

CEDAR CREEK NATURAL HISTORY AREA
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BETHEL, MINNESOTA 55005

Anim. Behav., 1982, 30, 461-474

EXTRA-PAIR-BOND COURTSHIP AND FORCED COPULATION
AMONG CAPTIVE GREEN-WINGED TEAL
(*ANAS CRECCA CAROLINENSIS*)

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Abstract. A 9½-week study of eight pairs of wild-caught, full-winged green-winged teal in flight pens showed that paired males both directed courtship toward, and attempted forced copulation on, females paired to other males. Chronology of activities in individuals indicated that: (a) this courtship was probably related to building of liaisons and subsequent mate-changes; (b) males were assessing female reproductive condition and selectively attempting to force copulation on females in laying or pre-laying condition; (c) attempts by males to force copulation on their own mates were associated with forced copulation attempts on the latter. Females tried to avoid forced copulations by fleeing and hiding from pursuing males; their mates attacked assaulting males and tried to dislodge them. A mixed male reproductive strategy involving sperm competition is indicated.

In the spring of 1973 we set out to document the characteristics of the breeding behaviour of *Anas crecca* as part of a comparative review of *Anas* social systems. Eight pairs of green-winged teals were released into two large flight pens that had been used successfully for earlier studies of shoveler (*A. clypeata*) (McKinney 1967) and mallard (*A. platyrhynchos*) (Barrett 1973). To our surprise, harassment of females by males trying to force copulations was so intense that only three females laid eggs, none completed clutches, and two died from stress or wounding. Although the breeding behaviour of these captives was grossly disrupted, the study led to hypotheses on the social system of this species (McKinney 1975) that have since been investigated in wild birds (McKinney, unpublished data). The flight pen data presented here are valuable in documenting the chronology of activities in birds of known breeding status. Also, the analysis of individual histories has led to more refined hypotheses on the significance of aerial pursuits and of participation by paired males in social courtship.

General Methods

Each of the two adjacent flight pens measured 27.5 × 27.5 × 3.6 m and contained a large pond surrounded by mowed grass. A strip of grass 1 m wide was left unmowed around the pen walls for nesting cover and a food pan was placed in each corner. These pens, located at the University of Minnesota's Cedar Creek Natural History Area, were described in detail by McKinney (1967).

The teal were captured at Salton Sea National Wildlife Refuge in California and had been held captive, without opportunities to breed, for several years, during which time they all became individually acquainted. In November 1972, four visually isolated flocks were established in the wintering house, from which eight strongly-bonded pairs were selected the following spring. Four 'strange' pairs were introduced to each flight pen on 25 April 1973, and from 26 April to 30 June one of us watched the birds, usually for 3 h, on two of every three mornings starting at first light. All-day watches were made on 9 May and 25 May. Observation periods on 43 days totalled 131 h. Individuals were identified by nasal discs (red, yellow, green, white) and named by colour and pen number (R1, Y1, G1, W1; R2, Y2, G2, W2). The pens were inspected every second day to check for nest-scrapes and eggs and to replenish food pans with commercial food. The birds also obtained some natural food from the ponds. They soon became adept at flying around the pens without crashing into the wire walls, and, although they never became tame, our visits to the pens did not cause extreme panics.

Terminology

Names for courtship displays and vocalizations are those used in previous papers (McKinney 1965, 1975), but several terms require comment.

Inciting. Ritualized threatening movements, accompanied by rattling calls, that indicate (to us

and presumably to other birds) a female's attachment to one male and her rejection of another. Similar displays occur in many kinds of waterfowl during and after pair-formation but, while they may 'incite' one male to attack another in some species (e.g. certain shelducks), this function is not implied in dabbling ducks (Lorenz 1951-53; Johnsgard 1965).

Persistent quacking. Repeated, loud quacks given by females of many *Anas* species on the days preceding egg-laying (McKinney 1967; Abraham 1974).

Liaison. A part-time pair-bond in which at least one partner is already paired to a different bird (McKinney et al. 1978).

Copulatory activities. For many years, the terms 'copulation' (between mates) and 'rape' (promiscuous and forced) were adequate to cover these activities (e.g. Lorenz 1951-53; Weidmann 1956; Leuret 1961; Raitasuo 1964). Then 'forced pair-copulation' was added for forced copulation behaviour between mates (Barrett 1973; McKinney 1975; Barash 1977). Recently, use of the word 'rape' in animal studies has become controversial and we no longer use it for the following reasons. 'Rape' has moral and legal implications for humans and, like 'murder', it has sensational qualities that make it unsuitable as a descriptive label in waterfowl studies; a neutral term seems especially desirable now that forced copulation is being viewed as a male reproductive strategy in certain waterfowl (i.e. it is a 'profitable' way for males to behave); the term 'rapist' can be misleading because it suggests a certain type of individual, a specialist in a particular kind of behaviour, but such specialization is not known to occur in any waterfowl species.

Monogamous pair-bonding is the basic element in *Anas* mating systems but, in species such as the green-winged teal, paired males also engage in promiscuity via forced copulation. The incidence of forced copulation and mixed male reproductive strategies in waterfowl is reviewed elsewhere (McKinney et al., in press). Copulatory behaviour between mates has characteristics fundamentally different from those seen in promiscuous interactions, and this dichotomy has influenced our choice of terms.

(a) *Pair copulation*. The members of a firmly-bonded pair of green-winged teal spend most of their time together. They synchronize many daily activities (e.g. bouts of feeding, preening, bathing, sleeping) and they use pre-flight intention

movements to achieve simultaneous take-offs. When separated, they communicate by loud contact calls and usually respond to them by coming together. Females perform inciting beside the mate only, thereby rejecting rival males. Mates usually perform copulations by mutual agreement. Such pair copulations take place only while both birds are swimming, they are preceded by pre-copulatory head-pumping displays by one or both members of the pair, and the female adopts the prone posture before or as the male mounts. They are usually followed by male post-copulatory displays.

(b) *Forced pair copulation*. This behaviour was noted by Bezzel (1959) and Raitasuo (1964) and studied by Barrett (1973) in the mallard, and we now have records of similar behaviour in other species of dabbling ducks. These incidents, reported here for the green-winged teal, differ from normal pair copulations in the absence of pre-copulatory pumping and in the fact that they can occur on land. The male rushes at his mate and attempts to mount without the usual preliminaries. The female's response is variable; often she moves away, showing mild resistance, but she does not make energetic attempts to flee. The male's behaviour is also variable, and often he abandons his attempts to mount. A milder word than 'forced' might be more appropriate for such interactions, but it seems best to retain Barrett's term which is already widely used.

(c) *Forced copulation*. Females do not solicit or willingly accept copulation from males other than the mate. Therefore, to achieve forced copulation a male must pursue, grasp and overpower the female, and intromission occurs in spite of resistance by the female. Indications that intromission has occurred are bending of the male's tail around the side of the female's body, a deliberate pelvic thrust by the male, and subsequent direct departure by the male, often with repeated tail-wagging. Male post-copulatory displays have not been recorded and we do not believe that their presence or absence can be used as a criterion for 'successful' forced copulation in this species. A male-female chase in which the chasing male grasps the female but does not succeed in copulating, or a chase of this kind in which the outcome is uncertain, is called a 'forced copulation attempt'.

Chases involving one or more males after a female may or may not end in forced copulation attempts. The female may be grasped before she is able to escape by flying or diving, but she

usually takes wing. We scored three types of 'male-female chases' for analysis: those in which the female only flew in retreat ('1-bird flight'), those in which the chasing male flew after her ('2-bird flight'), and those in which the female's mate flew after them as well ('3-bird flight'). Males do not chase their own mates, so that all these flights are extra-pair-bond interactions.

Behaviour Recorded

During observation periods, locations of all birds were plotted on outline maps of the pens every 15 min. We attempted to record all occurrences of the following behavioural events in all eight pairs, the time and location, and identities of all birds involved in interactions. The outcome of interactions that took place in nesting cover could not always be determined. Displays are described in McKinney (1965); for other activities see discussion of terms above.

Contact calls between mates: male, repeated calls (a series of burps); female, decrescendo call.

Pair copulation: pre-copulatory pumping, mounting attempt, copulation, post-copulatory displays.

Forced pair copulation: mounting attempt, copulation, post-copulatory displays.

Courtship: bout of social courtship including such displays as grunt-whistle, down-up, head-up-tail-up), isolated bridling, isolated grunt-whistle, isolated down-up.

Aggression: open-bill threat, peck, swim-off, surface chase on land or water, fight, male bill-up, female inciting.

Nesting: pair flight around pen, persistent quacking, walking in cover, scrape-making, egg-laying.

Forced copulation: 1-bird flight, 2-bird flight, 3-bird flight, mounting attempt, forced copulation, mate-defence, female diving, female hiding in cover (time in and time out), male searching.

Results

There were marked changes in behaviour during the 94-week study, and although these changes undoubtedly were influenced by many factors, we have analysed them primarily in relation to the breeding schedules of the females (Fig. 1). In particular, the dates on which females began nest-site selection and laid their first eggs proved to be key dates in interpreting the pattern of interactions.

From the start, pair copulations were frequent, and there were many bouts of social courtship. In the third and fourth weeks, five females

showed pre-nesting behaviour and a few males showed mild hostility toward other males. As in other *Anas* species, pre-nesting behaviour entailed spontaneous flights by the female (with or without an accompanying mate), bouts of persistent quacking before and during these flights, excursions on foot into long grass in search of nest-sites, and excavation of nest-bowls or scrapes. During this pre-nesting period males directed many chases at females of other pairs, often flying after them around the pen a few times in characteristic 2-bird flights. In the fifth week, three females stopped persistent quacking and started egg-laying. At this point, many pursuits developed into 3-bird flights ending in forced copulation attempts. In association with this switch in male behaviour, some females took to hiding and some males were seen to attempt forced pair copulations.

The following sections deal with four kinds of behaviour which show variations in form and/or frequency in *Anas* species and thus are especially important for comparative purposes. These are behaviour relating to pair-bonds, territoriality, courtship, and forced copulation.

Pair-bonds

All eight pairs remained firmly bonded after they were introduced into the flight pens. Mates spent most of the time together and females consistently gave inciting beside their own mates. If they drifted apart while feeding and lost sight of one another, pair members soon gave contact calls (series of burps by the male, decrescendo calls by the female) and came together again.

The persistence of pair-bonds was confirmed by the incidence of copulatory behaviour (Table I). Precopulatory pumping without subsequent mounting was very frequent, especially during the pre-nesting phase (Fig. 1). In two pairs (R2, G2), the male gave many bouts of pumping without eliciting a response from the mate, but in most pairs the female usually participated as well (Table I). All pairs were seen attempting copulation and seven pairs appeared to succeed on at least one occasion (judging by the occurrence of a male thrust and subsequent male post-copulatory bridling display).

Territoriality

Males were never seen to pursue one another in flight and, apart from the struggles associated with the frequent forced copulation attempts, we saw only one fight. Brief rushes by one male at another occurred infrequently on land or water

Table I. Breeding Performance of Females and Pair Copulations

	Breeding performance	Pre-copulatory head-pumping bouts ♂+♀ (♂ only)	Pair copulations (attempts)	Span of copulatory activity
R1	Laid 3 eggs	21 (17)	3 (9)	4/26-5/27
Y1	Laid 3 eggs	63 (13)	7 (3)	4/26-6/16
G1	Made scrape	73 (29)	5 (0)	4/26-6/01
W1*	Pre-laying behaviour	11 (17)	1 (3)	4/29-5/18
R2	None	23 (54)	2 (0)	5/02-6/23
Y2	Made scrape	53 (10)	2 (3)	4/26-6/22
G2*	Laid 2 eggs	7 (51)	4 (1)	4/26-6/09
W2	Pre-laying behaviour	19 (10)	0 (1)	5/02-6/13

*W1♀ died on 25 May; G2♀ on 20 June.

(two to 15 were recorded for seven of the eight males). Low-intensity hostile behaviour was quite common; for example, at the feeders. At close range, males threatened one another with bill-up postures and chattering calls, females gave inciting beside their mates, and pecks, open bill threats, and brief swim-offs were recorded also. Most of this male hostility appeared to be associated with courtship and mate-defence (see p. 465).

The only male to show any territorial behaviour (Y1) was recorded in 37 chases during the pre-nesting period. For about 1 week he chased mostly G1♂, especially when the G1 pair entered the corner of the pen where both Y1 and G1 pairs were exploring cover for nest-sites. Also, on these same days, G1♂ repeatedly chased females, including Y1♀, and this could have contributed to Y1♂'s intolerance of him during this period.

Courtship

Unpaired birds. The two males whose mates suddenly died during the study became very active in courting other females, especially during the 5 to 7 days immediately following the deaths. W1♂ lost his mate on 25 May. He had directed single displays to Y1♀ on 12 May and 18 May and after his mate died he actively courted Y1♀ (and to a lesser extent G1♀). This sequence suggests that, while still paired to W1♀, W1♂ was interested in Y1♀ and that this interest increased after he lost his mate. W1♂'s courtship was unsuccessful (both Y1 and G1 pair-bonds remained intact), and he was unpaired throughout the rest of the study.

G2♀ died on 20 June and on about the same date Y1♀ moved from pen 1 to pen 2 (apparently

through a hole in the fence). In pen 2, she was courted by Y2♂, R2♂, and G2♂ and she paired rapidly with the unpaired male G2. The reasons for Y1♀'s move are unknown but we allowed her to remain in pen 2 leaving Y1♂ unpaired in pen 1.

Paired males. Many bouts of courtship that were not related to the activities of the unpaired males occurred in both pens. Indeed, most courtship activity occurred while the eight pairs were strongly bonded.

Courtship bouts involving paired birds started in several different ways. (a) Many began when two pairs came together on the water (e.g. near one of the feeders) and the males assumed hostile bill-up postures ($N = 27$) or when larger groups assembled with similar signs of hostility between males ($N = 45$). In these cases, bill-ups led first to down-ups and then the birds began circling and manoeuvring in typical social courtship fashion giving more down-ups as well as grunt-whistle, head-up-tail-up, nod-swim, turn-back-of-head, and other displays. (b) Other bouts started when a paired male left his mate and approached a different pair, showing interest in the female ($N = 26$). The initiator's mate often joined the trio and thereafter most of his displays were directed toward her. (c) Some bouts were triggered by an alarm (e.g. caused by a bird of prey flying nearby) ($N = 6$). In these cases (probably commoner than we recorded), several pairs swam or flew out to the centre of the pond, the males gave a burst of repeated calls, and then social courtship displays followed.

In all of these gatherings of paired birds, no matter how they started, there were signs of hostility which indicated rivalry over mates. A female would frequently give inciting movements and calls, threatening a nearby male (often the

same one repeatedly) while moving along close to her mate. In addition to performing displays, males threatened one another with bill-up postures, manoeuvred tensely at close range, swam after or briefly chased one another, and moved to avoid one another. At one time or another, seven of the eight males were seen to direct displays at females other than their mate (Table II). Of the three males seen to do so on five or more occasions, two gave displays to one other female in the pen (Y1♂ to R1♀, W2♂ to G2♀) while the third (Y2♂) gave displays to all three females available. This extra-pair-bond courtship was certainly much more frequent than our small sample suggests. Table II includes only instances where we felt certain that we had identified the target female correctly.

In certain situations a male directed one or two displays from the social courtship repertoire at his own mate, but no social courtship followed. Three displays were involved (bridling, grunt-whistle, down-up), but the contexts and chronology for each were somewhat different and they will be considered separately.

Isolated bridling. Performed by a male on land when his mate approached after a separation. This context, and its occurrence very early in the study (9 of 10 records were in weeks 1 and 2), suggest that these displays functioned to reaffirm the male's interest in his own mate during the period when pair-bonds were strengthening prior to breeding attempts. (Note that when bridling was performed by a male courting a female to which he was not paired, the display also was often an isolated occurrence, independent of social courtship bouts.)

Isolated grunt-whistles. These were recorded on two occasions only (two displays in succession in each case) by a male courting his own mate. Both incidents occurred in the middle of the study (week 5), after the first breeding attempts had been abandoned. Both pairs concerned were making frequent flights around the pen and pre-

sumably these females were in the 're-nest interval' and the displays were associated with the reaffirming of bonds.

Isolated down-ups. These occurred later in the study (weeks 5 to 8) and were apparently associated with specific, high-intensity rivalry situations. On 17 occasions, a paired male gave a down-up (sometimes several) as he swam beside his mate when another male approached. Characteristically the long body axes of all three birds were parallel, the mates were close to one another (e.g. 0.3 m), the rival male farther away (e.g. 1-2 m). Most often the rival was unpaired, and had been directing courtship displays at the female ($N = 10$). Sometimes he was a paired male, apparently interested in attempting forced copulation on the female, judging from his behaviour before and after the encounter ($N = 4$). On three occasions we were uncertain about the rival's intentions. These down-ups appeared to be effective threat signals directed toward unpaired courting males (who usually responded by keeping at a distance from the pair and then moving away), but they did not deter males intent on making forced copulation attempts. The broadside orientation of the paired male to his mate when he performs isolated down-ups may mean that the displays have a simultaneous bond-reinforcement function in addition to their threat function.

Behaviour Associated with Forced Copulation

Male-female chases. Close to the date on which each female began pre-nesting behaviour, males began to make rapid approaches to them, forcing them to fly. If the male did not fly in pursuit, usually the female flew only a short distance and alighted in full view (1-bird flight) ($N = 36$). Often the male then swam towards her, repeating the 'flushing' pattern. More often, after approaching and pecking toward or rushing mildly at her, the male pursued her in flight. Both birds then circled the pen one or several times (2-bird flight), the male alighted first, the female

Table II. Orientation of Courtship Displays (Grunt-whistle, Head-up-tail-up, Down-up, Bridling) by Paired Males to the Mate* and to Other Females

	R1♀	Y1♀	G1♀	W1♀	R2♀	Y2♀	G2♀	W2♀
R1♂	21*	0	0	0	R2♂	57*	0	1
Y1♂	22	28*	1	1	Y2♂	6	27*	3
G1♂	1	1	22*	0	G2♂	1	1	32*
W1♂	0	2	0	16*	W2♂	0	0	12
								49*

a few seconds later in a different part of the pen. Repeated flushing of the same or other pre-nesting females by the pursuing male often followed. In 2-bird flights, the male rarely made serious attempts to grasp the female (only in 4% of 266 observed 2-bird flights). His objective seemed to be to make her fly and to fly after her but only for a short distance. Normally the female's mate paid close attention to these chases, watching the flying birds, giving repeated calls and swimming to join the female after she alighted.

These male-female chases showed no relationship to locations within the pens and they could

not have been a result of territorial intolerance. There were obvious signs of individual differences in the responses of males and females, and these changed during the study. Some females were chased more often than others on certain days but on other days different females were the prime targets. While the study was in progress we did not have a satisfactory explanation for these chases, and their high frequency over a period of about 3 weeks was puzzling. Now we suspect that Derrickson's (1977) interpretation of similar chases in northern pintails (*Anas acuta*) applies also to green-winged teal. The males may be 'testing' females by forcing them to fly and

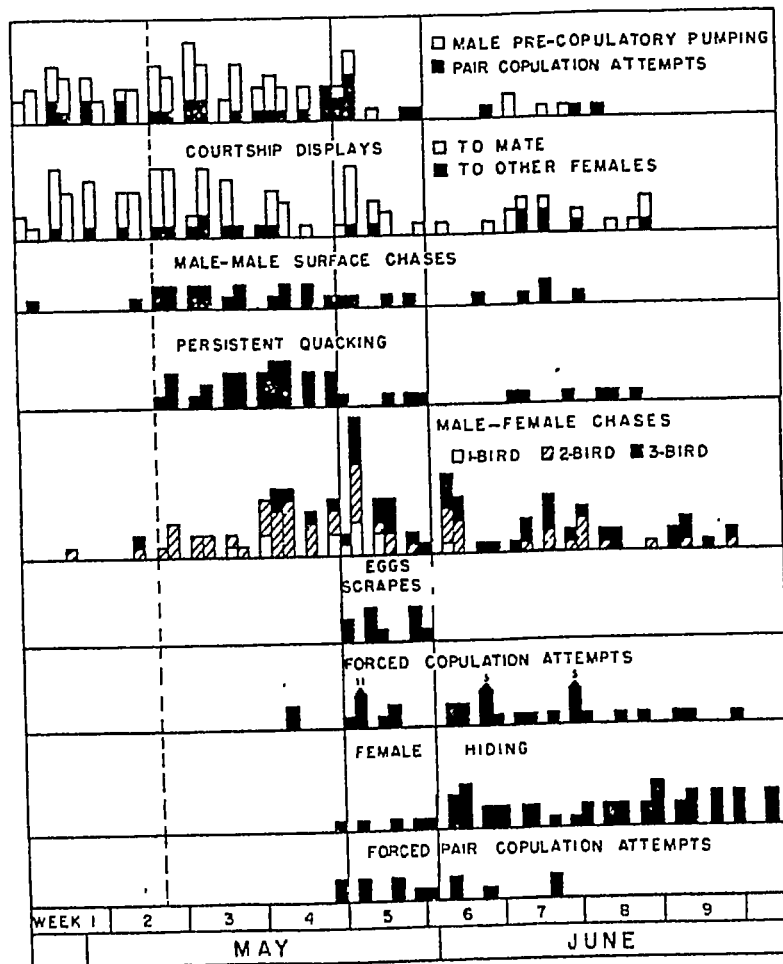


Fig. 1. Chronology of breeding behaviour in five pairs that laid eggs or made scrapes (R1, Y1, G1, Y2, G2). Histograms represent number of birds recorded in each activity on observation days. Vertical lines mark the start of pre-nesting behaviour (dashes) and the period of first breeding attempts (solid lines).

perhaps the responses elicited influence the vigour of the male's forced copulation attempts (see Discussion).

Two-bird flights were frequent during the pre-nesting period but once laying started the mates of chased females usually joined in the aerial pursuits (Fig. 1). In general, this change to 3-bird flights coincided closely with the date of the first forced copulation attempts on the females concerned (Fig. 2). Three-bird flights usually involved prolonged pursuit and energetic evasive manoeuvres by the female, and when they developed into forced copulation attempts (27% of 126 flights), other males in the pen often joined in the chase (65% of 57 forced copulation attempts).

Status of chasing males. All eight males initiated and joined in pursuits that led to forced copulation or forced copulation attempts while they were paired birds (Table III). The two males that lost their mates during the study (G2 and W1) actively courted other females. G2♂ made one forced copulation attempt 1 week after his mate died, but by then he was already re-paired to Y1♀. W1♂ did not have an opportunity to court an unpaired female (as G2♂ did), and although he courted firmly-paired females he remained unpaired for the rest of the season. He initiated several forced copulation attempts on the day his mate died but thereafter he was seen to join in only three forced copulation attempts during the following month. These findings agree with those for several other *Anas* species showing that attempts to force copulation are made by paired males while un-

paired males are primarily interested in forming pair-bonds (McKinney et al., in press).

Status of chased females. The behaviour of the three females that laid eggs changed abruptly when laying started. They stopped giving persistent quacking and they no longer made spontaneous flights and excursions through cover on foot. At the same time, males abruptly increased the vigour of their aerial pursuits and began to make forced copulation attempts. In turn, males guarded their mates more closely and forced pair copulation attempts began to occur (see below). These changes are documented for five females in Table IV.

Once begun, forced copulation attempts continued to be made throughout the following 5 weeks (Fig. 1), but they were not directed at all females indiscriminately. This is illustrated by certain females that made late attempts to breed. Three of these females (Y1, G2, Y2) had abandoned early attempts to breed and spent most of the time hiding in cover (Fig. 2B). When, 4 to 6 days after emerging from hiding, they again gave persistent quacking, two (G2, Y2) were subjected to chasing and harassment and returned to hiding. Another female (W2) was not recorded giving persistent quacking during the first period of breeding activity in late May, although she was chased by males and there were forced copulation attempts on 2 days. On 13 June she did give persistent quacking and thereafter she was chased, forced copulation attempts were made on subsequent days, and soon she took to hiding (Fig. 2C).

Table III. Records of Individual Males and Females Involved in Forced Copulation (FC) Activities

Pair	Males				Females		
	Initiates pursuit	Joins in pursuit	FC	Defends mate	FC attempt by 1 male	FC attempt by 2-3 males	FC
R1	11	1	0	6	2	6	1
Y1	7	4	1	0	0	1*	0
G1	5	4	0	12	14	4	0
W1	6†	5	0	2	2	0	0
R2	7	6	0	0	1	0	0
Y2	7	6	2	4	3	7	0
G2	10	4	1	2	4	1	1
W2	4	5	0	7	6	4	2‡
	57	35	4	33	32	23	4

*Y1♀ was then paired to G2♂ in pen 2 (see text).

†W1♂ was unpaired when 3 FC attempts were made (see text).

‡by G2♂ and Y2♂ in one incident.

Table IV. Relative Frequency of Activities Associated with Forced Copulation (FC) in Five Females After the Start of Egg-laying

Activities	Periods*										Total	
	Pre-laying (9 May–23 May)					Total	Egg-laying (24 May–6 June)					
	R1	G1	Y1	G2	Y2		R1	G1	Y1	G2		Y2
Persistent quacking†	7	3	10	8	3	31	0	0	0	0	4	4
1-bird flight	12	1	11	2	1	27	0	1	1	0	0	2
2-bird flight	52	5	40	14	5	116	5	4	3	6	10	28
3-bird flight	0	2	0	7	0	9	25	9	2	10	7	53
FC and FC attempts	0	1	0	0	0	1	7	9	0	4	6	26
Forced pair copulation attempts	0	1	0	0	0	1	3	6	0	0	0	9

*Counts during a total 42 h for each period.

†Number of days when persistent quacking was recorded (maximum of 10 days in each period).

The histories of three other females do not seem to show such a relationship between pre-laying behaviour and the incidence of forced copulation activity (R1, G1, Y1 on Fig. 2) and must be considered separately.

(1) After abandoning her first breeding attempt (three eggs), R1 went into hiding for the rest of the study period. She gave no signs of initiating a second attempt, hid very efficiently, and was harassed only rarely by males. The factors responsible for the very low rate of chases and forced copulation attempts on this female are impossible to determine. Perhaps she hid so successfully that she was in fact 'unavailable' to be chased.

(2) After an initial attempt to start breeding (a scrape was made), G1 remained active and visible during the remainder of the study but no late burst of persistent quacking was recorded. She did make flights and explore cover on 6 June and we may have missed her calling. Thus two of the periods (2–5 June, 11–17 June) when she was subjected to chasing and forced copulation attempts were preceded by pre-nesting behaviour. This female was guarded closely and actively by her mate and she did not show any ill effects from the frequent forced copulation attempts that she received. Her history suggests that performance of persistent quacking is not an essential trigger for male forced copulation attempts, but possibly she did call on mornings when we were not observing. Here again the factors responsible for the high rate of forced copulation activity are unclear; the visibility of this female may well have been important.

(3) Y1 female gave late-season bouts of persistent quacking but these were not followed by forced copulation attempts. This could be attributed to the ability of her mate to deter other males. He was the most aggressive male and only one FC attempt was recorded on her during the whole study period.

At the beginning of the breeding season, males did not initiate forced copulation attempts on females as soon as they began to exhibit pre-laying behaviour (e.g. persistent quacking); with one exception, forced copulation attempts did not begin until the day when egg-laying began. Once they had started, however, forced copulation attempts continued throughout the study period and were directed especially at females showing a recrudescence of pre-laying behaviour. While males seem to have been able to identify the latter females, we cannot say which clues they used to do so.

Tactics. When vigorous pursuits started in week 5, females used various escape tactics. After making flights around or across the pen, they often pitched into long grass instead of alighting in full view. Or, if they alighted on water and were pounced on, they either flew again immediately or dived, swam underwater, and sneaked away, with the head low and outstretched as they surfaced. There was no emergent cover in the pens so that diving females were usually spotted by the watchful males and the pursuit continued.

Once females began to hide from their pursuers, forced copulation attempts could occur

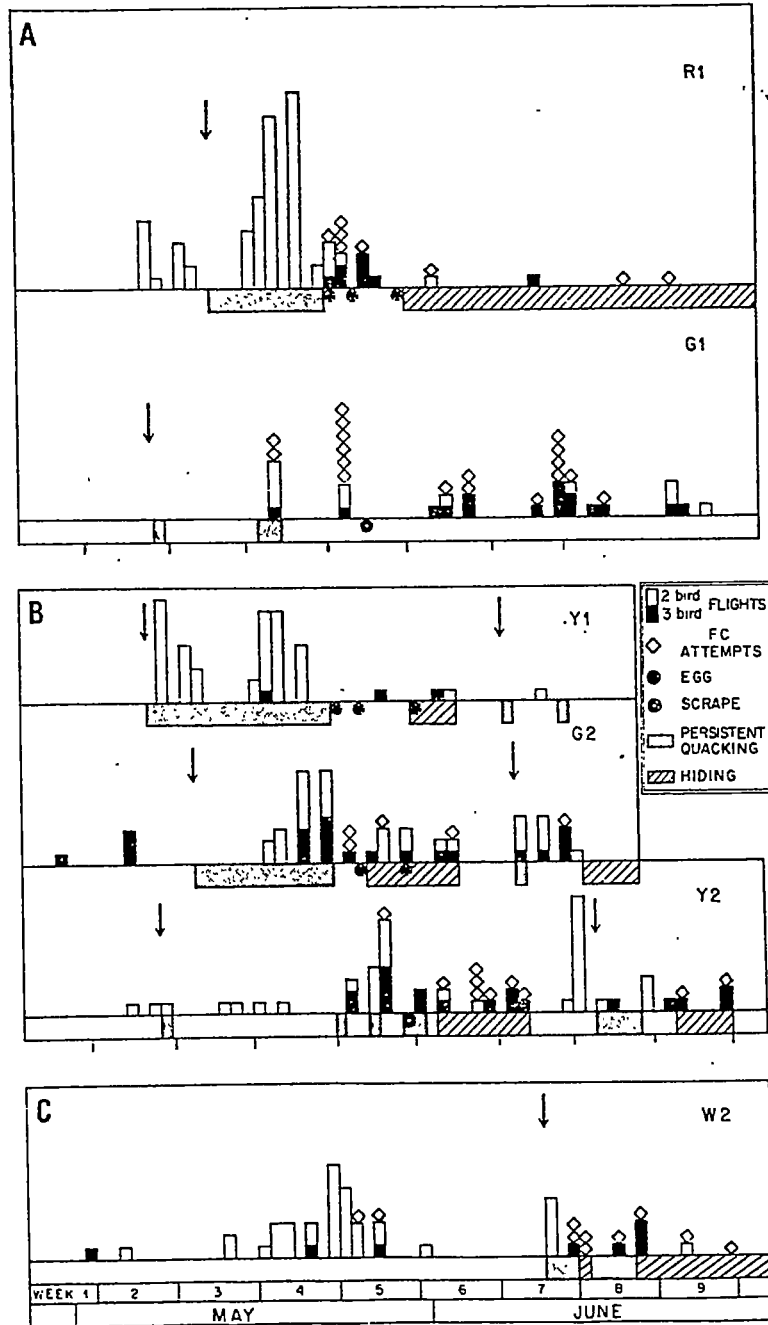


Fig. 2. Chronology of flights and forced copulation attempts on females of (A) two pairs that made only one early attempt to breed, (B) three pairs that made two attempts and (C) one pair that apparently made a late attempt. The start of persistent quacking (indicated by arrows) is considered to represent the beginning of each breeding attempt.

without any aerial chasing ($N = 12$). Some females became very reluctant to leave cover at all and during many morning watches they remained in hiding for much of the time. Males deliberately searched for hiding females, walking along with head high, peering into cover and dashing onto the female if they found her. Males often lost track of where their own mates were hiding and they searched for them persistently, moving around with head erect and giving repeated calls. The sight or sound of a scuffle in the grass immediately attracted the attention of searching males and they rushed to the scene.

Sequences involving a hiding female could lead to 'sneaky' behaviour by her mate and/or a male intent on forced copulation. One male made repeated attempts to approach a hiding exhausted female, although her mate chased him off vigorously each time and a prolonged interaction resembling a 'cat and mouse game' followed. The male attempting forced copulation appeared to take indirect routes in order to enter cover without being discovered by the female's mate, but the latter was constantly vigilant for the return of his rival and moved to intercept him if there was a movement in the grass on one of the usual approach routes. Defending males sometimes crouched beside the mate to avoid being seen by an approaching male. On the whole, hiding tactics by any of the birds did not appear to be effective for long; the pens were too small and the cover not very dense. Observations in Alberta, however, have indicated that these tactics are probably very important in wild birds (McKinney, unpublished data).

Mate-defence behaviour varied in intensity with the vigour of the aerial pursuit and the persistence of the chasing males. Compared to the pre-laying phase, when mild approaches and brief pursuits evoked little or no defence behaviour, the first vigorous pursuits and their consequences were a dramatic change. Thereafter, males followed closely (in 3-bird flights) but were never seen to interfere with a chasing male during the aerial pursuit ($N = 85$). If the female came down on land or water and was caught by a pursuer, her mate did not attack until the female was grasped by the nape or neck feathers and mounting was in progress ($N = 33$). At this point, he attacked vigorously, pecking at the mounted male's head and beating him with wings. Often such attackers were successful in dislodging the male, allowing the female to escape. Typically the two males continued to fight for several seconds before separating; the

chasing male then resumed his pursuit of the female, or her mate had to defend her from assault by a different male.

Only one of our eight females appeared to be so well protected by an aggressive mate (Y1) that she was subjected to few forced copulation attempts. (None were observed, but she was noted as being in hiding for several days.) Later, when this female moved to pen 2 and paired with G23, we did see one forced copulation attempt on her.

If one or both of the other males in a pen joined in a forced copulation attempt (65% of 57 pursuits), the female was sometimes mounted by more than one male in sequence. In these situations, fighting between males was usually a consequence of defence by the female's mate. Usually, after making his attempt, each male departed and showed no further interest in what was happening to the female. In one instance, however, after apparently successfully achieving forced copulation, a male attacked a rival male as the latter attempted to mount the female.

Intromission during FC attempts. In many cases it was difficult to determine if intromission occurred during a forced copulation attempt. At first, females remained in full view and their mates defended them strongly and effectively, but after they had been assaulted repeatedly, females relied mostly on hiding. Subsequent forced copulation attempts usually took place in the tall grass around the edge of the pens. On four occasions, we felt sure that intromission occurred because the male's tail was seen to move around the side of the female's tail and there was a pronounced thrust. Several times during a forced copulation attempt on land we saw a male apparently achieve intromission and then prolong it by maintaining his hold on the female's nape feathers, even after his body had slipped off the female's back and he was lying on his side adjacent to the female. This contrasts strikingly with the characteristic momentary intromission involved in pair copulations.

We noted what we believe to be other signs that a male had succeeded in a forced copulation attempt. Quite often, after an incident had occurred out of sight in cover, a male walked away from the female, tail-wagged repeatedly, and then swam or flew away. Judging from this behaviour, it seems likely that such males had achieved intromission and ejaculation, and this was further indicated on a number of occasions by the observation of an everted phallus which was subsequently reinverted during tail-wagging.

Although they provide circumstantial evidence only, these observations convinced us that males were indeed succeeding in forced copulation more often than our counts might suggest.

Forced pair copulations. On 14 occasions, between 23 May and 11 June, attempts by males to force copulation on their mates were recorded in five pairs. Only three of these attempts (all by male G1) were judged successful and all three were followed by post-copulatory bridling. Six attempts were abandoned by the male and most of these incidents appeared 'half-hearted'. Two were interrupted by another male and the outcome of three was uncertain.

All of these incidents took place during the period when forced copulations were going on (Fig. 1). Nine of them occurred within 11 min after a forced copulation attempt on the female (five within 1 min), and another three were on days when the females concerned were being chased or were hiding. Most incidents occurred in water, and four involved diving by both birds followed by underwater mounting attempts. In four cases, they occurred primarily on land where normal pair copulations do not take place.

Discussion

Extra-pair-bond Courtship

Seven of the eight paired males studied showed extra-pair-bond courtship, and it is unlikely that the behaviour was an aberration of certain individuals in captivity. Two males showed consistent preference for courting specific females other than their mates, and five other males were recorded directing displays at various females other than their mates. Recent field studies on individually-marked birds have shown that extra-pair-bond courtship occurs also in wild green-winged teal on the breeding grounds in southern Alberta in May and June (McKinney, unpublished data).

There is strong evidence, for dabbling ducks in general, that when a male directs courtship displays at a specific female he is showing his interest in forming or reaffirming a pair-bond with her (e.g. Johnsgard 1960; Weidmann & Darley 1971; McKinney et al. 1978). Analyses of body-orientations, distances between birds, and dominance relations in social courtship groups of green-winged teal have shown that each display occurs in distinctive contexts, and have suggested that each serves a range of specialized signal functions (McKinney 1965, 1975; Laurie-Ahlberg & McKinney 1979). The displays seem

to enable individual males to (a) attract the female's attention, specify interest in her, and encourage her to pair, and (b) compete with rival males in achieving these goals. Female displays apparently indicate and reaffirm preferences.

Participation by paired males in social courtship gatherings during the winter months was noted in the mallard by Weidmann (1956), Leuret (1961), Raitasuo (1964), von de Wall (1965) and others, but the phenomenon has been little studied. We were surprised that it was so frequent in our flight pen study and that it continued so late into the breeding season. The proximate causes of this activity among paired birds and the adaptive value to the individuals concerned remain questions for detailed study and our discussion here is preliminary.

In a species such as the green-winged teal, in which males combine pair-bonding with promiscuity by means of forced copulations, courtship by paired males directed to females other than the mate might be related to either or both facets of the male mating system. In a preliminary discussion of the study reported here (McKinney 1975), the question was left open but now we feel that the evidence favours a relationship with pair-bonding rather than promiscuity. We believe that extra-pair-bond courtship reflects a paired male's interest in acquiring a new mate. In theory, this could be advantageous for a male if (a) his first mate dies, or (b) he can switch to a mate of higher quality, or (c) he can acquire more than one mate.

Females of many ground-nesting duck species are vulnerable to mammalian predators while they are on the nest. For example a study of bird remains at rearing dens of red foxes (*Vulpes vulpes*) in North Dakota showed a preponderance of females (75 to 100%) among the remains of seven species of dabbling duck, including the green-winged teal (Sargeant 1972). Unless the breeding season is too far advanced, the mates of such females may be expected to seek new partners, and this tendency was shown by our captives. After their mates died on 24 May and 20 June, males W1 and G2 actively courted other females and the G2 male quickly formed a new pair-bond.

Many species of *Anas* form new pair-bonds each year (e.g. Sowl 1955) and, although some residential species can have bonds that last longer than one year, individuals are capable of switching mates quickly when the need arises (McKinney et al. 1978). Renewed courtship of females during the re-nest interval, after they

lose their early clutches, is a widespread occurrence in dabbling ducks (Sowls 1955; McKinney, unpublished data). Perhaps much of the extra-pair-bond courtship we saw in our pen study falls in this category. After females aborted their initial laying attempts, males paired to other females continued to show an interest in many of them as potential mates. We documented one case of pairing following extra-pair-bond courtship (W1♂), and the case histories of liaisons and mate-switches in African black ducks (*Anas sparsa*) (McKinney et al. 1978) illustrate how similar events could occur in green-winged teal.

Although harem polygyny occurs in the African comb duck (*Sarkidiornis melanotos melanotos*), a member of the perching duck tribe Cairinini (Siegfried 1979), polygyny does not appear to have been recorded for any *Anas* species under field conditions. We have observed bigamous behaviour in captives of certain species but not in green-winged teal, and it seems unlikely that extra-pair-bond courtship has to do with the acquiring of additional mates in this species.

In trying to understand courtship involving paired birds, we can distinguish probable 'interests' of the various participants. In bouts that begin when a paired male approaches the female of another pair and directs displays at her, there are at least four parties involved but perhaps only one of them (the initiator) benefits in the long run from the encounter. The behaviour of the other three birds could be unavoidable reactions to the situation. Participation by the initiator's mate was common but by no means invariable, and in some instances females remained sleeping on shore while their mates courted other females in full view. If such a neglected female did join the group, her mate usually directed subsequent displays toward her, thereby reaffirming his pair-bond with her.

The courted female's response appeared to be rejection of the courting male and a simultaneous show of allegiance to her own mate (by means of inciting). But such rejections did not deter courting males from continuing to direct displays at these females. Perhaps inciting is the only signal a female can give so long as her main interest is in preserving her current bond. She could still be gaining information about courting males that she will use later.

The courted female's mate usually responded to the courting male with threat displays (bill-up and down-up), but also he directed courtship displays to his own mate. These reactions sug-

gest that the female's mate may have no better way of protecting his pair-bond than to join in active courtship in the presence of a rival. His behaviour probably varies with the seriousness of the rival's threat, however, and this seemed to be a major factor in the situations in which isolated down-up displays were performed (p. 465).

There remains the question of the benefits to be gained by the initiating male. He might be (a) gaining information about the female and her current bond (e.g. by testing her interest in him and the vigour of her mate's response to him); (b) advertising to the female his interest in her; and perhaps (c) establishing a personal relationship with her: all of which could be of value to him if a mate-change becomes necessary or advantageous.

Forced Copulation

Smith (1968) showed that the aerial pursuits of northern pintails (*A. acuta*) peak in frequency during the laying period, and suggested that forced copulation could play a role in the fertilization of eggs. Experimental proof of this relationship has recently been obtained for mallards in flight pens (Burns et al. 1980) and evidence of many kinds supports the view that forced copulation is a secondary reproductive strategy of paired males of several species (reviewed by McKinney et al., in press). Our flight-pen studies indicate that the green-winged teal is one such species.

There are four lines of evidence. (a) While maintaining essentially monogamous pair-bonds and copulating with their mates, all eight males also made forced copulation attempts on other females, and at times they apparently succeeded. (b) Forced copulation attempts started when the first females started to lay, and three females that gave late bursts of persistent quacking in mid-June were harassed thereafter. (c) Males defended their mates by attacking males attempting forced copulation. (d) During the peak period for forced copulations, males were seen trying to force copulation on their own mates, at times immediately after a forced copulation attempt had been made on the mate, suggesting that sperm competition was going on. Thus paired males evidently inseminated their own mates through pair copulations (and perhaps forced pair copulations) and tried to prevent insemination of their mates by other males. Simultaneously, these same paired males were trying to inseminate other females on the days

when those females were most susceptible to being fertilized, namely just before and during egg-laying.

If the timing of forced copulations is indeed critical, we might expect males to have the ability to assess the reproductive condition of females. We can recognize females in pre-laying condition by their conspicuous nest-site selection behaviour (pair flights, walking into cover, persistent quacking), and it would be surprising if male green-winged teal do not respond to these clues. Males might also be able to detect a female's laying condition by her body-shape and/or behaviour in flight. Female ducks become heavy in the belly ('dropped', as aviculturists call it) when laying. As Derrickson (1977) has suggested for northern pintails, we believe that our male teal were obtaining information about the condition of females when they flushed and pursued them for short distances in 2-bird flights. Experiments are needed to determine if this is the case and, if so, which clues males are using.

We might expect the timing of male mate-guarding to be attuned to variations in the likelihood of being cuckolded. The increase in close attendance by the male on his mate, reflected in the change from 2-bird to 3-bird flights, is not surprising if a male recognizes that the early 'testing' chases of other males will not develop into real forced copulation attempts. The usual pattern seemed to be that during the 2-bird flight phase the female's mate watched what was going on but saved his energy by swimming to join his mate after she alighted rather than flying along with her. When the intensity of the pursuits increased, he joined in and stayed close to the chaser and to his mate by flying along with them. If the pursuit ended in a forced copulation attempt, he was on hand to defend his mate. Delaying his attack until the male had actually mounted and was about to make the copulatory thrust seemed to be an effective tactic. From the defending male's point of view this is the crucial moment, and he may be expected to delay as long as possible to conserve his energy and reduce risk of injury.

One puzzling aspect of mate-guarding was the rarity of forced pair copulations (considering the high frequency of forced copulation attempts) and the seemingly half-hearted nature of many of the attempts we observed. Of course, when the female hid in cover, the activities of the pair were difficult to observe and forced pair copulation may have been more frequent than we recorded. Furthermore, as Derrickson (1977) sug-

gested for pintails, pair copulations to which the female 'agrees' might be occurring later in the day and they may be as effective antidotes to rival sperm as are forced pair copulations. The timing of competing inseminations could be very important.

The female green-winged teals made vigorous attempts to avoid forced copulation. The main escape methods were diving underwater and plunging from flight into tall grass and hiding there. There was no evidence that females encourage males to pursue them and compete for copulations as Christoleit (1929a, b) suggested (and as might be expected, on theoretical grounds). Furthermore, when many males are involved simultaneously, several may achieve inseminations and it is difficult to imagine how females could have any control over which male fertilizes their eggs.

In comparison with other *Anas* species studied so far, the green-winged teal's social system most closely resembles that of the northern pintail (Smith 1968; Derrickson 1977) in that breeding males do not defend territories and forced copulation attempts are frequent and energetic. The characteristics of the breeding habitats of these two species are very different, however, and there are important differences in behaviour associated with the demands imposed by these habitats. These will be discussed in the report of the field study.

Acknowledgments

The study was supported by the Graduate School, University of Minnesota, and by the National Science Foundation (Grant BNS 76-02233). We are grateful to the California Department of Fish and Game for supplying the teal, to Deborah Buitron and Kimberly Cheng for helping with the analysis, and to Michael Anderson, Jeffrey Burns and Nick Collias for helpful comments on the manuscript.

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(Received 16 March 1981; revised 18 August 1981;
MS. number: A2625)