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BREEDING BEHAVIOR OF CAPTIVE MALLARDS

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INTRODUCTION

Field observations on dabbling ducks (tribe Anatini) have suggested that there are important specific differences in the behavior shown by breeding pairs. In some species, such as the Shoveler (Anas clypeata), paired males are very aggressive and defend territories; pair bonds are strong and long-lasting; paired males rarely attempt forced matings ("rape") with other females. Other species, most notably the pintail (Anas acuta), do not defend territories; pair bonds are weak and break early; paired males spend a great deal of time trying to rape other females. These variations in the characteristics of Anas social systems are thought to have evolved as the group radiated to occupy a variety of niches. As yet, these adaptive strategies are poorly understood but it seems likely that they have their basis in characteristics of feeding ecology, habitat, and relationships to predators (McKinney, 1973).

Much of the information required to investigate social systems and behavioral adaptations must be obtained through field studies. For example, we need to know about dispersion of food in time and space, vulnerability of nests to predation, characteristics of the home range of breeding pairs. In order to make statements about the relative development of aggressiveness and raping activity in different species, counts of interactions are needed. To be comparable, such counts should be in the form of rates (by the hour, day, week, or season) and they should be representative of each species. In

practice, this type of information is extremely difficult to collect in the field, because of the many variables influencing the observed frequency of activities. Thus the probability of interactions between breeding pairs must vary with such factors as the density of the populations, mobility of the birds, and their visibility to one another in different habitats. One approach to these problems is to measure rates of activities in captives, where such variables can be controlled.

During the spring and summer of 1968 and 1969 a study was made of the breeding behavior of Mallards (A. platyrhynchos) confined in large flight pens. The birds were full-winged, of known age, and each was marked individually for quick identification. Breeding behavior was quantified throughout each season, with special attention to aggressive and sexual interactions. The results are intended for use in cross species comparisons and preliminary comparisons are made with an earlier study of Shovelers carried out in the same pens (McKinney, 1967 and unpublished). Since my study was carried out, interactions between American Wigeon (A. americana) have been studied in these pens by Andrew Saunders (Ph.D. thesis in preparation) and a study is now in progress on the American Green-winged Teal (A. crecca carolinensis). Part of the objective of my study was to explore methods of analysis for data collected in the flight pens.

The limitations of behavior studies on captives are obvious and results must be interpreted with caution. In these flight pens, the ducks are fed largely on artificial food; individuals

are confined together for a long time and must learn to know each other very well; long flights cannot be made and escape from a pursuer may be impossible. Nevertheless, results with penned Shovelers and Mallards suggest that many aspects of breeding behavior proceed in much the same way as they do in the wild birds and conclusions about species characteristic behavior are possible.

METHODS AND MATERIALS

The Flight Pens

The flight pens used in this study are described in detail by McKinney (1967). Two adjacent pens, each measuring 90 feet X 90 feet X 12 feet high, are overlooked by one blind. Each pen provides nesting cover along the perimeter, extensive mowed grassy areas, and a large central pond with four peninsulas. Food was presented in feeders located on land in four corners of each pen until the third week in May when they were replaced with adjacent floating feeders. Thereafter, the birds fed much more often from the floating feeders. Food was replenished every other day, and cover was examined for nests at the same time. The birds were tame and were alarmed only briefly by these intrusions. Nesting hens flushed off their nests as I walked by but late in incubation they often sat tight.

The grass in the pens was not mowed until after the eggs had hatched; nesting cover around the periphery of each pen was not touched throughout the season.

In 1968 the nesting cover was very sparse until the end of May, and birds in the cover prior to this time were not concealed at all from the view of other birds. Two hens did not initiate nests until the cover growth was luxuriant, but this may not have been the only stimulus involved. The start of their nesting effort began one week after the floating feeders had been put in use and the consumption of high-protein feed greatly increased.

In 1969 the cover was less sparse and most nests were fairly well concealed. Some nests were hidden initially but the sitting bird became conspicuous as she removed all the surrounding grass in the process of nest construction. Hidden or not, the location of the nest sites were learned by some if not all of the birds in each pen.

The Study Birds

In September 1967, 40 wild Mallards were captured in bait traps at the Roseau River Refuge in northern Minnesota. There were 20 males and 20 females, all young of the year. The birds were transferred to a wintering house at the Carlos Avery Game Farm where they were separated into four visually isolated groups of five males and five females. In early April 1968, the four groups were transferred to holding pens at the Cedar Creek Natural History Area in Bethel, Minnesota. The birds were observed for a week to determine which had formed strong pair bonds. One pair was chosen from each of the four groups and,

after weighing and marking, they were released into flight pen 1. A second pair from each of the four groups was then chosen and released into flight pen 2. Thus each of the four pairs in each flight pen had not been together since their capture. In fall 1968 the four groups were reformed and the birds returned to the wintering house.

Pairs were marked with red, green, white, and yellow nasal discs similar to those described by Bartonek and Dane (1964) so that individuals could be distinguished without the aid of binoculars. Birds are identified in this thesis by a code combining the nasal disc color and the pen number. Thus, the pen 1 birds are R1, G1, W1, and Y1 and the pen 2 birds are R2, G2, W2, and Y2. The nasal discs were never observed to interfere with the activities of the birds.

In April 1969 the process of selecting pairs was repeated. The 1968 pen 1 pairs had all reformed except one. The three old pairs were marked as before and a new fourth pair was chosen and marked the same as the 1968 fourth pair. These birds were released into pen 1 on April 18. On the morning of April 30, one pen 1 male, W1, was found dead. Autopsy revealed that he died of avian amyloidosis, a stress disease (Cowan, 1968). Two days later his mate repaired with another male in the pen, identified as Y1, and so a trio was formed.

Three of the 1968 pen 2 pairs reformed in 1969 and were marked as before. A new fourth pair was chosen and was marked the same as the 1968 fourth pair. On April 21 the R2 male became lame with a foot disorder known as "bumblefoot", and

was removed for treatment from April 25 to 29. On the day of his removal, his mate (R2) laid her third egg and on the next day she began accompanying the Y2 male during the times that she was not on her nest. The Y2 pair appeared to accept the new female joining them. The Y2 female initiated her nest on April 26. When the R2 male was returned to the pen on April 29 he was apparently ignored by his old mate until May 6 when she was seen performing Inciting (Lorenz, 1953) beside him after she was chased by another male. This date was four days after the appearance of her last egg. On May 8, the R2 female Incited beside the R2 male as the Y2 male approached them. These performances of Inciting indicate that the R2 pair-bond was reestablished, at least to some degree.

Procedure During the Breeding Season

In 1968 the birds were introduced to the flight pens on April 24. Daily observations were made for four hours beginning at sunrise from April 25 to June 13, and casual observations continued until mid-July. The starting date of the study was determined largely by local weather conditions and the accessibility of the road to the pens. Nevertheless, on the first day of observations the ponds were nearly totally ice-covered. Data were collected on 46 days, spanning 50 calendar days. I stopped making daily observations in June when the birds began to spend nearly all of the time sleeping or out of sight in the cover.

In 1969 the birds were introduced into the flight pens on April 18 and daily observations were made from April 19 to

June 12. This period spanned 56 calendar days and data were recorded systematically on 49 of these days. Casual observations were continued until late July. Again weather conditions largely governed the starting date, although it snowed the afternoon of the day the ducks were put into the pens.

Five dawn to dusk watches and one 24-hour watch were conducted throughout the study. The all-day watches established that the birds had two peaks of activity during the day, one lasting until three or four hours after sunrise and another in the early evening ending soon after sunset. On June 12, 1969 the birds were active throughout the night. There was little moonlight due to cloudcover and, although the birds were heard to fly about the pens, it was too dark to see what behavior they performed.

The positions of birds were recorded on outline maps of the pens. Every ten minutes I noted the location of each bird and whether it was asleep. These data were transferred to punch cards for analysis by programs written for a CDC 6600 computer. The programs were written previously for other studies but could be used without changes for the duck pen data. The study generated about 36,000 animal locations.

Notes were made on the activities of each individual along with the time and location of their occurrence. Activities recorded included prenesting behavior, nesting, copulation, rape attempts (Raitasuo, 1964), chases, fights and other encounters between birds. In 1969 I did not record the location of many of these activities so that I would be able to observe the behavior involved more carefully.

RESULTS

Seasonal Distribution of Activities

In the following sections I will summarize my observations on each aspect of breeding behavior in turn, noting especially the frequency and seasonal distribution. This treatment, however, tends to obscure significant temporal associations between different activities. Since each bird was on a different breeding schedule, and its behavior could be greatly influenced by other birds, it is necessary to trace the seasonal changes in behavior for each pair separately. With this in mind, I plotted the seasonal distribution of major breeding activities for each pair in composite figures (Figs. 1-4). Frequent reference will be made to these figures throughout the thesis.

Figures 1-4. Composites of a number of activities in each pair of Mallards observed from April 25 to June 13, 1968 and from April 19 to June 12, 1969. Gaps in the baselines indicate days of no observations. The vertical scale for all four figures is included on Figure 1.

KEY

- A Copulations: above line successful, below line unsuccessful attempts. Forced pair-copulations are blacked in.
- B Rape attempts: above line made by the male, below line directed at the female.
- C Male-male chases: above line made by the male, below line directed at the male.
- D Male-female chases: above line made by the male, below line directed at the female.
- E Fights: above line not associated with a rape attempt, below line associated with a rape attempt.
- + Day first egg was laid.
- + Day last egg was laid.
- + Day eggs hatched.
- MM Occurrence of Persistent Quacking.

Figure 1. Composite of activities in 1968 Pen 1.

Figure 2. Composite of activities in 1968 Pen 2.

Figure 2. Continued.

Figure 3. Composite of activities in 1969 Pen 1.

Figure 4. Composite of activities in 1969 Pen 2.

Pair Bond and Male Sociability

During the week before the study began each spring pairs were selected on the basis of the strength of their bonds. Bonds were identified by the occurrence of the Inciting display of the female, given beside a preferred male, followed by the male's performance of a Belly Preen or Preen-Behind-Wing beside the female. Strongly paired birds spent much of their time together. After introduction to the flight pens, all bonds remained intact, the members staying close together, except for periods when hens were on their nests, until the pair bond disintegrated. Pair bonds are probably reinforced through almost constant close association of the members, copulatory behavior, Inciting by the female, and through the performance of Rabrab Palavers (Lorenz, 1953).

The strength of the pair bond apparently decreases as the degree of sociability between males increases. Beginning on May 7, in both years, the males began to spend time near each other without any overt signs of aggression. By May 20, 1968 all males could be described as essentially "sociable".

In 1969 the males commonly spent time together from May 11 onward. In the early stages of male sociability, males frequently approached each other on water, giving the Rabrab call while holding the bill up (Abraham, 1971). As they met, head to head, they moved their bodies parallel to each other and began to apparently drink. After this initial meeting and drinking the males would swim, feed, or rest together. During the early stages of male sociability, the birds would frequently associate quietly

one moment then chase each other the next. An obvious interference with male sociability was the presence of a female. A male behaving socially with other males either left them or became aggressive toward them as his mate approached.

In 1968, pair bonds were more and more difficult to detect as male sociability increased. In addition, the non-nesting females began to join the group of males. At this time, the nesting females were usually on their nests throughout my observation periods. By the time hatching began, the adult birds without young were in a flock, and hens with broods avoided the other birds. It should be noted that in the pens the members of a pair were rarely out of sight of one another, even when the female was on the nest. Males were not removed from the pen at mid-incubation - the time when pair bonds apparently disintegrate in the wild. In fact, three males routinely rested within three feet of their mates who were on nests. One of these males did not give up that resting spot until the 18th day of his mate's incubation when he left and joined the other males.

In 1969 pair bond strength did not decrease with the onset of male sociability. The males became sociable according to the pattern exhibited in 1968 but they also continued to spend time with their mates late into the study season. In fact the pair bonds never did disintegrate to the point where pair members were no longer found together at some times, although females with broods did chase away former mates as well as any other adult bird that approached. This added distraction led to the hens giving less than usual attention to their broods. This may be

one explanation for the high brood mortality of 1969. In the previous year, the males appeared to ignore the hens with broods and all but one duckling (which I accidentally killed) lived to maturity.

Prenesting Behavior

The female Mallards performed similar prenesting activities to those reported for other Anas species (McKinney, 1969). These included bouts of Persistent Quacking (Abraham, 1971), moving about the cover with a halting walk and a horizontal body posture, and brief flights alone or with the mate that were frequently accompanied by Persistent Quacking. The calling was usually given while the female was beside her mate and was most frequent just before sunrise. The vocalizations did not appear to attract attention from other birds.

In 1968 three of the four nesting females gave Persistent Quacking (Figs. 1-4). But one, a very late nester, gave these calls on only one occasion. The three females giving this call stopped on or before the day the first egg was laid. In 1968, three females that did not nest also gave this call, two of them being heard calling on only one occasion. The third female called over an 11 day period, being the first hen in the pen to give the call. She ceased calling on May 6, one day after her only nesting penmate began to lay eggs. This Persistent Quacking non-nester was unique in that she occasionally gave the call while in a sleeping posture, with the bill tucked back under the wing.

In 1969 six of the eight nesting females performed Persistent Quacking. All but one ceased on or before the day the first egg appeared; the other stopped on the day after she laid her first egg.

Normal Copulations

Male Mallards practice three different methods of inseminating females: normal pair copulations, forced pair-copulations, and rape attempts (see Figs. 1-4). Sixty-nine apparently successful normal copulations and 32 unsuccessful attempts were recorded during the study. "Normal copulations" were preceded by Head-pumping and were recorded as "apparently successful" if followed by the male post-copulatory displays (Bridling and Nod-swimming) (Raitasuo, 1964). An "unsuccessful attempt" involved mounting but no male post-copulatory display followed and usually the male's tail did not pass around the female's tail.

Pairs occasionally copulated successfully twice during a four-hour morning watch. Normal copulations were not recorded regularly every morning for any pair but, on average, it is likely that each pair made daily attempts. Whole day watches showed that as many as four attempts were made by some pairs in the early part of the season.

The proportion of copulation attempts that were successful (Table 1) varied from pen to pen and from year to year but sample sizes are too small to reveal correlations to explain these variations.

TABLE 1. Relative success of normal copulation attempts
and forced pair-copulation attempts.

Pen 1, 1968

	Successful	Unsuccessful	Total
Normal	21	6	27
Forced	2	6	8
Total	23	12	35

Pen 2, 1968

Normal	17	1	18
Forced	1	0	1
Total	18	1	19

Pen 1, 1969

Normal	13	2	15
Forced	7	10	17
Total	20	12	32

Pen 2, 1969

Normal	8	1	9
Forced	1	6	7
Total	9	7	16

OVERALL TOTALS

			% SUCCESS
Normal	59	10	85
Forced	11	33	33

Successful copulations, both normal and forced pair-copulations, were performed by breeding pairs from one to 35 days before the first egg was laid (Table 2). More than half of these copulations were within eight days before laying began. During the laying period five pairs performed eight normal copulations while two pairs performed seven successful forced pair-copulations (Figs. 1-4). No normal successful copulations were recorded involving an incubating hen. Comparison of successful copulation records for the Mallards with similar data for Shovelers shows a striking difference (Table 2), the frequency being much higher for Shovelers.

Forced Pair-Copulations

Eight different pairs of birds were seen to attempt copulations without precopulatory Head-pumping movements, the male trying to mount his mate after grasping her back or wing feathers and pulling her to the water. The female attempted to free herself by struggling but little chasing was involved. Three of these forced pair-copulations occurred on land, two of which were apparently successful, the male giving Post-copulatory Bridling (with whistle) and Nod-swimming movements. Three forced pair-copulations immediately followed attempts by other males to rape the female (see p. 30). Forced pair-copulations are noted on Figures 1-4, along with the number of copulations by each pair throughout the season.

The forced pair-copulations, in general, appear toward the end of the period when a pair was copulating in a season. Among

TABLE 2. Copulation frequency in breeding Mallards in relation to egg-laying compared with similar data for Shovelers (from McKinney, 1967). The counts for both species include apparently successful copulations only (both normal and forced pair-copulations in the case of the Mallard). Eight pairs of each species were studied for two consecutive seasons in the same pens.

<u>Days before first egg is laid</u>	<u>Number of pairs observed</u>	<u>Pairs observed copulating</u>	<u>Number of successful copulations</u>
--	---	--	---

MALLARDS (301 hours observation)

1-4	47	8	9
5-8	34	8	9
9-12	18	3	3
13-16	16	2	3
17-20	16	1	1
21-24	15	1	2
25-28	12	2	2
29-32	12	1	1
*33-35	5	2	2

*= 3 days
only

SHOVELERS (267 hours observation)

1-4	13	13	28
5-8	13	12	26
9-12	8	7	9
13-16	6	3	3
17-20	3	3	6

breeders, all but four of the 25 forced pair-copulation attempts observed occurred before the onset of incubation. I do not consider this behavior to be a sign of a weak pair bond. Pair bonds appeared firm at this time.

Only eleven of 33 forced pair-copulation attempts were successful compared to 59 of 69 normal copulation attempts (Table 1). One male (R1) performed forced pair-copulation attempts much more frequently than any other male: this pair also performed many normal copulations. Thus, in 1969, six of the 14 apparently successful copulations performed by this pair were forced pair-copulations.

On five occasions pairs performed both normal and forced pair-copulation attempts on the same day. I can find no temporal association between the two events in four of the cases. The fifth was part of a sequence of events leading to the pairing of the two birds involved (1969 W1 female and Y1 male).

On 16 days during the study a female received both rape attempts and forced pair-copulations (Table 3). (A female received both rapes and normal copulations on only five days). In 11 cases the forced pair-copulations followed the rape attempt within the hour. Three rape attempts at females were immediately followed by forced pair-copulations.

Interrupted Copulations

Because of the relatively small size of the pens the possibility of copulation attempts being interrupted by other birds was high. I was unable to determine how often precopulatory

TABLE 3. Temporal association of forced pair-copulation
(FPC) and rape attempts at females.

		FPC FOLLOWED RAPE			FPC PRECEDED RAPE
	<u>Date</u>	<u>Female</u>	<u>immed.</u>	<u>less than 1 hour</u>	<u>more than 1 hour</u>
1968	April 29	R1		X	
	May 10	Y1			X*
	May 14	R2		X	
1969	April 21	R1		X	
	April 28	R1	X		
	April 29	R1			X
	May 1	G1		X	
	May 2	W1	occurred in pair formation sequence with Y1 male		
	May 3	R1			X*
	May 4	R1		X	
	May 5	G1	X		
	May 7	G1			X*
	May 11	W2		X	
	May 12	W2		X	
	May 18	W2		X	
	May 23	W2	X		
			<hr/>	<hr/>	<hr/>
			3	8	1
					<hr/>
					3

* = FPC occurred within first 30 minutes of observation period, and
an unobserved rape could have preceded FPC in these cases.

Head-pumping was stopped because of approaching birds, but birds were interrupted only occasionally while attempting to mount. This happened three times in 1968, in all cases involving pair Y1 interrupted by G1 male who was, with his mate, occupying the same small part of the pen as the Y1 pair at the time. In 1969 there was only one instance of an obvious interruption.

Rape Attempts

In this study, rape attempts (Figs. 1-4) often began with a lengthy vigorous chase, the female often being detected in the cover or elsewhere on land before she was able to take flight. She usually resisted the attackers, walking along, pecking at the one or more males attached to her feathers. On other occasions the males began the pursuit after she had drawn attention to herself while making some obvious position change in the pen. The males mated to females being pursued often followed along on these encounters.

The chasing was largely aerial, and at higher speeds than usual with the females flying directly into the wire walls of the pen in their attempts to elude the followers. (On other flights in the pens the birds avoided touching the walls.)

If the group landed on water the female often dove and swam a distance under water in an escape attempt. In the next stage one or more males grasped the feathers of the hen's nape or back of the head and attempted to mount her. It was not unusual for all four males to be attached to the female and each other in this way. Once mounting was accomplished the female's escape

attempts ceased and her tail raised up to one side as in a reflex movement (Weidmann, 1956). Males frequently then dropped their wings to either side of the female, probably as an aid to balance, as they moved their tails downward and around the female's. Frequently cloacal contact appeared to have been made but on only four occasions were post-copulatory displays observed after a rape attempt (an apparent sign of the success of normal pair copulations). It is impossible to determine on which occasions sperm were actually transferred.

Earlier studies (McKinney, 1965; Raitasuo, 1964; Lebre, 1961) based on non-captive, unmarked birds suggested that the peak of rape attempts at females occurred toward the midpoint of incubation when pair bonds in the wild are believed to be dissolving. In this study, rape attempts peaked in frequency during the days when females were laying eggs, as Smith (1968) found in the Pintail.

It should be noted that the penned birds were at an abnormally high density and females had no means of escape. Nest locations were learned by males and they regularly sought a female to rape by visiting nests. While making rape attempts on other females each male was neglecting to escort his own mate, thus increasing her vulnerability. Also, in the wild, males would have left the area when pair bonds broke but in the pens they were confined with their mates throughout the study. Under such conditions I expected the rape behavior to begin early and to go on throughout incubation with possible mortality of females through raping as Weidmann (1956) reports. Instead, after peaking during the

period of egg-laying, rape behavior then diminished. This is shown in Figure 5 where rape attempts at all breeding females are considered together. An individual analysis of the behavior is presented in Table 4. Two incubating hens (1969 W1 and G1) experienced a number of rape attempts. This is reflected in the similar counts of rape attempts at laying and incubating females in 1969.

In 1968 pen 2, two hens nested late in May at a time when the early nesting female was late in the incubating stage. The mate of this female made 10 of the 14 rape attempts experienced by the late nesting hens. In addition, the late nesting hens experienced rape attempts at the time the early nesting hen was laying eggs as well as the time when they were laying eggs themselves.

As might be expected there was a great deal of individual variation in the amount of raping activity experienced by females as well as in the number of rape attempts performed by males. I believe the presence and/or activities of females preparing to lay eggs is the primary trigger for rape attempts by males. This may be modified by the behavior of an individual female as well as by the behavior of her mate toward her and toward other males.

For example, only eight females received rape attempts while actually sitting on their nests (one effectively resisted by backing tightly up against the wall of the pen). On 39 occasions hens were flushed from their nests by drakes and immediately raped. Had they remained in the nest many could probably have repelled the attackers, or perhaps if they had not so easily

Figure 5. The number of rape attempts at females in relation to the nesting cycle, spanning 66 days.

TABLE 4. Frequency of rape attempts (A) performed by males in relation to the stage of their mate's breeding cycle and (B) directed at females in relation to the stage of their breeding cycle. (Only breeding birds are included).

Pair		A				B			
		mate pre-laying	mate laying	mate incubating	mate post-incubating	pre-laying	laying*	incubating*	post-incubation
<u>1968</u>	Y1	0	2	4	0	0	19	2(1)	0
	R2	0	5	10	0	0	5	4	0
	G2	4	2	0	0	7	6(4)	0	0
	W2	<u>5</u>	<u>2</u>	<u>0</u>	<u>0</u>	<u>2</u>	<u>5(3)</u>	<u>0</u>	<u>0</u>
Year Totals		9	11	14	0	9	35	6	0
<u>1969</u>	R1	1	7	7	2**	3	10	2	4**
	G1	4	7	14	4	1	13(13)	8(7)	2(1)
	W1	1	-	-	-	2	1(1)	9(6)	2
	Y1	1	13	4	1	3	2(2)	4	0
	R2	1	0	1	0	1	0	4	0
	G2	2	1	3	0	1	1(1)	3	2
	W2	5	0	2	0	10	1(1)	0	0
	Y2	<u>0</u>	<u>3</u>	<u>6</u>	<u>0</u>	<u>0</u>	<u>0</u>	<u>1</u>	<u>0</u>
Year Totals		15	31	37	7	21	28	31	10
TOTAL		24	42	51	7	30	63	37	10

*Figures in parentheses refer to cases where female was chased off the nest by males and raped.
 **Rape attempts occurred during the renest interval.

flushed no attempted rapes would have followed at all. This was especially the case with the 1969 G1 female. Frequently one male chased her from the nest while a second immediately attempted to mount her. The strength of a male's tendency to launch a rape attempt may be influenced by the stage of his mate's breeding cycle and the strength of his pair bond but this is difficult to determine. I believe that the stimulus of seeing other females in the pen preparing to lay eggs is of primary importance. Since the mating system of male Mallards involves a combination of pair bonding and promiscuity, they encounter special problems in protecting their mates and strategies may be expected to have evolved through competition among males for the opportunity to fertilize eggs. My observations suggest that Mallards use two such strategies: (1) attempting to drive off the rapers by fighting with them (Table 5) and (2) forcefully copulating with their own mates soon after a rape attempt at their hen.

Four males reacted with fighting during more than 50% of the rape attempts at their females. This fighting appeared to greatly decrease an attacker's chances of mounting and thus fertilizing the female.

Nesting

During the two years, hens initiated 13 nesting attempts, including one hen (1969, R1) who abandoned her first nest and later made a second attempt. In addition, the 1968 R2 female laid two eggs in a nest in an area where many chases passed

TABLE 5. Frequency of mated male fighting with males
attempting to rape his mate.

		<u>Number rape attempts on mate</u>	<u>Number of fights with other males</u>	<u>% of rape attempts where mated male fights other males</u>
1968	R1	13	3	23
	G1	1	0	--
	W1	7	3	43
	Y1	21	3	14
	R2	9	2	22
	G2	13	2	15
	W2	7	5	71
	Y2	3	0	--
1969	R1	19	15	79
	G1	24	18	75
	Y1-W1	14	5	36
	Y1	9	3	33
	R2	5	1	20
	G2	7	4	57
	W2	11	5	45
	Y2	1	0	--

nearby, causing her to frequently jump out of the nest. Without missing a day, she began laying in a second nest about 25 yards away. Ducklings were produced from 11 of the 13 clutches, but in only eight cases did the broods survive more than one week. All ducklings that attained one week of age grew to maturity.

Detailed breeding records are presented in Table 6.

In 1968, when the birds were yearlings, four females nested; one in pen 1 and three in pen 2. Two of the pen 2 nesters did not begin to lay eggs until late May when nest cover growth finally became luxuriant, and soon after the change to floating feeders resulted in increased consumption of high protein feed. Hatching success ranged from 38% to 89%. Of the 23 ducklings hatched, 22 survived (96% success): I accidentally killed the other.

In 1969, when the birds were two years old, all females nested. The first nest was initiated on April 22 (this female was the first nester in 1968 also). The last nest initiation, a renesting attempt, began June 7. Hatching success, omitting abandoned nests, ranged from 38% to 90%, with all but one of the lower successes occurring with the females that had not had previous nesting experience. Of the 44 eggs hatched only 27 ducklings survived to maturity. In pen 1 the young of the second nesting attempt of the R1 female all survived and the one experienced female lost only one young while the other two broods hatched in the pen were all dead within four days of hatching. In pen 2, three complete broods were raised while one brood did not survive longer than three days. Duckling survival in 1969 was 61%.

TABLE 6. Breeding records of Mallards in flight pens
beginning April 24, 1968 and April 18, 1969.

<u>Pairs</u>	<u>Date of first egg</u>	<u>Clutch size</u>	<u>Days of incubation</u>	<u>Eggs hatched</u>	<u>Young raised</u>	<u>No. eggs removed</u>
1968						
Y1	May 5	10	25	8	8	0
R2	May 2	8	26	3	3	3
G2	May 28	6	24	4	3	0
W2	May 30	9	23	8	8	*0
1969						
R1	April 26	10	20	ABANDONED		10
R1	June 7(renest)	9	23	8	8	0
G1	April 25	11	25	6	0	5
**W1	May 12	9	25	5	0	2
Y1	April 25	9	25	7	6	0
R2	April 22	9	24	5	0	2
G2	April 24	10	24	9	9	1
W2	May 22	4	18+	ABANDONED		3
Y2	April 26	10	24	4	4	0

*The W2 female apparently removed two eggs laid by a previous occupant of her nest.

**W1 female paired with the Y1 male.

Egg Removal

In 1968, one hen (W2) laid nine eggs in an abandoned nest which already contained eggs. The two foreign eggs disappeared from the nest and were later recovered from the pond bottom. The first removed egg was found floating on the water within one hour after the W2 female laid her first egg (May 30), and the second one disappeared from the nest on June 24, the 18th day of W2's incubation of her own eggs. Each egg had a hole in it of a size and shape suggesting that it was made by a duck's bill. When both of these eggs were in the nest they were very dark and when found in the pond they smelled decomposed. One egg disappeared from another 1968 clutch three days before the rest of the eggs hatched. The egg in question when found in the pond bottom showed no apparent signs of development.

In 1969, two females were seen carrying eggs from the nest into the water. On April 29 the R2 female went to her nest, poked her head in while making a whimpering noise, then walked to the water carrying an egg in her bill. She dropped the egg into the water. This occurred one day before she began to incubate. A second observation involved the G1 female. On the day after she laid her last egg she walked to her nest and immediately walked back to the water's edge carrying an egg. She entered the water and swam out into the pond where she dropped the egg. Egg removal has also been reported for penned Shovelers (McKinney, 1967).

During the two seasons 26 eggs were found in the ponds, each pierced with a hole apparently made by a duck's bill. Twenty-three

of these eggs were found in 1969, 17 of them in pen 1. The 1969 eggs of R1 female were the only ones known to be cracked before removal. In 1969 the two females that removed most eggs were chased off their nest more than the other females with one exception. Also, five of the eight females apparently removing eggs made 90% or more of their nest departures as a result of being chased off by other birds. As far as I could determine, the discarded eggs would not have hatched had they been left in the nests.

Renesting and Nest Failures

There was one instance of renesting in the two years. In 1969 the R1 female was recorded being chased off her nest 224 times, 203 times by the Y1 male, and eventually she abandoned her effort, 20 days after the last egg was laid. The nest was clearly visible from the front, a result of her removing the grass to incorporate it into the nest. The day she abandoned was also the day the last of her 10 eggs disappeared, apparently by removal. Some of her eggs were cracked, just prior to their disappearance into the pond, presumably by the force of her launching from her nest as she was chased off. The mate of this female was unable to prevent males from approaching her nest and chasing her off. He typically met the chaser male, especially Y1, as he approached the nest. They would then run together toward the nest while calling Rabrab until the female left. This pattern continued until she abandoned the nest.

This was an obvious case of a male learning the location of a nest. Frequently the Y1 male would sneak up (flattened posture, halting gait) to the R1 nest and the female would not be there. Also this Y1 male appeared to chase only this female. During the nest period, when he chased her off the nest 203 times, he attempted to rape her only four times. The R1 renesting attempt began on June 7 and was 100% successful.

Two other nest failures also occurred in pen 1 during the 1969 study season. Some of the eggs were removed from both of these nests and when the remaining eggs hatched the young did not survive beyond four days of age. The two nests belonged to W1 and G1, but the G1 female was the female incubating the eggs at the time of hatching in both cases. (Five days after the young in the G1 nest were hatched and they were all dead, the G1 female displaced the W1 female from her nest. The G1 female was equally unsuccessful at raising a second brood.) These two females received more rape attempts during incubation than any other hens.

Many of the dead young had head or body lacerations but only one observation was made of a duckling being killed. The G1 female was brooding the young on the nest when several males attempted to rape her. In the confusion, one of the young wandered about a yard away from the nest. As the hen returned to the nest she did not appear to notice the stray young and the duckling followed the nearby G1 male into the water. As they swam the male did not make any apparent movement toward the duckling. As they neared the Y1 female and brood, the G1 duckling joined the brood

and the G1 male swam on by. In less than two minutes the Y1 female made several forceful jabs at the head of the strange young. It then swam to shore, hobbled up onto land and into the cover where it was found dead at the end of the observation period. In 1968, however, I recorded one instance of a strange duckling being successfully incorporated into a brood.

There were also nest failures in pen 2 during the 1969 study. Three eggs were found in the pond and five ducklings were found dead, some with lacerations. In addition, one nearly fully developed egg was found in the Y2 nest with part of the shell removed. The embryo was still moving under the membrane. Two days later this egg was found broken in the pond with the badly lacerated duckling and some yolk hanging from it. Raitasuo (1964) also refers to the intolerance of females toward strange ducklings. I agree with Titman (1969), who cites overcrowding as an aggravation of this intolerance by the females.

Harassment of Females on the Nest

Nesting females often did not spend the entire observation period on the nest. During the period of egg laying they often did not go to their nests until two to three hours after sunrise. Also hens were frequently chased off the nest by males (Table 7). At least 70% of the times that females left their nests there was a male chasing them. One male was responsible for 45% of the chases at females on nests. This high level of harassment of females was undoubtedly a major artifact of the pen situation.

TABLE 7. Nest leaving and egg removal by females. Data for four hens (*) are incomplete: the 1968 G2 and W2 females as well as the 1969 W2 female had not finished their nesting effort by the end of the study. The 1969 W1 female was displaced from her nest by another hen before her eggs hatched.

	<u>Bird</u>	<u>Total nest departures</u>	<u>No. involuntary departures</u>	<u>%involuntary departures</u>	<u>No. eggs removed</u>
1968	Y1	33	23	70	0
	R2	11	8	73	3
	*G2	7	6	86	0
	*W2	5	5	100	0
1969	R1	228	224	98	10
	G1	83	76	92	5
	*W1	10	9	90	2
	Y1	35	26	74	0
	R2	49	46	94	2
	G2	24	19	79	1
	*W2	4	1	25	3
	Y2	20	16	80	0
		<u>509</u>	<u>459</u>		

Table 8 indicates how many times each male chased each female off the nest and shows that there was much individual variation both in the numbers of chases made by males and in the number of chases experienced by females. These differences can probably be attributed to cues given by the females, cues given by their mates, and relative locations of the birds at the time. Included in "cues" would be the social rank of the individuals. The visibility of the nests also seems to have been important, but I suspect that the location of every nest was learned by each individual in the pen. Some males immediately followed these chases with attempts to rape the nesting hen. On rare occasions (eight times) rape attempts were made right at the nest.

Mates of the nesting hens responded in a variety of ways to their females being chased off their nests. When one hen underwent a high rate of chases off her nest her mate began to rest in the cover at the nest edge. This was his usual position during observation periods until his mate's 18th day of incubation. His presence alone apparently deterred any further chasing. Some other drakes rested at or near their mate's nest and chased away any approaching birds. A third type of mate response was discussed above in the case of the R1 male in 1969 who accompanied the chaser male to his hen's nest and did not deter the chase in any way.

TABLE 8. The number of times identified males chased females off their nests in 1969.

Female	No. chases by males at laying hen		Rate per day	No. chases by males at incubating hen		Rate per day
R1	Y1	38	3.8	Y1	165	8.2
	G1	2	.2	G1	16	.8
G1	Y1	22	2.0	Y1	40	1.6
				R1	13	.5
W1	G1	2	.2	G1	13	.5
				R1	1	.04
Y1	G1	13	1.4	G1	14	.6
	R1	2	.2			
R2	W2	9	1.0	W2	23	1.0
	Y2	8	.9	Y2	1	.04
	G2	1	.1			
G2	Y2	7	.7	W2	9	.4
				Y2	3	.1
				R2	1	.04
W2	Y2	1	.2	Y2	2	.1
				R2	1	.1
Y2	G2	4	.4	W2	11	.5

SUMMARY

Males chasing females that are:

	<u>laying</u>	<u>incubating</u>
Y1	60	203
G2	17	43
R1	2	14
W2	9	43
Y2	16	6
G2	5	0
R2	0	2
	<u>109</u>	<u>313</u>

Females chased while they are:

	<u>laying</u>	<u>incubating</u>
R1	40	181
G1	22	53
W1	2	14
Y1	15	14
R2	18	24
G2	7	13
W2	1	3
Y2	4	11
	<u>109</u>	<u>313</u>

Encounters Between Males

Hostile encounters between males varied greatly in intensity. An approach by one bird could cause another to move aside. Slight forward movements of the head could develop into open-bill threats and these could grade into chases involving a rapid rush at another bird. While low intensity forms of threatening were frequent they proved to impossible to record consistently and my counts of male hostile behavior were classified simply as either "chases" or "fights".

Chasing. A chase is defined as rapid swimming or running at another bird. The chaser can adopt a posture with the bill on the breast and pointing slightly downward or he can stretch his open bill toward the other bird. Males seldom flew to chase other males but they often did when chasing females.

During the two year study, 1983 male-male chases were recorded. This represents 45% of chases performed by males, the others being directed at females. Seasonal trends in chasing activity are summarized in Figure 6 for each pen and in Figures 1-4 for individuals. Chase rate totals were calculated as an index of aggressiveness. This reflects the number of chases per male hour for each day.

Pen 1, 1968. The rate of male-male chases was low (60.5 chase rate total for the year). Only two males (W1 and R1) were recorded chasing during the first 11 days; thereafter all four males chased and were chased. There was only one laying hen and her

Figure 6. Daily male-male chase rate totals throughout two study seasons. Total chases by all four males in a pen during each observation period as expressed in chases per hour. (Gaps in the baseline signify days when no observations were made.)

mate contributed little to the chasing total. He did not begin to chase until the day after his mate laid her first egg, but male-male chases in the pen increased during the mid-incubation period for this hen. Forty-one percent of male-male chases occurred during the early peak.

Pen 2, 1968. There were two peaks of chasing activity. At the start of the season, one male (R2) chased almost exclusively and his mate laid first. The high level of chasing by this male ceased on the day that his mate laid her first egg and thereafter two other males (W2 and G2) did most of the chasing in the pen, R2 becoming the subordinate male. The second peak of chasing was on the days before G2 and W2 females began to lay. Chasing stopped one day before the first ducklings hatched. The chase rate total for the year was 206, 45% of chases occurring during the first 17 days. On the days when the three hens were laying, their mates were the most aggressive males in the pen (or they shared this rank with another male).

Pen 1, 1969. Chasing was much more frequent between these four males than it was in 1968 (118.9 chase rate total compared to 60.5 for 1968). The first striking decrease in chasing occurred on the day after the last clutch was initiated (May 12). 64% of the chase rate total for the year was before this date.

No male was "the most aggressive" for more than five consecutive days. Also, male W1, a very aggressive bird in 1968, never became the most aggressive bird in 1969, and on April 30

2

this bird was found dead. Each of the other three males was the most aggressive male (or he shared that position with another male) on the day his hen laid her first egg. Male Y1 had two mates which began laying in sequence and he chased for an unusually long period.

Pen 2, 1969. Seasonal changes in male-male chasing activity were less clearly correlated with the breeding activities of females. The chase rate total for the year was lower than in 1968 (135.78 compared to 206), and there were few obvious peaks. In general, however, males chased before and during the laying periods for their hens and two males showed increases in chasing at the time of hatching. One male (G2) chased frequently during the first week of his hen's incubation period, but most were directed at the Y2 male for some unknown reason.

Data dealing with males chasing males were recorded similarly for Mallards and Shovelers. Analysis reveals that as a group, Shoveler males chased males more than Mallards did (Fig. 7). Considering the rates of chasing done by individuals (Table 9) the highest rate for any of the Mallards (15 considered) was 46.8 chases per hour. Of the 16 Shovelers considered, six of them chased more than 52.4 times per hour.

Fighting. Fights between males occurred both on land and water and included breast-jostling, wing-beating and bill-tugging as described by Weidmann (1956). These encounters were often preceded by Rabrab calling while holding the bill up by both

Figure 7. Male-male chases per hour by Mallards and Shovelers
(omitting each third day).

TABLE 9. Individual Mallard and Shoveler males chasing
males per hour for each two out of three days
(season totals: Shovelers observed 267 hours,
Mallards observed 301 hours).

1968 Mallards

R2 46.83

G2 44.09

W2 39.50

W1 14.92 $\bar{x} = 23.64$
Range = 41.08

G1 14.67

Y2 13.08

R1 10.33

Y1 5.75

1969 Mallards

G2 36.91

Y1 30.67

Y2 30.51

G1 26.75 $\bar{x} = 25.19$
Range = 26.99

R1 25.11

W2 16.50

R2 9.92

1965 Shovelers

80.1

62.2

52.4

34.2 $\bar{x} = 38.9$
Range = 68.4

30.6

22.4

17.9

11.7

1966 Shovelers

81.8

63.2

52.4

34.9 $\bar{x} = 39.6$
Range = 69.4

31.6

22.4

18.4

12.4

males (Abraham, 1971). I was usually unable to identify the initiators or the winners of fights.

Fights were generally associated with disputes between well-balanced aggressive males or with rape attempts. In some pens, 37% of fighting occurred when a male engaged other males which were attempting to rape his female. Usually such a fight began when a mated male, after Rabrab calling, grasped one of the raping males by the nape and began beating him with his wings. In the confusion, it often looked as though the mated male was attempting to rape one of the other males! Fights in this context were generally one-sided.

In aggressive situations between two males, fights appeared to occur when neither bird would retreat. Often both birds ran or swam along side by side calling Rabrab, with bills raised; then they either fought or engaged in feeding, drinking or resting without obvious signs of hostility. Many particularly prolonged bouts of balanced conflict of this type occurred between males Y1 and R1 in 1969. In addition to Rabrab calling side by side, these males spent long periods (lasting up to 11 minutes or so) almost motionless a few inches from one another. They also frequently made movements resembling feeding, dabbling with the bill in the grass or bank at the edge of the pond. Films showed that swallowing motions seemed to occur but the behavior differed from normal feeding in being more jerky and slower. The feathers on the back and scapulars were erected and the birds ignored other events in the pen (even a rape attempt directed at the mate of one of them). Many of these encounters took place when Y1 male approached close

to R1 female's nest; this often resulted in R1 female being chased off her nest and may have been a major factor in the failure of this female's first nesting attempt.

I have no evidence that fighting between males resulted in changes in dominance relationships or areas occupied, although in one case (R2, 1968) fighting behavior appeared immediately after the male dropped from supremacy. Each male usually returned to the area he had been occupying before the fight or else the two birds continued to associate with one another without signs of overt hostility. Fighting between a male attempting rape and the mate of the hen being attacked appeared effective in preventing a successful rape. Thus the mated male could protect his "investment" of genes in his female by fighting with an attacker. Mated males were not very successful in preventing harassment of their hens by males attempting rape, but they were quite successful in preventing the rape attempt from resulting in insemination. There was considerable variation in both the context of the fights and the adversaries. This is detailed in Table 10.

Male-female Chases

Encounters involving pursuit of a female by a male were classified as either "chases" or "rape attempts". These are purely descriptive terms for pursuits with different characteristics and I will avoid the controversial issue of male motivation. The "results" of the two types of pursuit were different and this was the primary criterion for distinguishing them: "chases" did not end in grasping of the female with an attempt to copulate with

TABLE 10. Frequency of fights between males associated with rape attempts (A, B, C, D) and not associated with rape attempts (E, F, G, H). The W1 male died on day ten of the 1969 study season.

1968

	R1	G1	W1	Y1	
R1	-	1	1	1	
G1		-	2	1	
W1			-	3	
Y1		total 9		-	A

	R2	G2	W2	Y2	
R2	-	2	6	1	
G2		-	0	0	
W2			-	0	
Y2		total 9		-	B

1969

	R1	G1	W1	Y1	
R1	-	20	1	6	
G1		-	0	14	
W1			-	0	
Y1		total 41		-	C

	R2	G2	W2	Y2	
R2	-	2	0	0	
G2		-	1	3	
W2			-	4	
Y2		total 10		-	D

	R1	G1	W1	Y1	
R1	-	0	0	0	
G1		-	0	17	
W1			-	0	
Y1		total 17		-	E

	R2	G2	W2	Y2	
R2	-	4	3	5	
G2		-	2	1	
W2			-	0	
Y2		total 15		-	F

	R1	G1	W1	Y1	
R1	-	14	1	15	
G1		-	12	26	
W1			-	1	
Y1		total 69		-	G

	R2	G2	W2	Y2	
R2	-	1	1	3	
G2		-	3	17	
W2			-	14	
Y2		total 39		-	H

her, "rape attempts" did. It is quite possible that some "chases" were low intensity "rape attempts".

Chases involved running, fast swimming or flying. In these pursuits both birds took wing much more frequently than in male-male chases. Females usually retreated when chased but occasionally they did not respond in this way. For example, on May 3, 1968, R2 male ran at the W2 female five times. Her response was to remain perfectly motionless. The male responded to this by stopping abruptly within three feet of her, then walking away. On two of these occasions he very slowly and deliberately touched the ground with his bill several times before walking away. On the previous day his 22 rushes at this female resulted in her rapidly moving away from him. A second case of a female not retreating when a male rushed at her involved a hen with a bad head injury. Her response to an oncoming male was to open her bill as in the gesture of Repulsion (Lorenz, 1953), given by an incubating hen. The opening of the bill was accompanied by a soft whimpering sound. This deterred most chase attempts. The onrushing males stopped short and walked away.

Incubating hens were frequently chased by males of other pairs when they were off their nests. These birds typically responded by giving Repulsion behavior but this did not discourage pursuit.

Most chases directed by males at females did not lead to involvement of the female's mate i.e. paired males did not appear to "rush to their mate's aid" in these situations, a reaction that is very frequent in the Shoveler. In wild Mallards, male-female chases very often entail aerial pursuits of considerable length,

the female's mate typically following behind but not attempting to fight with the pursuer in the air. This is the well-known "three-bird flight" and, for lack of space, pursuits of this type were impossible in the flight-pens.

A situation producing a male-female chase was an intrusion by a female into an area of the pen controlled by the male. This often happened as a female fed or searched cover for nest-sites. At other times, males would approach females as they sat quietly beside their mates, initiating a chase spontaneously without provocation by the female.

"Rape attempts" often began in similar ways but typically they often involved more than one chasing male, the pursuit was more determined and prolonged, and in the end the female was assaulted by the males. Pursuits with this ending have been discussed separately (p. 26).

The chase rate total at females (Figure 8) for 1968 in pen 1 was 95.5, a rather low rate. Chasing activity peaked during the second and third weeks, then declined, but there was a secondary peak in June. In pen 2, the rate was much higher (212.93), largely because of the energetic chasing of the dominant male R2. The seasonal distribution of all chases reveals a similar bi-modal pattern with an early period of frequent chases and a later resurgence of chasing in June.

Chase rate totals for 1969 were 236.17 (pen 1) and 134.61 (pen 2) and again the bi-modal pattern is exhibited when data for all females in each pen are grouped.

Figure 8. Daily male-female chase rate totals throughout two study seasons. That chases by all four males in a pen during each observation period as expressed in chases per hour (gaps in the baseline signify days when no observations were made).

The overall seasonal distribution pattern of male-female chases revealed by grouping the data for all birds in each pen seems to result from a number of interacting factors, the relative importance of which may well have varied from pen to pen. While there are some clues, the problems of distinguishing causal relationships from activities associated by chance are formidable.

The initial peak of chasing occurred at the time when many females were preparing to nest and while they were laying. At this stage, females are exploring cover and are likely to intrude in areas occupied by males. Also they are much more "available" to be chased than after they have begun to incubate. However, some females (1968 G2 and W2) delayed nesting and although they were "available" for chasing they were rarely disturbed after the clearly dominant R2 male greatly decreased his chases at females.

Chasing in Relation to Other Activities

Clearly the seasonal distribution of chases must be examined in the light of events in each pen and the interactions of individuals. The relationship between male-female chases and other types of interactions (male-male chases, fights, rape attempts) is of particular interest and one way to investigate this problem is to compare the seasonal distribution of the various activities in individuals (see Figures 1-4). For this, only breeding pairs will be considered.

In pen 1 in 1968 only the Y1 female laid eggs. She was chased regularly until her clutch was completed. Her mate did

not begin to chase females until after she began to lay, then he nearly ceased before the onset of incubation. The Y1 male rarely chased males but he was chased more than ever during his mate's laying period. The female experienced most of her rape attempts during the days she was laying.

In pen 2 in 1968 the timing of the aggressive activities of the dominant R2 male greatly influenced the activities of the other birds. I suspect that R2 male displayed the behavior most closely resembling that of an average wild male living under natural conditions of all the birds in the study. This male was extremely aggressive toward both males and females from the start of the study until his mate had laid about half of her clutch. At this point the other males began to chase the R2 male (but not his mate) while he all but ceased to chase them. The R2 male continued to chase females but to a lesser degree. Rape attempts were directed at the R2 females on these days as well as on the days that other females were laying eggs.

The G2 male began to chase males frequently as the R2 male stopped chasing. The G2 male was the male chased least by the R2 male, and he received only a low level of chasing throughout the season. The G2 male chased females most during the time the R2 male chased females most, but to a lesser degree. During this same time the G2 female experienced the bulk of the chases directed at her during the 1968 study. This female was noted to give Persistent Quacking on one morning early in the study on one of the days she was chased a lot. Her nesting attempt was delayed until the end of May, perhaps partly due to the high levels of

chasing she experienced when she first demonstrated a tendency for egg laying. She experienced several rape attempts at this early time as well as several more at the time she was laying eggs.

The pattern shown by the W2 female closely paralleled that of the G2 female except that she did not experience rape attempts early in the study near the time she had given Persistent Quacking. The chasing activities of the W2 male appeared to be suppressed by the superdominant R2 male; he was chased a great deal at the onset of the study, but then he chased other males as soon as the R2 male ceased to chase him. The W2 male's chases at females were at a low level throughout the season except for a two-day period when he chased the G2 female nearly exclusively. The cause of these chases was not apparent.

In pen 1 in 1969 few clear patterns emerged. The birds were all a year older but no individual male was clearly dominant or subordinate. Fights between males (not involved in a rape attempt situation) were more frequent than in the previous year. The R1 male chased both males and females more before the onset of this mate's incubation than after, and he was not chased a great deal by other males at any time. The R1 female was chased more than any other female, especially during her days of incubation. In fact, her first nesting effort ended in abandonment of the nest, apparently because she was so frequently chased from it, particularly by the Y1 male. Most rapes experienced by this hen occurred during her egg-laying period, a time when her mate was also attempting to rape other females.

The G1 male also chased both males and females more before his mate began to incubate than after, although he did continue to chase females at a moderate rate until June 2. He was chased most at the same time as he was chasing other males (i.e. before the onset of his mate's incubation). The G1 female experienced most of her rape attempts during the days she was laying eggs.

The W1 male was found dead on April 29. Before that date he was quite inactive. Just prior to the day he died, his mate was chased a great deal but she was not seen to be raped by other males. The chases were neither lengthy nor vigorous but they prevented her from resting in her one favored place near her mate for any great length of time. During the May 2 observation period she paired with the Y1 male who already was well paired to his own mate. At this time, however, the Y1 female was preoccupied with egg-laying.

During a 2-hour and 45 minute period the activities of the Y1 male and W1 female began with an attempted rape, followed 20 minutes later by the male performing pre-copulatory Head-pumping before grasping her nape feathers. Then she performed Inciting beside him, and soon after there was a normal copulation attempt. Following all this, but still within the 2 3/4 hour time period, the Y1 male performed courtship displays near the W1 female, then a half hour later they successfully copulated.

Throughout the duration of this trio the male appeared to be equally strongly paired to each of the two females. In addition the Y1 male chased the R1 female at a high rate until he finally disrupted her first nesting attempt. The W1 female experienced

only one rape attempt during egg-laying and several during incubation. The Y1 male chased other males at a moderate rate until the fourth day of his second mate's incubation. There was a slight increase in his chasing activity at the time the Y1 female laid the second half of her clutch and he was forming his second pair bond (with the W1 female). Neither female mated to this male experienced much chasing or raping.

In pen 2 in 1969 the pattern of chasing is not very revealing, probably for the same reasons given for pen 1 in 1969. The activities of the R2 male were inhibited by his lameness and subsequently he was removed from the pen for five days. In addition his mate joined the Y2 pair during his absence. The R2 female was chased most during the days just before and after the day she laid her first egg. She did not experience any rape attempts during my observation periods on the days she laid eggs.

The G2 male chased males at a moderate rate from the start of the study until just before the end of his mate's incubation. In addition, he chased the Y2 male at a much higher rate for a period of four days at the time both of their mates began incubation. The G2 male chased females most until the day his hen laid her third egg. The G2 female was chased most just before she began to nest, and on the days she was heard to give Persistent Quacking. This hen was seen to experience only one rape attempt on a day that she laid an egg.

Both the W2 male and female experienced a higher rate of chases at the start of the study. The male chased males and the

female was chased by males until she began to nest on May 22. The nest was abandoned after the 13th of June and after the female removed three of the four eggs. She received one rape attempt during the laying period.

The Y2 male chased males at a moderate rate from the start of the study until his mate had nearly completed her clutch. At that point chases directed at him increased noticeably. Many of the chases he experienced were by one male (G2). The Y2 male chased females more frequently at the start of the study than did any other male. These chases diminished greatly after his mate began to nest. The Y2 female experienced few chases (and only one rape attempt) during the study.

Localization

Data were also collected on the locations of each bird in the pens, once every ten minutes, as well as the locations of birds when they were performing certain activities. As the results were being analyzed, I decided to give priority to what the birds were doing and at what stage of the breeding season, rather than where they were when they performed the activities.

In general, each of the Mallards ranged over the entire pen at the start of the study season. Within a few days birds demonstrated site attachment, spacing themselves out over the area available to them. There was, however, considerable overlap of these occupied areas. The Shovelers followed a similar temporal pattern, but in contrast to the Mallards each maintained discrete areas with little overlap. In addition, the Shoveler males

maintained these areas in part by boundary fights (McKinney, 1967), a rare activity in the Mallard. Throughout each study season both the Mallard and Shoveler pairs moved from one preferred area to another one or more times and toward the end of the season all birds ceased to show a preference for any one area, moving all over the pen together.

SUMMARY

The breeding behavior of eight pairs of wild-caught, full-winged Mallards was observed closely in large flight pens for two consecutive seasons (mid-April to mid-June). Special attention was given to interactions between pairs and promiscuous mating attempts of males, and the relationships of these activities to breeding chronology. The results provide baseline information on the characteristics of the social system for comparison with parallel studies on other species of Anas. They are intended to complement field studies on this species and to contribute to comparative study of the adaptive radiation of social behavior in the Anatini.

The captive Mallards maintained firm pair-bonds which were reinforced by a variety of activities. Males became sociable with each other, while still paired, soon after the females began to lay eggs and incubate them. Laying females joined their mates on leaving the nest, and at such times, males once again became aggressive toward each other. Late in the season pair-bonds appeared to dissolve.

Pairs copulated regularly especially during the week preceding egg-laying; some copulated several times during one whole day watch at this stage of the cycle. In addition to these matings, which were preceded by pre-copulatory displays ("Normal copulations"), males also attempted rape-like matings with their own mates. I have called these "Forced pair-copulations". They have been noted only incidentally in the literature and have not been clearly distinguished previously. Both of these types of pair-copulations occurred from the start of the study each year and continued until the pair finished egg-laying. The relative frequency of the two types changed, however, during this period, forced pair-copulations becoming more common.

All paired males, in addition to copulating with their mates, made attempts to rape females paired to other males. These attempts were most frequent at females in the laying stage of their nesting cycles. On days when certain females were subjected to both rape attempts and forced pair-copulations, the latter tended to follow the former within the hour.

The onset of nesting was signalled, in many cases, by the occurrence of Persistent Quacking by the hens. All but one of the hens had discontinued this calling by the time they had laid the first egg. Thirteen clutches of eggs were laid in the two years. There was a high nesting success in the first year, but in the second there was a great deal of duckling mortality. I attribute this largely to a high level of aggressive behavior among the overcrowded hens with broods. Only one female was harassed at the nest so much that she abandoned it.

Male Mallards chased both males and females. The chases at males occurred on the ground, while chases at females were primarily aerial. The chasing resulted in spacing out of the birds in each pen. In addition, high rates of chasing by some males tended to suppress the activities of the others, allowing a dominant male and his mate to use the available area relatively undisturbed by the others.

Fighting occurred between males also, in two contexts:

(1) when two males were evenly matched and neither would retreat in a hostile interaction, (2) during rape attempts, when the female's mate attacked a male attempting to mount her.

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