

## FORCED COPULATION IN CAPTIVE MALLARDS (*ANAS PLATYRHYNCHOS*): II. TEMPORAL FACTORS

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**Abstract.** A study of temporal trends in forced copulation was conducted in flight-pens with eight pairs of captive mallards to test the hypothesis that forced copulation is an evolved breeding strategy in waterfowl. Significantly more forced copulation attempts were directed at females during egg-laying than during the non-laying period preceding laying, and few forced copulations occurred after the laying of the last egg of the clutch. Most forced copulations occurred in the morning when the females were leaving the nests after egg-laying. Thus, forced copulations occurred at times when fertilization was most likely to result, supporting the insemination strategy hypothesis.

Pair-bonding is characteristic of mating systems in all tribes of Anatidae with only a few exceptions (Heinroth 1911; Delacour & Mayr 1945; Kear 1970). Males perform pair copulations, which are typically preceded and followed by characteristic displays (Johnsgard 1965). In many species of ducks, however, paired males also pursue other females and forcibly copulate with them (McKinney et al., in press). Heinroth (1911) believed that in species such as the mallard (*Anas platyrhynchos*), males are combining pair-bonding with promiscuity in what Trivers (1972) has called a 'mixed male reproductive strategy'. The idea that forced extra-pair copulations<sup>1</sup> could contribute significantly to the fertilization of eggs gained support from Smith's (1968) finding that in northern pintails (*A. acuta*), pursuits by males after females peaked in frequency immediately before and during the egg-laying period. Similar observations were made by Barrett (1973) and Cheng et al. (1979) on captive mallards and by McKinney & Stolen (1982) on captive green-winged teal (*A. crecca*). Recently, Burns et al. (1980) showed that eggs of captive mallards can be fertilized by forced copulation (FC).

In order to test further the hypothesis that paired males of these species of dabbling ducks

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<sup>1</sup>Waterfowl ethologists have generally followed Lorenz (1951-53) in calling this behaviour 'rape'. Although apt and convenient, this term has moral and legal implications and sensational overtones that many people find objectionable. If this behaviour proves to be an evolved reproductive strategy of males in certain species, it seems better to use a neutral, descriptive term free from anthropomorphic implications (e.g. Gladstone 1979; Fujioka & Yamagishi 1981).

are adopting a mixed reproductive strategy, we predicted that forced copulation attempts should (a) be directed primarily at females in pre-laying and laying condition, and (b) be most frequent at times of day when the chances of successful fertilization are highest. These predictions were tested in the following study of captive mallards.

### Methods

#### Flight-pen Study

This study was carried out concurrently with the experiment reported by Burns et al. (1980). In April 1978, two pairs of a wild-type male and dusky female (WM+DF) mallard combination and two pairs of a dusky male and dusky female (DM+DF) combination were introduced into each of two adjacent flight-pens each measuring 27.5 m × 27.5 m × 3.6 m high with a large centre pond and four peninsulas, allowing space for all pairs to set up small breeding territories (described in McKinney 1967). The dusky trait is a recessive plumage mutation (Jaap 1934; Lancaster 1963), and was used as a genetic marker for determining paternity of the progeny in the study reported by Burns et al. (1980). The birds had been allowed to pair during the previous winter by free choice of mates. Each bird was individually marked with a coloured nasal saddle (Doty & Greenwood 1974) so that it could be identified from the blind overlooking both flight-pens.

From 17 April to 21 June, 1978, we made daily 3-h observations starting at sunrise. Whole-day observations (from sunrise to sunset) were also carried out on 17 May, 25 May, and 3 June, during the peak of the breeding season.

All major interactions (e.g. chases, pair copulations, and forced copulation attempts) and nesting activities of each female were recorded.

In the case of each male-female pursuit, we noted the position of the female at the beginning of the chase and the incidence of (a) bodily contact between the chaser and the female, (b) grasping by the pursuing male of some part of the female with his bill, (c) mounting, (d) bending of the male's tail around one side of the female's tail, (e) thrusting by the male following tail-bending, and (f) post-copulatory displays by the male during or after dismounting.

The pens were inspected every other day for nests and eggs. Eggs laid by the females were collected, labelled, and replaced with wooden dummy eggs. The dummy eggs were removed and the nest destroyed on the third or the fourth day after the clutch was completed to encourage re-nesting. After laying their third clutches, females were allowed to incubate the dummy eggs until the end of the experiment.

#### Data Analyses

For the purpose of data analyses, the days within a clutch cycle of a female were labelled. The first egg of the clutch was laid on day zero (0). Previous days (—) were counted backwards and days thereafter were given positive values (+). The latter were the days when the female was laying or starting to incubate, and the total number of days in a clutch cycle varied from female to female and from clutch to clutch. The day after each clutch was removed became the first 'negative day' for the next clutch.

All pursuits in which a female was chased by a male (or males) other than her mate were included in the statistical analyses. Chases were classified in six categories depending on the outcome. These categories represent progressive stages leading up to forced copulation and we use them to allow separate analyses of chases in which the male's 'intention' was unquestionably to attempt forced copulation (i.e. mounting occurred) from those chases for which other interpretations are possible (i.e. mounting did not occur).

The six categories are: (1) All; all chases of a female by a male other than her mate. (2) Contact; there was bodily contact between male and female. (3) Grasp; some part of the female was grasped in the male's bill. (4) Mount; the male mounted the female's back. (5) Tailbend; the male mounted and bent his tail around the female's tail. (6) Forced copulation (FC); after tailbending, the male performed a pronounced copulatory thrust, remained in this posture briefly, dismounted and swam or walked away,

usually tail-wagging as he left. In the following text and tables, FC refers only to a male-female chase that ended in apparently successful copulation; a male-female chase in which there was contact but the male did not succeed in copulating, or a chase of this kind in which the outcome was uncertain, is referred to as an 'FC attempt'.

Thus each category of chases was not mutually exclusive but a subset of the previous category. Data from each category were summarized and expressed as frequency of chases per female per observation period (3 h). The six categories were analysed separately using the Least-Squares Method outlined by Harvey (1975) with the aid of a computer program (Program No. An. Sci. IBM/360-LSA 10 and CDC/6600-LSA 10, St. Paul; University of Minnesota Computer Center). Such procedure considers all effects simultaneously to free these effects from confounding due to disproportional subclass frequencies. The general statistical model is:

$$Y_{ijklmnp} = \alpha + F_{ij} + P_j + L_k + C_l + S_m + O_n + E_{ijklmnp}$$

and  $i = 1, 2, 3, 4$ ;  $j = 1, 2$ ;  $k = 1, 2, 3, 4$ ;  $l = 1, 2, 3, 4$ ;  $m = 1, 2$ ;  $n = 1, 2, 3$ ; where  $Y_{ijklmnp}$  = one of the six dependent variables (All, Contact, Grasp, Mount, Tailbend, or FC).  $Y_{ijklmnp}$  is the frequency of chases of the  $i$ th female in the  $j$ th pen, in the  $k$ th stage of her  $l$ th clutch, observed by the  $n$ th observer during the  $p$ th observation period,  $\alpha$  = the theoretical population mean,  $P_j$  = effect of the  $j$ th pen,  $F_{ij}$  = effect of the  $i$ th female in the  $j$ th pen,  $L_k$  = effect of the  $k$ th laying period (see Results section for designation of the four periods),  $C_l$  = effect of the  $l$ th clutch,  $S_m$  = effect of whether the female has laid the last egg of the clutch,  $O_n$  = effect of the  $n$ th observer, and  $E_{ijklmnp}$  = random error.

#### Results

##### Differences Between Different Periods Within a Clutch Cycle

Data were summed over 24 clutches of eggs (eight females, each with three clutches). We divided the days within each clutch cycle into four periods for comparison:  $L_k$ ,  $k = 1, 2, 3, 4$  where (1) = the non-laying period (days — 13 to — 7); (2) = the pre-laying period (days — 6 to — 1; female exhibits nest-searching activities, gives 'persistent quacking' (Abraham 1974; McKinney et al. 1978), and makes nest scrapes during this time); (3) = laying period (days 0 to 10; female lays one egg a day during part or all

Table I. Mean Number of Chases Per Female Per 3-h Observation Period During Different Periods of the Clutch Cycle

Chases	Periods			
	Non-laying	Pre-laying	Laying	End-of-clutch
	Days: - 13 to - 7	- 6 to - 1	0 to 10	11 to 18
	N: 41	147	237	86
All ( $P < 0.005$ )	$2.80 \pm 0.40$	$3.01 \pm 0.21$	$2.32 \pm 0.17$	$1.49 \pm 0.28$
Contact ( $P < 0.01$ )	$0.38 \pm 0.17$	$0.53 \pm 0.09$	$0.79 \pm 0.07$	$0.78 \pm 0.12$
Grasp ( $P < 0.05$ )	$0.36 \pm 0.14$	$0.52 \pm 0.08$	$0.62 \pm 0.06$	$0.34 \pm 0.10$
Mount ( $P < 0.05$ )	$0.30 \pm 0.13$	$0.42 \pm 0.07$	$0.54 \pm 0.05$	$0.25 \pm 0.09$

of this period; clutch size varied from clutch to clutch but ranged from 8 to 12 in this study, and arbitrarily we used day 10 as the cut-off point); (4) = end-of-clutch period (days 11 to 18; a female finishes laying her clutch and starts incubation during this period). There were significant differences between the periods for four of the six categories (All,  $P < 0.005$ ; Contact,  $P < 0.01$ ; Grasp,  $P < 0.05$ ; Mount,  $P < 0.05$ ) (Table I). Orthogonal comparisons showed that females were chased (All) more frequently during the non-laying and pre-laying periods than the laying and end-of-clutch periods. However, most of these chases ended without contact between the male and female. Chases that ended with at least grasping or mounting (Grasp and Mount) showed a significant quadratic effect ( $P < 0.05$  for both categories), indicating that these chases were more frequent during the pre-laying and laying periods than during the other two periods. For the remaining two categories (Tailbend and FC), the differences between the four periods were not significant, probably because of their rare occurrences. However, FC's were significantly more frequent on females before than after laying the last egg of the clutch ( $P < 0.025$ ). Mean number of FC's per female per observation period before and after completion of the clutch was  $0.25 \pm 0.02$  and  $0.0042 \pm 0.04$  respectively. This difference was consistent over all clutches.

### Time Of Day

During the whole-day observations, males were more successful in FC in the morning (from morning, 14 resulted in FC. In contrast, only one FC was recorded from 59 chases observed in the afternoon ( $\chi^2 = 8.4$ ,  $df = 1$ ,  $P < 0.005$ ). sunrise to noon) than in the afternoon (from noon to sunset). Of 83 male-female chases in the morning, there were three pair copulations in the morning and 10 in the afternoon.

Observations of frequencies of FC after chases that started in various situations are presented in Table II. Males were 21% successful in those chases that began as a female left her nest, compared to less than 10% success in all other situations.

### Other Factors Affecting Frequencies of Chases

The between-pens and between-observers effects were not significant in all six categories of chases. Individual females in pen 1 were chased with significantly ( $P < 0.05$ ) different frequencies and FC occurred significantly ( $P < 0.05$ ) more often on one particular female than on the other three. In pen 2, the variation in frequencies of chases was small and there were no significant differences in the frequency of FC on the four females. Frequency of chases (All) was highest

Table II. Total Number of Forced Copulations Resulting From Male-Female chases That Started in Different Situations

Chases	Position of female when chase started					
	Leaving nest	On nest	Nest-site searching	In the open	Hiding in cover	Pre-laying flights
All	19	54	20	884	7	32
FC*	4	31	1	32	2	1
% success	21	9	5	4	11	3

\*The total number of FCs observed was 71 and not 58 as reported in Burns et al. (1980).

( $3.34 \pm 0.20$ ) at the beginning of the breeding season (first clutch) and declined as females laid their second ( $2.59 \pm 0.21$ ) and third ( $1.93 \pm 0.20$ ) clutches ( $P < 0.005$ ). On the other hand, there was no significant decrease in FC over the same period.

#### Discussion

Data on seasonal variations in the occurrence and frequency of aerial pursuits and FC attempts in dabbling duck species under natural conditions are scarce, but those that are available show close correlation between FC and the egg-laying periods. This relationship was found in urban mallards by Weidmann (1956), Leuret (1961), and Raitasuo (1964), and in northern pintail by Smith (1968) and Derrickson (1977). Flight-pen studies on green-winged teal (McKinney & Stolen 1982), red-billed pintail (*A. erythrorhynchos*) and white-cheeked pintail (*A. bahamensis*) (McKinney, unpublished data) indicate that FC does not begin until females are about to start egg-laying and that it continues through the laying period. Under our experimental conditions, FC was not only generally associated with the laying season but also with the egg-laying cycle of individual females. Male-female chases that ended in grasping or mounting occurred most frequently during an individual female's pre-laying and laying periods. Furthermore, within a clutch cycle, almost all FC's observed were made on females before they laid their last egg, despite the fact that these females were chased just as frequently after they laid the last egg ( $All = 2.75$  before and  $2.06$  after the female laid the last egg, non-significant Least-Squares test). This indicates to us that the males were sensitive to the laying status of the females and were making determined FC attempts on days when they were most likely to fertilize eggs. Our data are compatible with the suggestions of Derrickson (1977) that males may be obtaining information about the reproductive condition of females when they flush and pursue them for short distances.

Physiologists working with domesticated birds know that sperm competition can occur in chickens and turkeys (Allen & Champion 1955; Payne & Kahrs 1961; Lake 1975). Studies on chickens indicate that fertility declines with the age of the sperm and that the most recent of competing inseminations is likely to be most effective (Compton et al. 1978). Mallard females may store viable sperm for up to 17 days (Elder & Weller 1954). An artificial insemination study

with mallards (Cheng et al., in press) has shown that a similar pattern of fertilization exists in ducks. In the species of dabbling ducks studied to date, the frequency of FC appears to be low compared to the frequency of pair copulations. Even though males are attempting FC on females during their laying periods, sperm from infrequent FC are unlikely to compete effectively with sperm from repeated pair copulations. In order for FC behaviour to benefit males, precise timing of insemination may become an important factor. In chickens, turkeys, quail, and ducks, ovulation normally occurs about 15 to 75 min after the laying of the previous egg (Sturkie 1976). The ovulated ovum remains fertilizable for about 15 min before albumen is deposited around the yolk (Gilbert 1971). In chickens, sperm reached the ovum in as little time as 26 min after insemination (Mimura 1939). Sperm that were introduced into the vagina of turkey hens reached the infundibulum within 15 min (Howarth 1971). Because of their intermittent organ ('phallus', King 1981), the distance to be travelled by sperm and thus the time needed for fertilization may be shorter in waterfowl. Thus it seems likely that sperm introduced within an hour or so after egg laying may have the best chance of fertilizing the next egg in the clutch. In our flight-pens, significantly more FC occurred in the morning than in the afternoon. Moreover, there seemed to be a higher proportion of male-female chases that resulted in FC when male(s) started chasing a female as she was leaving her nest, as compared to chases that started in other situations. Female mallards usually lay their eggs in the morning and, at least for the first few eggs of the clutch (Caldwell & Cornwell 1975), thereafter leave their nests to join their mates. Sperm freshly introduced through FC at this time may have a higher likelihood of fertilizing the next egg despite probable pair copulations later in the day. Sperm from these later pair copulations may not be introduced in time to compete successfully for the fertilization of the next egg, although they may compete effectively for the fertilization of eggs to be laid later in the clutch.

In summary, we found that FC attempts were mainly directed at fertilizable females and FC tended to occur more frequently at times when the chance of fertilizing an egg is highest. Thus, the mixed reproductive strategy predicted by Trivers seems to fit the situation in mallards, and perhaps it applies to other species of dabbling ducks.

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