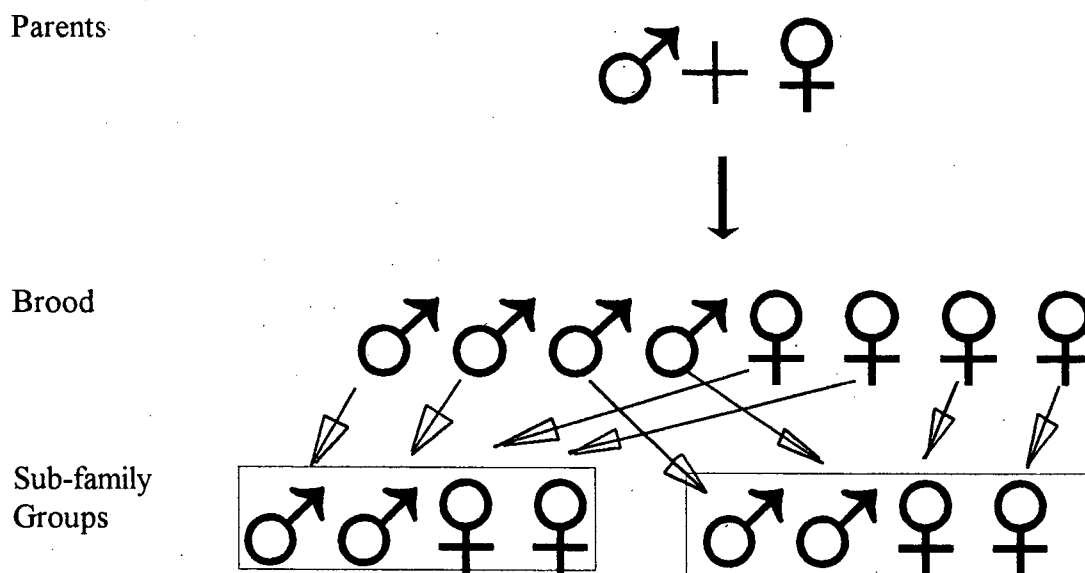
Fig. 2.1   Composition of sub-family rearing groups.

The experimental birds were shipped to the San Rafael Aviary in August 1993, after the youngest had fledged. Males and females were housed separately in two large, visually isolated groups. To prevent the formation of homosexual pairs, each group was provided with birds of the opposite sex, housed in an adjoining pen, to allow visual and auditory interaction but no direct physical contact. These birds were not used in any mate preference trials. All birds were fitted with nasal saddles (supplied by McGraw Game Farm, Dundee, Illinois) for identification. The birds were wing-clipped to prevent injury from in-flight collision with the holding pen walls.

Two tests of mate preference were conducted at the San Rafael Aviary in the spring of 1994. Preference Test I, a test for intial preference, was conducted in early February. Preference Test II, of longer duration, was conducted in late March. Preferences of both males and females were examined. Both preference tests involved four choices:

(FS)   a sibling with which it was reared (familiar sib)

(NS)   a sibling it had never seen before (novel sib)

(C)   a first cousin (cousin)

(U)   an unrelated bird (unrelated)

PREFERENCE TEST I

The number of trials that could be conducted was determined by the number of individuals that had a complete set of a familiar sib, a novel sib, and a cousin, all of the appropriate sex. Originally, 60 males and 43 females fulfilled these requirements.

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Unfortunately, over-winter mortality and avoiding birds in obviously poor condition reduced the sample size considerably. Initial preferences of 31 males and 17 females were tested in early February of 1994. The males comprised 13 inbred and 18 outbred birds; the females, 3 inbred and 14 outbred individuals. Each bird was tested once.

Two pens with four compartments each were constructed (Fig. 2.2), modelled after the design used by Cheng *et al.* (1978). The position of each choice (FS, NS, C and U) was randomized for each trial. For each trial, the choices were placed in their pre-assigned compartments 15 minutes before the subject was introduced into the trial pen. The subject was caught from the rearing pen and placed in an opaque plastic box (approx. 20cm x 20cm x 30cm) positioned at the release point in the trial pen. The subject was released by means of a trap door at the front of the box controlled by the observer in the tower using a string and pulley system.

Trials lasted 60 minutes and observations were recorded with a MacIntosh computer using a program (MateChoice 4.1) developed by Dr. Michael Sorenson of the Smithsonian Institute National Zoological Park. For each trial, all courtship (pre-copulatory head-pumping, female inciting) and aggressive pecking behaviours performed by the subject and choices were recorded. Time spent by the subject in the scoring zones in front of each choice was also recorded (Cheng *et al.* 1978).

Preferences were determined both by analyzing the time spent (minutes) in each zone by ANOVA and by assigning a preference rank. A rank of 1 indicates most preferred (most time spent in that zone) and that of 4, least preferred. Half ranks (i.e. 1.5, 2.5, or 3.5) were assigned to cases where approximately the same amount of time (a difference of <1 minute)

was spent with each of two choices. In 10 trials (8 males and 2 females) the subjects spent <5 minutes total in the scoring zones and those trials were not included in the analysis.
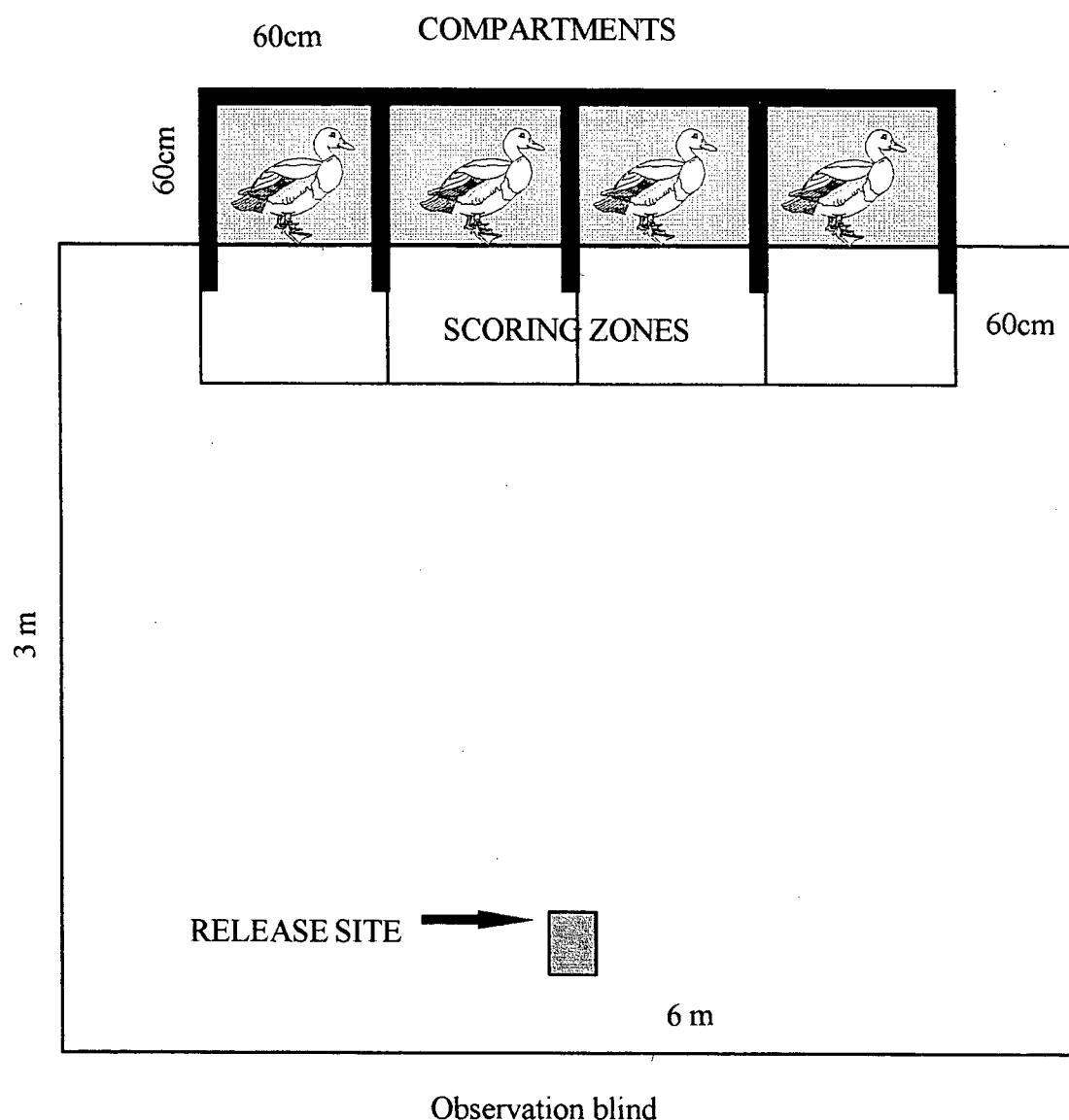
Fig. 2.2   **Observation pen for Preference Test I, a one-hour mate choice test of captive-reared wild mallards (*A. platyrhychos*).**

Mate preference of 19 males (8 inbred, 11 outbred) and 11 females (3 inbred, 8 outbred) was tested in late March of 1994. Each bird was used as a test subject only once in this test but all birds had been previously been subjects in Preference Test I.

The observation pens were wedge-shaped, with the observation tower at the apex and a pond near the base of the wedge (Fig. 2.3). There were three adjacent observation pens available so it was possible to conduct three tests simultaneously. The pens had plywood walls from ground level to 1.2 m high so birds in adjacent pens were visually isolated from each other.
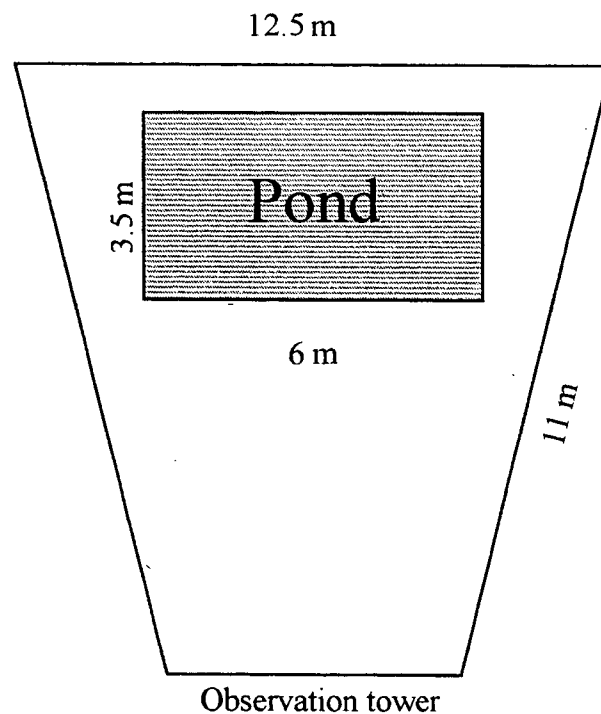
Fig. 2.3   **Observation pen for Preference Test II, an overnight mate choice test of captive-reared wild mallards (*A. platyrhychos*).**

The test subject and four choices (FS, NS, C, and U) were introduced simultaneously into one of the observation pens in mid-morning. Shortly after the birds were introduced, a 10 minute preliminary observation was conducted to see that they were settling in well. The data collected during this observation were not analysed. Observation 1 (30 minutes) was conducted in the early evening of the day the birds were introduced into the pens, and Observation 2 (30 minutes) was conducted early in the morning of the following day. These observations were scheduled to coincide with periods when ducks are more active (Bluhm, pers. comm.). All performances of courtship behaviour (MHP, FHP, BHP, INC, MAT, COP) were recorded.

Every 10 minutes during an observation period, the location of each bird was marked on a diagram of the pen and the distance in map units between the test subject and each of the four choices was later measured. Preferences were determined both by analyzing these distances and by assigning a preference rank as in Preference Test I. The birds were removed from the observation pen following Observation 2.

STATISTICAL ANALYSES

The mean distance between each pair of mates in the compatibility study was calculated from the six estimates recorded during each of three observation periods. During the observation periods, displays of courtship and agonistic behaviour were infrequent. The frequencies of INC, MAT, and COP were extremely low so these variables were not analyzed. The frequencies of FHP, MHP, BHP, MPF, and MAG over the three observation periods were

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summed before being analysed. These behavioural variables and the reproductive variables measured for each pair (date of first egg, clutch size, and percent fertility) were analysed with *PROC GLM* (SAS, 1985) using the following statistical model:

$$Y_{ijk} = \mu + G_i + M_j + (GM)_{ij} + E_{ijk}$$

$$i, j = 1, 2$$

where Y = one of the variables measured, μ = the sample mean, G = mating type (inbred or outbred), M = mate choice (self-chosen or forced), (GM) = the two-way interaction, and E = residual error. Fertility data (percent) were normalized with an arcsine transformation before statistical analysis was performed. The percent of pairs within a group that laid eggs was analysed using paired Chi-square calculations.

Both preference tests were similar to the situation of a taste panel where an individual is asked to rank his/her preferences among several choices; therefore, traditional statistical methods used to analyse taste panel data (Kramer and Twigg, 1970) were used to analyse mate preference. The data collected during preference tests were first analysed with ANOVA (Kramer and Twigg, 1970), then ranked and analysed with Kramer's rank method (Kramer, 1960). This rank test gave equal weight to each trial. While not as powerful as the ANOVA, this test is a non-parametric test that frees the data from assumptions of normal distribution and equal variances, factors which may bias the outcome of the ANOVA (Kramer and Twigg, 1970). Preferences expressed by inbred males, outbred males, inbred females and outbred females were analysed separately.

The data from Preference Test I were analysed using this model:

$$Y_{ijk} = \mu + S_i + R_j + E_{ijk}$$

where Y = minutes spent in a particular scoring zone, μ = the sample mean, S = the effect of a particular subject, R = the effect of the relationship between the subject and the choices (familiar sib, novel sib, first cousin, or unrelated), and E = residual error.

The data from Preference Test II were analysed using this model:

$$Y_{ijk} = \mu + O_i + R_j + (OR)_{ij} + E_{ijk}$$

where Y = mean distance between the subject and one of the choices; μ = the sample mean; O = the effect of observation period I or II; R = the effect of the relationship between the subject and the choices (familiar sib, novel sib, first cousin, or unrelated); (OR) = the two-way interaction; and E = residual error.

RESULTS

MATE PREFERENCE

Males, outbred females and inbred females did not show any significant preference in Preference Test I, but inbred males tended ($P<0.055$) to spend more time with female cousins than with familiar sisters and unrelated females (Fig 2.4). When ranks were considered in Preference Test I, inbred males tended to spend the least amount of time with unrelated females, whereas outbred males tended to spend the least time with familiar sisters (Table 2.2). Neither the outbred nor the inbred females demonstrated any preferences. Courtship (MHP, FHP, BHP, INC) and aggressive pecking behaviours were very infrequent during Preference Test I so were not analysed.

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Outbred Males (N = 14)

Inbred Males (N = 9)

Outbred Females (N = 12)

Inbred Females (N = 3)
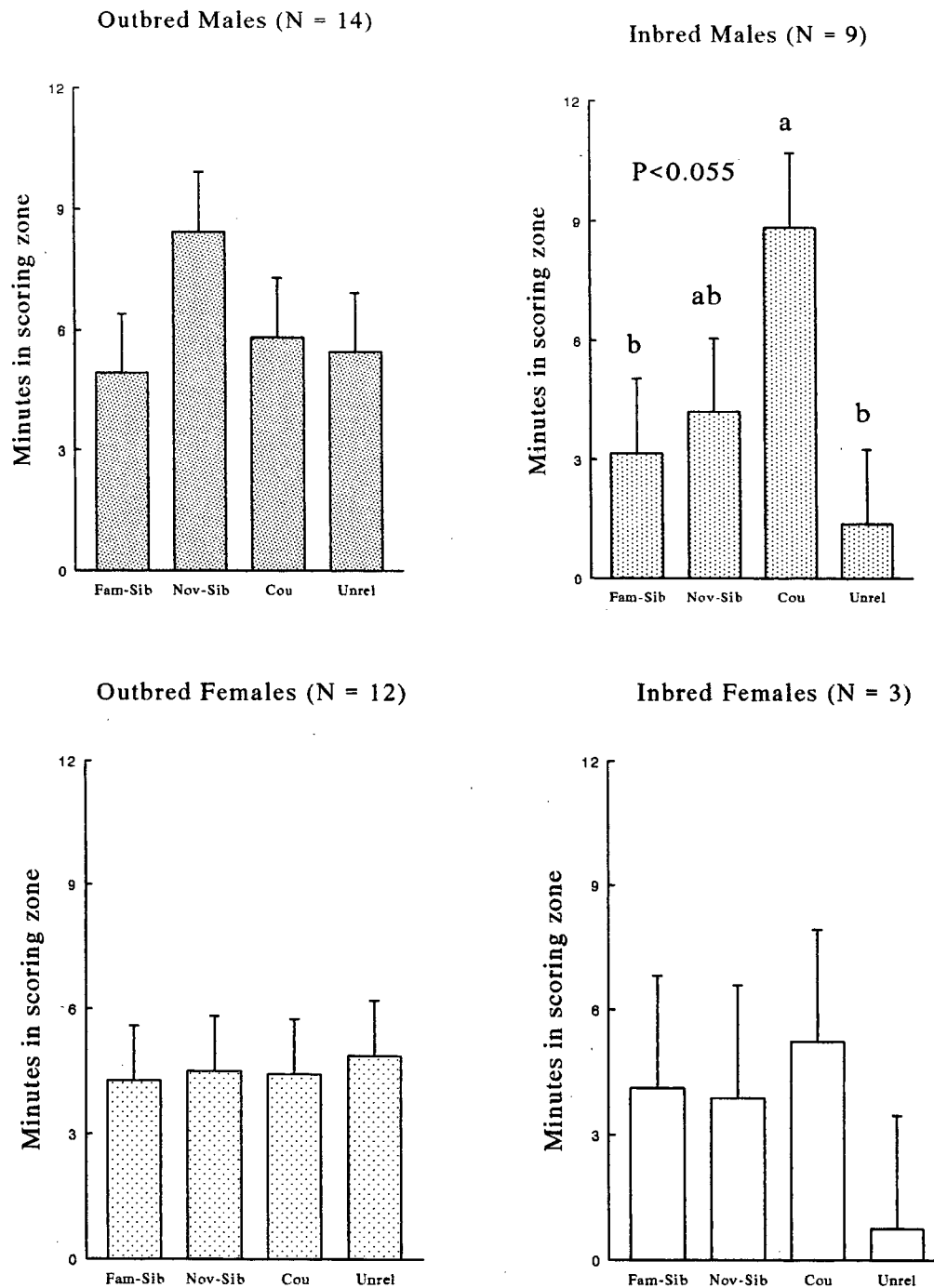
Fig. 2.4 **Mean time (minutes) spent by the subject in the scoring zones of the four choices during Preference Test I, a one-hour mate choice test of captive-reared wild mallards (*A. platyrhynchos*).**
Choices identified by different letters are approaching significance (P<0.055).
Data presented in this figure are given in Table III.i in Appendix III.

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Table 2.2   Accumulated ranks for male mallards in Preference Test I

males (n)	familiar sib	novel sib	cousin	unrelated	test range‡
outbred (14)	44*	28	33	35	26-44
inbred (9)	21	22	17	30*	15-30

‡ The highest or lowest accumulated rank must exceed this range to be significant (P<0.05).
* Approaching significance.

In Preference Test II, outbred males, outbred females and inbred females did not show any significant preference, but inbred males were significantly (P<0.001) closer to novel sisters and unrelated females than familiar sisters and female cousins (Fig. 2.5). There was no significant difference in the mean distance between the subject and the choices between the two observations.

With the rank test for Preference Test II, no significant preference was indicated by the females (either inbred or outbred). For the males, there was no significant preferences indicated during Observation 1; however, during Observation 2, inbred males showed significant preference for novel sibs (P<0.05) over the other choices (Table 2.3).

Table 2.3   Accumulated ranks for male mallards in Observation 2 of Preference Test II.

males (n)	familiar sib	novel sib	cousin	unrelated	test range‡
outbred (11)	26	20.5	32	31.5	19-36
inbred (8)	22.5	9.5*	24	24	13-27

‡The highest or lowest accumulated rank must exceed this range to be significant (P<0.05).
* Significantly preferred.

Outbred Males (N = 11)

Inbred Males (N = 8)
P<0.001

Outbred Females (N = 8)

Inbred Females (N = 3)
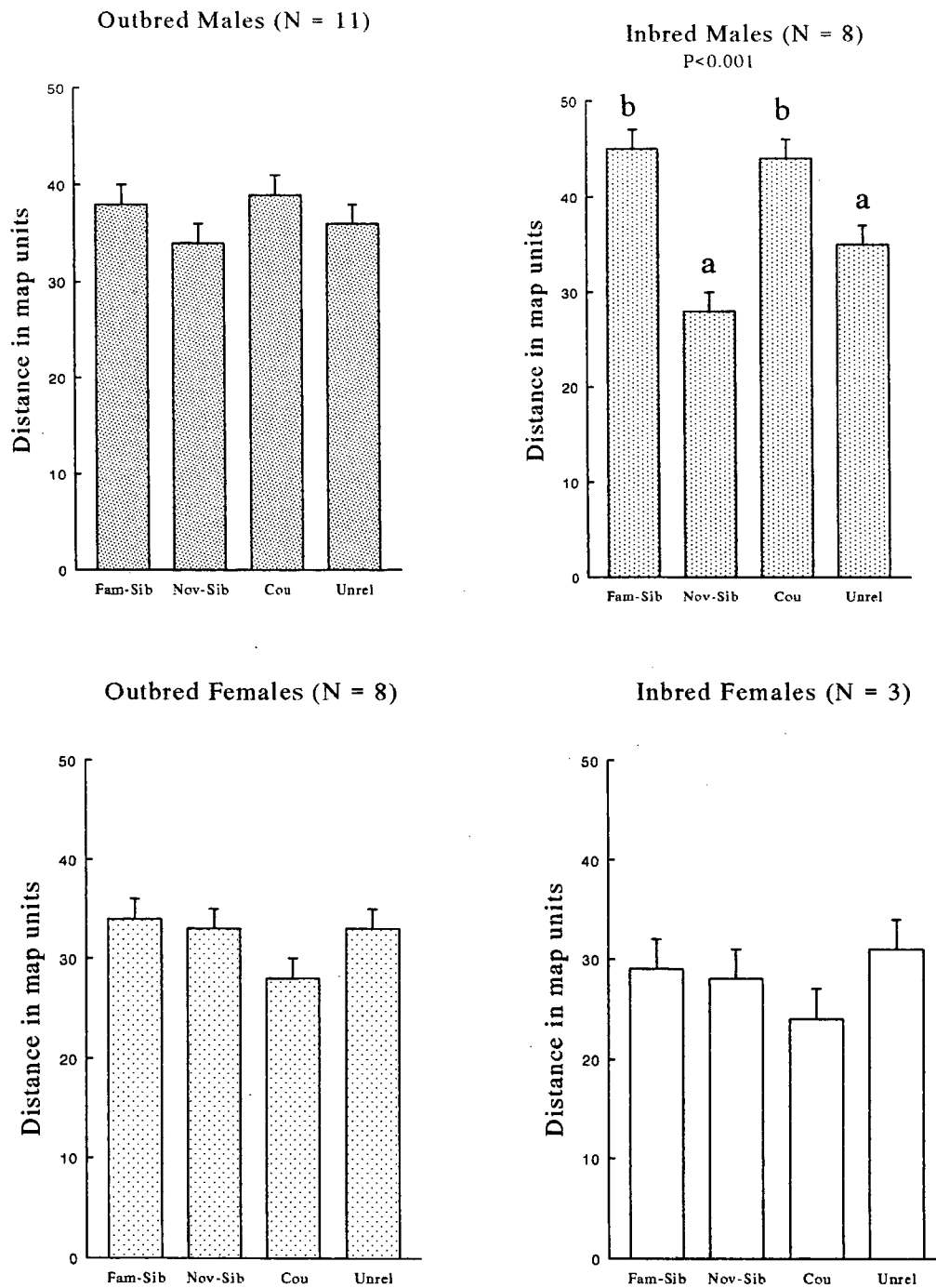
Fig. 2.5   **Mean distance (map units) between the subject and each of the four choices during Observation 2 of Preference Test II, an overnight mate choice test of captive-reared wild mallards (*A. platyrhychos*).**
Choices identified by different letters are significantly different (P <0.001).
Data presented in this table are given in Table III.ii in Appendix III.

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Self-chosen mates performed significantly higher frequencies of simultaneous head-pumping (BHP) than forced pairs (P<0.01) (Table 2.4). Males of forced pairs also pecked their mates significantly (P<0.01) more frequently than did males of self-chosen pairs. There was no significant difference between the two groups in frequencies of female head-pumping (FHP) and male head-pumping (MHP), nor between the two groups in the mean distance between mates measured during the observation periods. Although significantly more females from self-chosen pairs than forced pairs laid eggs (Table 2.5), there was no difference in the date of first egg, clutch size and percent fertility.

Table 2.4. **Frequency‡ of courtship† and aggressive§ behaviours of self-chosen versus forced mallard mates.**

mate type (n)	MHP	BHP	MPF	MAG
self-chosen (16)	1.8 ± 0.5	0.9 ± 0.2*	0.1 ± 0.1*	0.8 ± 0.2
forced (16)	0.9 ± 0.5	0.2 ± 0.2	0.5 ± 0.1	1.4 ± 0.2

‡ Frequency per 25 minutes of observation; least squares means ± s.e.
† Male head-pumping (MHP) and both head-pumping (BHP).
§ Male pecking female (MPF) and overall male aggression toward female (MAG).
* P<0.01

Table 2.5 **Reproductive variables‡ of self-chosen versus forced mallard mates.**

mate type (n)	day of first egg	% that laid	clutch size	% fertility
self-chosen (16)	12 ± 2	88*	11 ± 1	80 ± 20
forced (16)	13 ± 2	50	9 ± 2	60 ± 20

‡ Least squares means ± s.e.
* P<0.05; Chi-square test using actual numbers.

There was no difference in the frequency of courtship between pairs of siblings (both self-chosen and forced, SS and SF) and pairs of unrelated individuals (both self-chosen and forced, SU and FU) except that males from sibling pairs (SS and SF) performed head-pumping (MHP) significantly less frequently (P<0.01) than males from unrelated pairs (SU and FU; Table 2.6). There was also a significant two-way interaction (P=0.02) in overall male aggression towards female (MAG): males of self-chosen unrelated pairs (SU) were significantly less aggressive towards their mates than were males of all other pair types (SS, FS, and FU). There was no significant difference between the two groups in the mean distance between mates measured during the observation periods.

Table 2.6. Frequency‡ of courtship† and aggressive§ behaviours of sibling versus unrelated mallard mates.

mate type (n)	MHP	BHP	MPF	MAG
sibling (16)	0.5 ± 0.5*	0.6 ± 0.2	0.2 ± 0.1	1.2 ± 0.2
unrelated (16)	2.2 ± 0.5	0.5 ± 0.2	0.3 ± 0.1	1.0 ± 0.2

‡ Frequency per 25 minutes of observation; least squares means ± s.e.
† Male head-pumping (MHP) and both head-pumping (BHP).
§ Male pecking female (MPF) and overall male aggression toward female (MAG).
* P<0.01

There was no difference between sibling pairs and unrelated pairs in the 4 reproductive variables measured (Table 2.7). The date of first egg and the date of first fertile egg coincided in all cases except one where only the first egg of the clutch was infertile.

Table 2.7   Reproductive variables‡ of sibling versus unrelated mallard mates.

mate type (n)	day of first egg	% that laid	clutch size	% fertility
sibling (16)	15 ± 2	69	9 ± 1	80 ± 20
unrelated (16)	10 ± 2	69	11 ± 1	70 ± 20

‡ Least squares means ± s.e.

DISCUSSION

In this study, I tested several hypotheses to investigate whether mallards attempt to optimize the balance between inbreeding and outbreeding via mate choice. My results indicated that mate choice is affected by the degree of familiarity between the subject and the choices: males could distinguish a female sib that they had been raised with, from one that they had not seen before. While the results were inconclusive in the first preference test, in the second test, where the birds had a chance to mingle for > 20 hours, inbred males preferred a sister that they had never met before over a sister that they were raised with for the first 6 weeks post-hatch. Because the familiar sib and the novel sib were genetically similar, my results support Bateson's (1983) prediction that kin recognition is achieved through both filial and sexual imprinting (see also Kruijt *et al.*, 1982), rather than by an innate process (Yamazaki et al. , 1978).

The degree of relatedness between the subject and the choices also affected mate preferences: by the end of the second preference test, inbred males were physically closer to novel female sibs than to any other type of female. The apparent ability of the inbred males to differentiate novel kin from other novel individuals could depend on gradient stimulus

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generalization from a standard acquired during filial imprinting (Bateson, 1982). Because inbred males demonstrated a significant preference while outbred males did not, the null hypothesis that there is no difference in mate choice whether the subject is inbred or outbred cannot be accepted. The degree of inbreeding did appear to affect mate choice in this population of wild-stock mallards. The parents of the birds used in these preference tests were hatched from wild eggs and are assumed to be outbred individuals. When they were given an opportunity to choose siblings or unrelated individuals as mates, pair formation occurred both between brothers and sisters and between unrelated individuals.

Avoiding inbreeding by careful selection of a mate may be of more consequence to the inbred males as it seems the outbred males can afford to be less choosy. In a natural situation, male mallards would not be presented with these choices with a gradient of "familiarity". At best, they may fulfill the prediction of "choosing a mate that differed somewhat but not too much from one with which they had been reared" (Bolhuis *et al.*, 1989). It is possible that an inbred male's sibs would be very similar and therefore during filial imprinting, a more clear cut or well defined standard would be generated from which the male could generalize when choosing a mate. The same could not be said for the outbred males: their sibs should be much more variable, resulting in a more fuzzy standard and thus more flexibility in mate choice.

In the early part of the study, I set up self-chosen and forced pairs to test whether the former were more compatible. As expected, males of forced pairs were more aggressive to their mates than were males of self-chosen pairs (Stunden, 1996). There was also less mutual pre-copulatory head pumping (BHP) displayed by the forced pairs and a large proportion of the females of these forced pairs halted their breeding attempt and did not lay any eggs. To a

lesser extent, the males of sibling pairs were also more aggressive to their mates than were males of unrelated pairs. In addition, males of sibling pairs were not as aroused by their mates (significantly less male pre-copulatory head pumping) as were males of unrelated pairs. Hence, my results suggest that not only are self-chosen pairs more compatible than forced pairs, but also that outbred pairs are more compatible than inbred pairs (even if self-chosen). The results of the compatibility test confirm the findings of the mate preference tests that outbred males did not show a strong mate preference; nevertheless, males seemed to be less "enthusiastic" (Bateson, 1983) about their mate when she was a sister.

The overall results provided support for excessive inbreeding avoidance but did not provide strong support for optimal outbreeding. The mallard has holarctic distribution, and environmental conditions for reproduction vary among geographical populations. In North America, female mallards return to their natal grounds to breed (Hochbaum, 1960). The males follow the females they paired with, thus they do not necessarily return to their own natal breeding grounds, yet there still seems to be a restriction in gene flow across different populations because of the female natal-site fidelity. Batt and Prince (1978) reported differences in the onset of laying between females of 2 different geographical origins even though they were compared in the same environment. The mallards' migration pattern may already provide the mechanism to prevent excessive outbreeding and similar facilitation via mate choice may be unnecessary.

The small sample size of three inbred females did not really permit examination of whether the inbred females had any mate preference, although it can be said that the outbred females did not behave differently from the outbred males since neither sex demonstrated a

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significant preference. In the second preference test, the preference of the female, if any, may also be masked by male dominance and competition for a mate (Cheng *et al.*, 1979; Brodsky et al., 1988). Schutz (1965) argued that female mallards were incapable of sexual imprinting because their male parent left them before they hatched and their male siblings had not molted into their breeding plumage by the time the brood dispersed. Kruijt *et al.* (1982) and Cheng *et al.* (1978, 1979) also demonstrated that female mate choice was not based on sexual imprinting. That does not mean, however, that the female is the passive partner during pair formation (Collins, 1994). Cheng *et al.* (1979) observed that under some circumstances, the female may use criteria other than the interest of the drake to pick a mate. Holmberg *et al.* (1989) also found that female mallards based their choice on the male's courtship activities, plumage condition, and body size. More recently, Omland (1995) presented evidence that female mallards may discriminate males based on bill colour and speculum size, possible indicators of health status (see also Mateos & Carranza, 1995, for pheasants; Ligon & Zwartjes, 1995, for jungle fowl; and Buchholz, 1995, for wild turkeys).

CHAPTER 3

EFFECTS OF INBREEDING ON THE REPRODUCTIVE PERFORMANCE

OF CAPTIVE-REARED WILD MALLARDS

INTRODUCTION

In the previous chapter, I provided evidence that mate choice in mallards may reduce

severe inbreeding. Thus, it is of interest to examine the ecological effects of close inbreeding in

this population of mallards to show inbreeding avoidance.

The term *inbreeding* is used to describe matings of genetically related individuals (Hartl

et al., 1988). Individuals are said to be genetically related when their genomes contain genes

that come from a common ancestor. The degree of inbreeding of an individual lies in how

many ancestors are in common and how recently and how many times they appear in the

pedigree (Abplanalp, 1990). It also reflects the degree of homozygosity in the individual's

genome. In animal breeding, inbreeding usually describes the mating of extremely close

relatives (e.g. father-daughter, sister-brother) for several generations in succession. Close

inbreeding is often used to develop lines or strains within a certain breed, but it is believed to

occur only rarely in natural bird populations (Greenwood, 1987).

The term *inbreeding depression* describes the deterioration in fitness or performance of

individuals resulting from inbreeding (Hartl *et al.*, 1988). Many of the adverse effects of

inbreeding are due to the action of deleterious homozygous recessive alleles. Also, because

inbreeding results in greater homozygosity of both dominant and recessive alleles, the beneficial

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effects of over-dominance (where the heterozygous state confers greater advantage than either homozygous state) within the population may be diminished, thus contributing further to inbreeding depression (Falconer, 1960).

Fisher's fundamental theorem of natural selection (Fisher, 1958) predicts that traits that are major components of fitness (such as reproductive traits) contain little additive genetic variance when a population is in relative equilibrium with its environment. Such traits will have been subjected to extensive, prior selection that reduces additive genetic variance and favours the accumulation of non-additive (dominance and epistasis) genetic variance. Inbreeding depression therefore most severely effects fitness traits.

Most data on the effects of inbreeding on reproductive success come from studies of close inbreeding for several generations in domestic species (e.g. Sato *et al.*, 1983, 1984; Chaitanyam and Singh, 1985; Cheng *et al.*, 1985). For example, significant increases in incubation time and a marked deterioration in egg fertility and hatchability, viability and fitness were documented by Sato *et al.*, (1983, 1984) in Japanese quail (*Coturnix japonica*) inbred for four generations by full-sib mating. In contrast, in a study of 10 inbred lines of White Leghorn chickens (*Gallus gallus*), Chaitanyam and Singh (1985) found no effects of inbreeding on egg fertility and hatchability, chick mortality, 10-week body weight, age at sexual maturity and egg weight. However, significant declines in egg production and decreased weight at sexual maturity were observed in the same study. In domestic ducks (*Anas platyrhynchos*), Tai (1985) reported a 35% reduction in fertility, 30% reduction in egg production, and 38% reduction in hatchability when the population reached an inbreeding coefficient of 50%. Cheng *et al.* (1985) documented significantly lower frequencies of several mating behaviours

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by both sexes in an inbred line of White Leghorns as compared to a randombred line. Fertility and hatchability of eggs was also significantly lower in the inbred line. In a population of Great Tits (*Parus major*), significantly higher nestling mortality occurred among inbreeders than among outbreeders (27.7% versus 16.2%; Greenwood *et al.* 1978, 1979). However, in a different population of these birds, although nestling survival was lower for inbred clutches, eventual recruitment into the population was higher for clutches with one inbred parent (Van Noordwijk and Scharloo, 1981). While inbreeding depression can generally be detected, inbreeding studies in natural populations often yield conflicting results because the exact degree of inbreeding may be different in the different populations and the "fitness" traits are either defined or measured differently.

This chapter compares the embryonic and post-hatch development of inbred ducklings arising from full-sib matings to that of outbred ducklings arising from unrelated matings.

METHODS

EXPERIMENTAL BIRDS

Eggs produced by the 32 pairs of breeding birds (8 pairs each of Self-chosen Siblings, Forced Siblings, Self-chosen Unrelated birds, and Forced Unrelated birds) used to study mate compatibility (Chapter 2, p. 8) were used to examine embryonic mortality, percent hatchability, and duckling growth. The Gaylord Avicultural Laboratory protocol for incubation was followed (Bluhm *et al.*, 1993). Additional eggs from another 32 breeding pairs (SU), and eggs

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from 2-year old breeding pairs used for a concurrent study (SS and SU; Stunden, 1996) provided the opportunity to examine the effect of age of parents on duckling development. These additional breeding pairs were kept in similar conditions and fed the same diet as the breeding pairs in my study.

EMBRYONIC DEVELOPMENT

In total, 208 eggs from 23 clutches were incubated to examine embryonic development. Before being incubated, the eggs were measured with calipers to record length and diameter (± 0.02 mm). The eggs were candled weekly during incubation and the following data collected (Cheng *et al.*, 1978; Hanson, 1954): percent early embryonic mortality (fertile eggs dead by day 7 of incubation), percent late embryonic mortality (between day 7 and pipping), and percent pipping mortality (embryos that pipped but died in the shell); percent hatchability (percent of fertile eggs that hatched).

POST-HATCH DEVELOPMENT

Morphological measurements were taken on 302 ducklings (71 hatched from eggs used to examine embryonic development and 231 from eggs obtained from concurrent experiments). Of these, 134 were inbred ducklings arising from matings between full sibs and 168 were outbred ducklings arising from matings between unrelated birds. Mass was measured to the nearest 0.1 g on a *Sartorius I 6800 A* electronic scale, and was recorded four

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times during the rearing period: days 1, 15, 30, and 45. The remaining morphometrics were measured on day 1, and again on day 45, following Baldwin *et al.* (1931). Length of exposed culmen, length of tarsus (tarsometatarsus), and length of middle toe were measured to the nearest 0.02 mm with calipers. Length of (flattened) open wing was measured to the nearest 1 mm with a ruler.

STATISTICAL ANALYSES

Embryonic development was examined using first-clutch eggs, again using PROC GLM (SAS, 1985). I scored percent early embryonic mortality, percent late embryonic mortality, percent pipping mortality, and percent hatchability. These data were normalized with an arcsine transformation before being analyzed with the following model:

$$Y_{ijk} = \mu + G_i + M_j + (GM)_{ij} + E_{ijk}$$

$$i, j = 1, 2$$

where Y = one of the variables measured, μ = the sample mean, G = mating type (inbred or outbred), M = mate selection (self-chosen or forced), (GM) = the two-way interaction, and E = residual error.

Body mass, culmen length, tarsus length, middle toe length and wing length were analysed with PROC GLM (SAS, 1985) using the following statistical model:

$$Y_{ijkl} = \mu + G_i + A_j + S_k + (GA)_{ij} + (AS)_{ik} + (GS)_{jk} + (GAS)_{ijk} + L_{ijkl} + H_{ijkl} + E_{ijkl}$$

$$i, j, k = 1, 2$$

where Y = one of the variables measured; μ = the sample mean; G = mating type (inbred or outbred); A = parent age (1 or 2 years); S = sex of duckling; (GA), (AS), and (GS) = the two-way interactions between these factors; (GAS) = the three-way interaction; L = egg length as a covariate; H = hatch date as a covariate; and E = residual error. The effects of parent age, duckling sex, egg size, and hatch date were included in the ANOVA model for duckling growth to remove these sources of variation and allow a clearer examination of inbreeding effects. The results from the analysis of these factors are presented in Appendices I and II.

RESULTS

Percent early embryonic mortality was significantly (P<0.03) higher in eggs produced by sibling pairs than by unrelated pairs (Table 3.1.). There were no significant differences between sibling and unrelated pairs for percent late embryonic mortality, and percent pipping mortality. Approximately twice as many outbred ducklings hatched (87%) than did inbred ducklings (44%) (P<0.01). Of these progeny, only 3 neonates died: 2 from inbred matings and 1 from an outbred mating.

Table 3.1 **Embryonic mortality‡ and hatchability‡ of eggs produced by pairs of siblings versus unrelated mallards.**

mate type (n)	% early mortality	% late mortality	% pipping mortality	% hatchability
siblings (16)	16 ± 4*	34 ± 8	9 ± 5	44 ± 1**
unrelated (16)	2 ± 5	13 ± 9	4 ± 6	87 ± 2

‡ Least squares means ± s.e.   *P<0.03   **P<0.01

Ducklings from unrelated parents were no heavier than inbred ducklings on day 1 after hatching, but were significantly heavier on days 15 (P<0.04), 30 (P<0.003), and 45 (P<0.0001) (Fig. 3.1.). Thus, they had significantly larger gains in mass from the periods 1-15 days (P<0.04), 16-30 days (P<0.006), and 31-45 days (P<0.001) days (Table 3.2). Although there was no significant difference in morphological measurements between inbred and outbred ducklings on day 1, outbred ducklings had longer tarsi (P<0.02) and greater middle toe (P<0.0001) measurements on day 45 (Table 3.3).
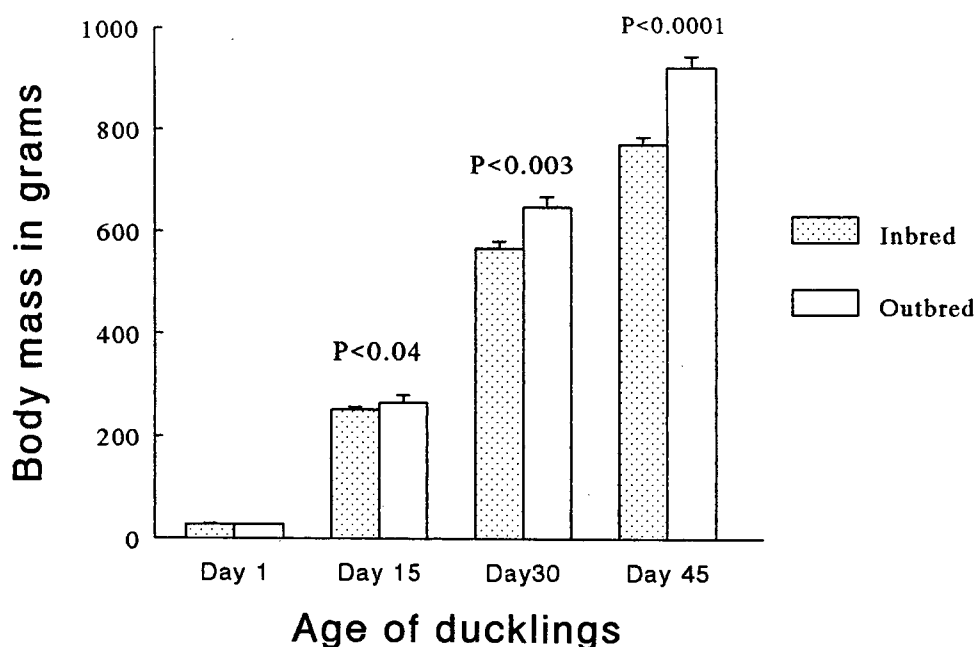
Fig. 3.1. **Effect of brother-sister inbreeding on body mass (g) of captive-reared wild mallard (*A. platyrhychos*) ducklings.**
Data presented in this figure are given in Table III.iii in Appendix III.

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Table 3.2   Effect of inbreeding on body mass gains‡ (g) of captive-reared wild mallard ducklings.

duckling type	1-15 days	16-30 days	31-45 days
inbred	225 ± 5* (85)	294 ± 11** (66)	201 ± 11*** (59)
outbred	239 ± 4 (123)	352 ± 15 (65)	272 ± 15 (75)

‡ Least squares means ± s.e. (n)   *P<0.04   **P<0.006   ***P<0.001

Table 3.3   Effect of inbreeding on duckling morphometrics‡ (mm) at 45 days old.

duckling type (n)	culmen	tarsus	middle toe	wing
inbred (56)	51.0 ± 0.4	59.0 ± 0.3*	62.7 ± 0.3**	188 ± 6
outbred (55)	51.7 ± 0.5	60.5 ± 0.5	65.4 ± 0.4	210 ± 8

‡ Least squares means ± s.e.   *P<0.02   **P<0.0001

DISCUSSION

There is evidence from this study that mallards suffered considerable inbreeding depression even with one generation of full-sib matings. This evidence refutes the null hypothesis that there is no difference in embryonic or post-hatch development of ducklings from inbred matings versus those from outbred matings. While there was no difference in the fertility of eggs from sibling pairs and unrelated pairs (see Chapter 2), there was significantly higher early embryonic mortality and lower hatchability of eggs from the inbred matings. Also, while body mass of inbred ducklings was not different from that of outbred ducklings when measured at 1 day, weight gains were significantly lower and inbred ducklings were significantly smaller throughout the rearing period.

Although the effect of full-sib matings was obvious in these mallards, the inbreeding depression suffered was less drastic than that reported for domestic ducks (Tai, 1985). The results indicated that there is sufficient heterozygosity maintained in this population of mallards that an occasional brother-sister mating would not necessarily result in a severe reduction in fitness. On the other hand, if an individual is already inbred, the benefit to avoid further inbreeding is great because inbreeding depression could be severe if further inbreeding occurs.

CHAPTER 4

GENERAL DISCUSSION

Payne *et al.* (1988) examined splendid fairy wrens and concluded that in these birds, there is no evidence of decreased fitness resulting from inbreeding, nor any active avoidance of inbreeding based on the recognition of kin. I examined whether these observations apply to waterfowl species, using mallards as a model. I also examined whether mate choice can be used by mallards to achieve optimal outbreeding, as predicted by Bateson (1982). My data indicated that at the individual level, inbreeding could reduce a mallard's reproductive fitness by over 50%, mostly through embryonic mortality. Whether inbreeding has an impact at the population level will depend on the frequency of mating of close kin. Inbred males in my study used mate choice to avoid mating with sibs but non-inbred males did not seem to avoid mating with close kin. However, because only the inbred males developed inbreeding avoidance, perhaps the Manitoba mallards are not adversely affected by occasional inbreeding.

Unfortunately, I could not use novel siblings in the test of mate compatibility, but it seems probable that the problems of behavioural compatibility between siblings are likely the result of familiarity, so that these problems would not be apparent between novel sibling mates. Of course, problems of genetic incompatibility (e.g. embryo mortality, etc.) would still be evident in matings between novel siblings, but, as discussed above, matings between sibling mallards would be unlikely under natural circumstances because only familiar siblings would be available.

My data also did not support Bateson's prediction (1982) that mate choice results in optimal outbreeding. Bateson (1983) suggested that as the level of inbreeding in the population increased, individuals would be more and more similar to one another and, based on the same gradient of generalization from a standard (template) obtained from filial imprinting, individuals would choose more distant relatives and non-kin as mates. Conversely, as the level of inbreeding decreased, individuals with the same relatedness would be more different than one another and closer related individuals would be chosen as mates. Thus the population would maintain its balance of inbreeding/outbreeding.

An aspect that was not considered is that at a given level of inbreeding of the population, individuals or families vary greatly in their inbreeding coefficients and thus differ significantly from the average inbreeding for that population. This situation is quite unlike that of a laboratory population where the same mating system (e.g. random, full-sib, half-sib, or parent-young mating) is applied to all members of the breeding group. I propose that, at least in mallards, members of an inbred family are more similar, and filial imprinting results in a more clear cut or definite standard for the individuals to use in mate choice. Consequently, the inbred male is able to "choose a mate that differed somewhat but not too much from one with which he had been reared". In a randombred or outbred family, family members are more variable which could result in a less clear cut standard from imprinting and more flexibility in mate choice.

In developing hypotheses for future research, we must distinguish between inbreeding at the population level and inbreeding at the individual level. Bateson (1983) is concerned that a system in which individuals choose a mate that differ somewhat but not too much from one

with which they had been reared would only slow down inbreeding and would not maintain the desirable degree of inbreeding. But as he has also pointed out other mechanisms, such as dispersal, can also play a part in maintaining optimal outbreeding. In the case of the mallards, natal site fidelity exhibited by females and not by males may be one such mechanism. Hypothetically, a system in which (1) males show filial and sexual imprinting to ensure mating with females of the same species while avoiding severe inbreeding, and (2) females show natal site fidelity and discriminate males based on dominance and health status (Holmberg *et al.* 1989; Omland, 1995), would be very efficient with minimum duplication of effort. Such system may be a good candidate for an evolutionarily stable strategy (ESS) and certainly warrants further examination.

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THE EFFECTS OF OTHER FACTORS ON DUCKLING GROWTH

The effects of duckling sex, egg size, hatch date, and parent age were included in the ANOVA models for duckling growth to remove these sources of variation and allow a clearer examination of inbreeding effects. The effects of these other factors are presented below.

RESULTS

DUCKLING SEX

Differences in body mass which were not apparent at hatch became obvious in later measurements with male ducklings being heavier than females on days 15 ($P<0.01$), 30 ($P<0.0001$), and 45 ($P<0.0001$) (Table. I.i) and having greater gains from periods 1-15 days ($P<0.01$), and 16-30 days ($P<0.004$) (Table I.ii). Males had shorter culmen ($P<0.0001$), tarsus ($P<0.0001$), but longer middle toe ($P<0.0001$) measurements on day 45 than did females (Table I.iii).

Table I.i   **Sexual dimorphism in body mass† (g) of captive-reared wild mallard ducklings.**

sex	1day	15 days	30 days	45 days
male	28.4 ± 0.3 (140)	268 ± 4* (111)	643 ± 14** (74)	904 ± 16** (67)
female	28.6 ± 0.3 (136)	252 ± 5 (97)	574 ± 14 (71)	790 ± 16 (69)
†least squares means ± s.e. (n)		* P<0.01	**P<0.0001	

Table I.ii   **Sexual dimorphism in body mass gains† (g) of captive-reared wild mallard ducklings.**

sex	1-15 days	16-30 days	31-45 days
male	224 ± 5* (111)	346 ± 11** (68)	254 ± 11 (67)
female	240 ± 4 (97)	300 ± 12 (63)	219 ± 11 (67)

†least squares means ± s.e. (n)   *P<0.01   **P<0.004

Table I.iii   **Sexual dimorphism in morphometrics† (mm) of captive-reared wild mallared ducklings at 45 days old.**

sex (n)	culmen	tarsus	middle toe	wing
male (55)	53.0 ± 0.4**	61.3 ± 0.3**	65.6 ± 0.3**	203 ± 6
female (56)	49.7 ± 0.4	58.2 ± 0.3	62.6 ± 0.3	195 ± 6

†least squares means ± s.e.   ** P<0.0001

EGG SIZE

Egg length was positively correlated with all morphological measurements of 1 day old ducklings (mass, culmen length, tarsus length, middle toe length and wing length) (P<0.0001). Egg length was also a significant co-variate of gain in mass from 1-15 days (P<0.0001) and mass on days 15 (P<0.0001), 30 (P<0.03), and 45 (P<0.03). Even at 45 days of age, egg length was a significant co-variate of middle toe length (P<0.02) and wing length (P<0.0002).

HATCH DATE

Hatch date was negatively correlated with mass on days 1 (P<0.03), 30 (P<0.0001) and 45 (P<0.0001). It was also negatively correlated with gain 30 (P<0.0001) and gain 45

(P<0.008). Hatch date also affected morphometrics of ducklings at 1 and 45 days. Both tarsus and wing length on day 1 were positively correlated with hatch date (P<0.0001). On day 45, culmen length was negatively correlated with hatch date (P<0.02) and wing length was positively correlated with hatch date (P<0.0001).

AGE OF PARENTS

Even corrected for egg size and hatch dates, progeny of 2 year old parents were significantly heavier than that of 1 year old parents on day 1 (P<0.0001) but significantly lighter on day 15 (P<0.05) (Table I.iv). However, gain in mass was significantly different only in periods 1-15 days (P<0.02), and 31-45 days (P<0.02) (Table I.v). Progeny of 2 year old parents had longer tarsus and middle toe measurements on days 1 (P<0.01, P<0.0005) (Table I.vi.) and 45 (P<0.03, P<0.002) (Table I.vii).

Table I.iv   **Effect of parent age on body mass† (g) of captive-reared wild mallard ducklings.**

parent age	1day	15 days	30 days	45 days
1 year	27.6 ± 0.3** (141)	264 ± 4* (125)	605 ± 12 (88)	811 ± 14 (82)
2 years	29.3 ± 0.3 (135)	251 ± 5 (83)	589 ± 18 (57)	856 ± 21 (54)

†least squares means ± s.e. (n)   * P<0.05   ** P<0.0001.

Table I.v   **Effect of parent age on body mass gains† (g) of captive reared wild mallard ducklings.**

parent age	1-15 days	16-30 days	31-45 days
1 year	235 ± 4* (125)	336 ± 14 (88)	204 ± 12* (80)
2 years	221 ± 5 (83)	378 ± 20 (43)	264 ± 17 (54)

†least squares means ± s.e. (n)   * P<0.02

Table I.vi   **Effect of parent age on morphometrics† (mm) of captive-reared mallard ducklings at 1 day old.**

parent age (n)	culmen	tarsus	middle toe	wing
1 year (105)	14.9 ± 0.1	26.1 ± 0.2*	25.9 ± 0.2**	37.4 ± 0.2
2 years (51)	14.8 ± 0.2	27.0 ± 0.3	27.1 ± 0.2	37.7 ± 0.4

†least squares means ± s.e.   * P<0.01   **P<0.0005

Table I.vii   **Effect of parent age on morphometrics† (mm) of captive-reared wild mallard ducklings at 45 days old.**

parent age (n)	culmen	tarsus	middle toe	wing
1 year (73)	51.6 ± 0.4	58.8 ± 0.3*	62.8 ± 0.3**	203 ± 5
2 years (38)	50.8 ± 0.6	60.7 ± 0.5	65.4 ± 0.5	203 ± 9

†least squares means ± s.e.   * P<0.03   **P<0.002

DISCUSSION

SEXUAL DIMORPHISM AND GROWTH

Although there is no difference between males and females in mass at 1 day of age, males are significantly larger when measured on days 15, 30, and 45. These results agree with those of Rhymer (1982) who conducted her studies on a similar population of mallards. Sexual dimorphism was found in all growth parameters measured by Knizetova et al. (1991) in a recent comparative study of 10 lines of domestic ducks. That sexual dimorphism in mass and morphometrics is not readily apparent at hatch has been previously documented in wild birds; recent examples include boat-tailed grackles (*Quiscalus major*; Bancroft, 1984), gadwall (*Anas strepera*; Blohm, 1987), black skimmers (*Rynchops niger*; Schew and Collins, 1990), and

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shelducks (*Tadorna tadorna*; Duettmann, 1993). Sexual dimorphism in growth has been documented in many bird species (e.g. Bancroft, 1984; Schew and Collins, 1990; Husby, 1991).

EGG SIZE AND GROWTH

As expected, egg length was a highly significant covariate of all morphometric measurements, including mass. That larger eggs result in larger hatchlings is a relationship that has long been recognized (Pinchasov, 1991; Davis, 1975); that egg size has a significant effect on morphometrics and mass of wild-stock mallards even to 45 days post-hatch has not been documented. Researchers studying domestic chickens have found that the correlation between egg size and body mass diminished after hatching but reported rates were quite variable. For example, Pinchasov (1991) reported that correlation between egg size and mass of broiler chicks became nonsignificant by day 5 after hatching, while Wyatt *et al.* (1985) reported significant correlation even at market age (7 weeks). In wild birds, while there have been many studies of relationship between egg size and fledging success or offspring mortality (Sæther, 1990; Rhymer, 1982), reports of correlations between egg size and body mass at different ages are scant (Davis 1975; Sydeman & Emslie, 1992). Whitehead *et al.* (1990) recently reported that larger magpie goose (*Anseranas semipalmata*) hatchlings from large eggs tend to maintain a size advantage, at least until fledging.

HATCH DATE AND POST-HATCH DEVELOPMENT

Hatch date was significantly and negatively correlated with body mass at all ages measured, but was positively correlated with tarsus length at day 1 and wing length at days 1 and 45. The negative relationship between hatch date and fledging success has been documented in several seabird studies (Harris *et al.*, 1994; Spear and Nur, 1994; Harris *et al.*, 1992; Perrins, 1966; Sullivan, 1996), with decreased food availability or environment quality often cited as likely explanations. In my study, where food was available *ad libitum*, ducklings hatching later in the season had a smaller fledging mass than those hatching earlier, but their wings developed faster. Smart (1965) found that primaries of late-hatched Redheads (*Aythya americana*) emerged a week earlier than those of early-hatching ducklings, and, consequently, late hatchers fledged at a younger age. It may be advantageous for late-hatching ducklings to develop faster than those hatching earlier and in order to develop the necessary flying skills before fall migration (Lightbody & Ankney, 1984). Janiga (1992) found that for feral pigeons in Slovakia, squabs hatched in the summer grew faster but feathered slower compared to squabs hatched in the winter. Ricklefs (1979) suggested that growth rate is inversely related to the rate of acquisition of mature function of tissues and that the rate of acquisition of flight may be limiting growth rate. My data seem to support this hypothesis. A likely candidate to facilitate the difference in development would be the pineal hormone, melatonin, the level of which changes with changing day length and has been found to affect many organs and tissues directly and indirectly (Reiter, 1991; and Cheng *et al.*, 1994). In many species of fish, it has been found that, independent of other environmental factors such as temperature, changing

photoperiod (both in rate and in direction) had profound effect on growth pattern (Jobling, 1994).

AGE OF PARENTS

A review by Martin (1995) acknowledges that the majority of bird species exhibit age-dependent survival and reproduction, with young birds or first time breeders performing at a lower and slower rate than older individuals (Batt & Prince, 1978; Bruggers & Jackson, 1981; Curio, 1982). Stunden (1996) also found that at the beginning of the breeding season, yearling mallard drakes did not differ in body weight from 2 year-old drakes, but yearling females were significantly lighter than 2 year-olds. Pairs where both partners were yearlings had lower fertility than 2 year-old pairs. However, there was no difference in egg size or clutch size, and, after the first clutch, yearling females gained weight and weighed the same as 2 year-olds. In many bird species, breeding success of older females is better than that of very young females (Lack, 1966; Sæther, 1990), not only in terms of bigger and more clutches, better fertility and hatchability, but also in heavier fledglings which survive better. Most researchers explain this phenomenon by pointing out that older females lay bigger eggs and have more experience and better resources (see Sæther, 1990). Although Martin's (1995) review did not specifically address the effects of parent age on offspring growth, she writes that "despite the fact that extensive numbers of papers suggest age-dependent foraging ability may explain age-dependent reproduction, it has been problematic to demonstrate whether or exactly how foraging ability or physiological maturation varies with age of breeding individuals. Likewise, many studies

invoke 'experience' as the reason for improvements in reproduction with advancing age. But surprisingly, observational and experimental studies have shown convincingly that previous breeding experience per se (independent of age) does not result in improved reproductive success."

Parental age affected variation in mass and morphological measurements of ducklings in this study. Even after correcting for egg size and hatch date, ducklings of 1 year old parents reared in the same environment with the same *ad libitum* feed were significantly smaller (smaller mass, shorter tarsus and middle toe) at 1 day than those of two year old parents. However, they grew faster during the first two weeks in life and were actually heavier at 15 days than ducklings from 2 year old parents. By day 45, there was no difference in body mass between the two types of ducklings This difference in growth pattern has not been previously documented in mallards and clearly shows that ducklings from 1 year old parents develop faster than those from 2 year old parents. The ducklings raised in this study were taken as eggs from their parents' nest boxes, then incubated artificially and raised in the avicultural laboratory. Both parents and ducklings were provided with *ad libitum* feed and water. Given these conditions, it should be obvious that parental foraging ability or previous breeding experience cannot account for the variation in duckling mass and morphometrics attributed to parent age. If these differences can be confirmed by further research, they will shed new light on current theories regarding optimal breeding age and parental investment.

APPENDIX II

THE EFFECTS OF PARENT AGE AND MATING TYPE ON EGG SIZE

STATISTICAL ANALYSES

The width and length measurements of eggs were analysed using *PROC GLM* (SAS, 1985) with the following statistical model:

$$Y_{ijk} = \mu + G_i + Aj + (GA)_{ij} + E_{ijk}$$

$$i, j = 1, 2$$

where Y = one of the variables measured, μ = the sample mean, G = mating type (inbred or outbred), A = parent age (1 or 2 years), *(GA)* = the two-way interaction, and E = residual error.

RESULTS

As expected, 2 year-old females laid slightly larger (~2% longer and wider) eggs than did 1 year old females (Table II.i). Unexpectedly, females mated to their brothers laid longer eggs than females mated to unrelated males. Furthermore, there was an interaction between parent age and mate type: the diameter of eggs laid by 2 year old females mated to their brothers was larger than those from 2 year old females mated to unrelated individuals ($P<0.03$) but no such difference was observed with one year old birds (Table II.ii).

Table II.i   **Size‡ (mm) of eggs laid by 1 and 2 year old female mallards.**

age of female (n)	egg length	egg diameter
1 year (140)	56.2 ± 0.03*	40.1 ± 0.1**
2 years (142)	57.3 ± 0.2	41.2 ± 0.1

‡ Least squares means ± s.e.   *P<0.002   **P<0.0001

Table II.ii   **Effect of the interaction‡* between age and mate type on egg diameter (mm).**

age of parents	sibling mates	unrelated mates
1 year	40.1 ± 0.2a (39)	40.2 ± 0.1a (103)
2 years	41.6 ± 0.2c (83)	40.8 ± 0.2b (57)

‡ Least squares means ± s.e. (n)
* Means followed by different letters are significantly different (P<0.03)

DISCUSSION

In my study, 2 year old females mated to their brothers laid eggs with a larger diameter than 2 year olds mated to an unrelated male. This difference was not observed in 1 year olds. A careful look at the records indicated that about 50% of the eggs from 2 year old, inbred pairs were second clutch eggs, whereas nearly all of the eggs from 1 year old pairs, as well as 2 year old outbred pairs were either first or third clutch eggs. Stunden (1996) found that in this population, eggs from second clutches were significantly larger than eggs from first and third clutches. This may well explain the unexpected association found in my study.

TABULATED DATA

Table III.i   Mean time† (min) spent by the subject in the scoring zone of each choice during Preference Test I.

subject	n	familiar sib	novel sib	cousin	unrelated	s.e.
outbred male	14	4.92	8.44	5.82	5.46	1.47
inbred male*	9	3.15b	4.18ab	8.84a	1.36b	1.87
outbred female	12	4.27	4.50	4.43	4.88	1.32
inbred female	3	4.12	3.88	5.24	0.76	2.70

† Least squares means.
* Means with different letters are approaching a significant difference (P<0.055).

Table III.ii   Mean distance† (map units) between the subject and each of the four choices during Preference Test II.

subject	n	familiar sib	novel sib	cousin	unrelated	s.e.
outbred male	11	38	34	39	36	2
inbred male*	8	45b	28a	44b	35a	3
outbred female	8	34	33	28	33	2
inbred female	3	29	28	24	31	3

† Least squares means.
* Means followed by different letters are significantly different (P<0.001)

Table III.iii   Effect of inbreeding on body mass† (g) of captive-reared mallard ducklings.

duckling type	1 day	15 days	30 days	45 days
inbred	28.7 ± 0.3 (122)	253 ± 5* (85)	567 ± 14** (65)	771 ± 16*** (61)
outbred	28.3 ± 0.3 (154)	267 ± 14 (123)	649 ± 20 (80)	923 ± 22 (75)

† Least squares means ± s.e. (n)   * P<0.04   ** P<0.003   *** P<0.0001