SOCIAL ASPECTS OF REPRODUCTIVE BEHAVIOUR IN THE BLACK DUCK (<u>ANAS RUBRIPES</u>) IN EASTERN NOVA SCOTIA

by

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Social Aspects of Reproductive Behaviour in the Black Duck (Anas rubripes) in Eastern Nova Scotia

ABSTRACT

Territories were established only after pairs were on the marsh 30-40 days. Females spent approximately 45 days on the territory and males 27-32 days. Males were almost always on the territory during the egg laying period but left the female and territory during mid-incubation. Pairs foraged almost continuously during the pre-territorial period. When the pair was together prior to laying, the female fed 35-40% more than the male. Similarly on the territory females fed 50-60% more.

Encounters between groups of unpaired males and pairs consistently resulted in social display by unpaired males. Single unpaired males seldom displayed but remained near pairs. Paired males threatened and chased unpaired males and generally remained near their mates.

Pursuit flights in five Anas species were analysed, compared and equated to the social system of each species. Pintail and shoveler flights were different while black duck and mallard flights were similar to each other but different from pintail and shoveler flights.

Les Aspects Sociaux du Comportement Reproductif du Canard Noir (Anas rubripes) dans l'Est de la Nouvelle-Ecosse

RESUMÉ

Les territoires sont établis 30 à 40 jours apres l'arrivée des paires. Au total, la femelle demeure environ 45 jours sur son territoire et le mâle de 27 à 42 jours. Le mâle passe presque tout son temps dans le territoire jusqu'à la fin de la ponte. Il laisse la femelle et le territoire lorsque la couvaison est a moitié complétée. Les paires se nourrissent presque continuellement jusqu'a ce que le territoire soit etabli. Avant la ponte la femelle se nourrit en moyenne de 35 a 40% plus longtemps que le mâle; sur le territoire de 50 a 60% plus longtemps.

Le comportement des mâles accouplés envers les mâles non-accouplés varie au cours de la saison. Les mâles accouplés ne poursuivent pas longuement les autres mâles. Les mâles solitaires sont souvent tolérés sur leur territoire.

Les vols de poursuite du canard noir et du mallard sont différents de ceux des autres espèces.

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TABLE OF CONTENTS

TABLES AND FIGURES

Page

I. TERRITORIAL BEHAVIOUR BY BLACK DUCKS (*ANAS RUBRIPES*)

PREFACE

This thesis consists of three manuscripts in the format suitable for submission to the Canadian Journal of Zoology. The content of the material contained in each manuscript is related but it is sufficiently different to warrant a separate treatment.

The first two manuscripts deal with the breeding biology of the Black Duck, Anas rubripes, in a tidal estuary in northeastern Nova Scotia. One manuscript elucidates details of territorial behaviour with particular reference to the pursuit flight. The other manuscript discusses details of the behaviour of unpaired males, particularly as it relates to the activities of paired females.

The third manuscript brings together data collected from 1968-1976 on the pursuit flight in five species of ducks belonging to the genus Anas, including the Black Duck. This is a comparative treatment of a behaviour pattern which is an integral part of the social behaviour of each species during the breeding season.

Although information on ecological parameters has been accumulating, details of the breeding behaviour of the Black Duck have not been elucidated. In particular, details are lacking on the role of the male in relation to his mate during the time that the pair bond is developed.

This study involved the observation of marked birds during the reproductively critical time prior to and during egg laying. The significance of the male in aiding the female to succeed in her reproductive effort was emphasized.

Males established territories prior to egg laying by the female and maintained them until mid-incubation. The pursuit flight was the main mechanism in the establishment and maintenance of territories and characteristics of this behaviour pattern are reported in detail.

The second manuscript deals with the behaviour of unpaired males in the same study population. There is little published information concerning the behaviour of unpaired males in any duck species and none for Black Ducks. The activity of these males was investigated to elucidate the influence that they had on paired birds, particularly females.

The third manuscript is a comparison of characteristics of pursuit flights in five species. The main objective is to elucidate the functional significance of this behaviour pattern in each species. In addition, the motivation of the chasing male is also considered.

Each of these manuscripts represents a contribution to original knowledge in that studies like this of marked, wild ducks are few. This is particularly so for the Black Duck, the main study bird. Several aspects of the study have special significance. The daily and seasonal activity budget of paired males and females, particularly during breeding, elucidates factors critical to the reproductive success of the pair. In particular details of activity schedules aid the observer in determining the relative importance of foraging, hostility toward conspecifics and other behaviour patterns in influencing the reproductive effort of the pair. These aspects were investigated and are discussed.

Another key aspect of the study was the determination that territorial behaviour is developed in this population of Black Ducks. This was determined primarily by the observation of marked birds. Much of the discussion here clarifies the situation in Black Ducks and attempts to clarify the functional significance of territory in ducks, a topic that is confusing in the literature.

In the introduction and also the discussion sections of each manuscript there is a brief historical statement of the relevant published work. This appears brief because, although various workers have made contributions in the past, most of the significant contributions have been made by contemporary researchers and their work is cited. In general though, the study of the breeding strategies of ducks has suffered due to a lack of intensive observation of marked birds and this is reflected in the literature.

TERRITORIAL BEHAVIOUR BY BLACK DUCKS (ANAS RUBRIPES)

ABSTRACT

Observations of wild marked birds provided a qualitative and quantitative description of hostile interactions between pairs throughout the breeding season. Interactions occurred first on the communal part of the marsh and later on territories. Changes in the form and intensity of hostility led to the spatial displacement of pairs. The pursuit flight by males was the main mechanism in the establishment and maintenance of territories.

Territories corresponded to tidal ponds (0.61-3.9 ha) at the marsh periphery and were established only after pairs were on the marsh 30-40 days. Territories were established approximately five days before egg laying began and females were responsible for their location. Females spent approximately 45 days on their territories and males stayed 27-32 days. Males remained almost continuously on their territories during the pre-laying and laying periods but left both their females and their territories during mid-incubation.

The activity of males and females of pairs was analysed and compared according to three activities: foraging, loafing and hostility. Pairs, and particularly the females, foraged almost continuously during the pre-territorial period. When a pair was together prior to laying, the female fed 35-40% more than the male. Similarly on their territories females fed 50-60% more. Hostility by territorial males toward intruding pairs provided seclusion for the resident pairs.

Territorial behaviour by black ducks (Anas rubripes)

INTRODUCTION

McKinney (1965) categorized the response of ducks encountering other ducks on the breeding grounds. However, for the black duck (Anas rubripes), description of these responses is lacking, particularly changes in response throughout the breeding season. The concept of territory in breeding ducks is controversial and there are no quantitative data suggesting that this behaviour occurs in black ducks, despite use of the term in the literature (Coulter and Miller 1968; Mendall 1958; Stotts and Davis 1960; Wright 1954). The objectives of this paper are to quantitatively describe encounters between pairs of black ducks, particularly changes in their form, frequency and intensity, from arrival on the breeding grounds to pair bond dissolution. In addition, details of territorial behaviour and activity schedules of pairs are described. Although encounters between pairs and unpaired males are described here, they are discussed in much greater detail in another paper.

The study area was an undisturbed 170 ha Spartina marsh at the upper end of a tidal estuary in Antigonish County, Nova Scotia (Figure I). The vegetation is the same as described by Nixon and Oviatt (1973) for a New England salt marsh. Tidal pools which ranged in size from 0.61 ha to 3.9 ha occurred in the marsh and at the periphery. These pools were permanently water-filled and free of emergent vegetation except at the edges. The marsh was free of ice two weeks or more before inland ponds and was the focal point for migrants and also residents which wintered in the permanently ice-free lower estuary. Birds used the marsh from mid March until ice forced them out in late December.

Several vantage points allowed virtually complete surveillance of the marsh and frequently many pairs could be watched simultaneously. Numbers and locations of birds were estimated each year (1972-1973) from counts made at two hour intervals (dawn to dusk) on three or four days each week from 15 March to 15 June. Individual pairs on territories were observed continuously for periods of 30 min to 5 h. A grid of wooden poles, placed approximately 100 m apart, was used to locate and follow the movement of birds. These grids each covered approximately 2 ha and were located on six of the most frequently used parts of the marsh. In addition similar grids were located on four intensively observed tidal pools. During the three years, 27 males and nine females were captured in wire mesh traps baited with grain. These birds were marked with nasal saddles (Bartonek and Dane 1964) and released. Both marked and unmarked birds were observed for 280 h during the pre-territorial period and for 420 h during the territorial period. Continuous periods of intensive observation (total 360 h) of seven marked males whose breeding schedules were known provided most of the data on territorial behaviour. Pursuit flights deal with both marked and unmarked paired and unpaired males as chasers. However, pursuit flights in which a territorial male chased an intruding pair from the territory are dealt with in most detail. Daily and seasonal flight frequencies for the population are based on the observation of 156 flights in 1974 while the description of pursuits and data analysed in relation to the breeding chronology are based on observations of 132 entire flights of 12 marked territorial males during 1973 and 1974. Additional reference is made to 42 pursuit flights observed in 1976.

RESULTS AND DISCUSSION

Black ducks in this population apparently employed three different breeding strategies; 1) nesting and foraging inland along streams, but rearing broods in estuaries, and having territories corresponding to the main foraging area; 2) nesting inland, but foraging and rearing broods in estuaries and having territories corresponding to a pond near the nest or a section of the marsh edge; and 3) nesting and foraging in the estuary, and having territories corresponding to tidal ponds. Results reported here apply to the third strategy.

The nesting period each year (1972-1974) was arbitrarily separated into pre-laying, laying and incubation periods based on observations of all pairs that nested on the study area and by location of nests. As Reed (1970) found in his black duck study, the onset of breeding was sufficiently synchronized each year, to determine a peak of nesting for the population.

Twenty of the 23 territories on the study area over the three years were located on six ponds at the periphery of the marsh that ranged in size from 0.6 ha to 3.9 ha (Fig. 1). Each pond was used by at least one pair during each year and three ponds were used by two successive pairs on two occasions. The remaining three territories were located along portions of approximately 9,000 m of marsh edge, not on the central part of the marsh which was a communal area (Fig. 1).

Interactions on the Communal Area

Pairs used the communal area throughout the breeding season but most intensively before they established territories. Pairs usually foraged when there and were quite mobile except prior to the second week of April when ice restricted movement. At this time pairs were relatively tolerant of each other and often foraged 3.0 to 4.5 m apart in locations where food appeared abundant. Even after ice no longer restricted movement and a measure of pair dispersal had occurred, there appeared to be a tendency for pairs to join other pairs to forage. Even pairs which defended territories elsewhere sometimes foraged within 9 to 15 m of other pairs. Flock feeding presumably assisted birds in the location of food and perhaps facilitated the detection of potential predators like bald eagles (Haliaeetus leucocephalus) which harassed them.

Probably most early hostility occurred between foraging pairs and seemed to be primarily a consequence of the shortage of foraging locations. Generally when one pair encountered another early in the season, the male of one or both pairs stopped, held his head high and swam away followed by his mate. However, obvious hostility was observed in 122 of 232 encounters between foraging pairs (Table 1). The participants in these encounters usually occupied an area of 5 or 6 square meters while foraging and a male threatened or chased only birds which approached within 9 m of him. Supplanted pairs usually moved only 5-6 m away from where the encounter occurred. When not feeding pairs usually loafed 15-30 m apart.

The site where these encounters occurred did not appear to have any significance to the pair beyond the time they foraged there (range 12-125 min per day). Pairs usually left the site when finished feeding and often loafed near other pairs with which they had earlier interacted. Often another pair swam to a site as soon as a pair vacated it. Furthermore, no territories were established in three heavily utilized locations where most early hostile encounters were seen.

Whenever pairs gathered at preferred foraging locations virtually continuous chasing and threatening occurred between nearby pairs and dominance often changed during bouts of foraging. Preferred locations were quickly occupied when deserted. Although supplanted pairs were not apparently inhibited from foraging and began feeding again immediately after being supplanted, 23 of 65 pairs swam about, apparently searching for a feeding place, from 17 to 60 min before they resumed feeding. After pair dispersal had begun, pairs supplanted while feeding usually swam further (20 to 90 m) away from the usurping pair than they had earlier in the season. The chasing male rarely chased the other pair more than 10 m from where he and his mate were foraging. Unlike most early encounters between pairs where hostility was associated with the occupation of a foraging location, later in the season hostility usually occurred whenever two pairs met, regardless of circumstances.

Changes in Hostility and Displacement of Pairs During the Season

Paired females appeared hostile toward other pairs earlier in the season than did their mates. This was expected since the first observed hostility occurred when paired females Incited during social display by unpaired males. During 1974, Inciting occurred in 46% of 402 hotile encounters between pairs. The first hostility by paired males toward pairs appeared to be initiated by the Inciting of females. Although Inciting occurred throughout the season, most occurred on the communal area before flock dispersal and before the female's mate reacted by threatening and chasing the other pair. Early in the season the mate reacted to Inciting by attacking primarily the male of the other pair. However after hostile encounters between pairs had occurred for approximately ten days, males reacted more quickly toward intruders and always attacked the female. Inciting occurred less frequently after the first week of April probably because pairs appeared to avoid each other and males left their females to swim toward approaching pairs. This was particularly so on territories where Inciting rarely occurred.

Intensity of male hostile behaviour provided a measure of the seasonal change in intolerance between pairs. McKinney (1965) noted that hostile behaviour in male ducks ranges from threat to the pursuit flight. Figure 2 compares changes through the breeding season in the relative occurrence of the following four subjective measures of intensity which are comparable to male hostility in the closely related mallard (A. platyrhynchos) and similar to hostility in the blue-winged ducks (McKinney 1970): (1) threat postures, (2) mild rush across the surface of the water, (3) overt attack, (4) pursuit flight.

Threat and mild rush were characteristic of the communal area and occurred most frequently before flock dispersal. The high occurrence of threat on the communal area probably reflects a conflict between escape and attack and also between attack and remaining with the female. Mild rush occurred early and only on the communal area and was characterized by one male following another pair. This did not develop into more overt hostility even when intruding pairs remained nearby. Overt attack on the communal area occurred later in the season, usually when males with territories elsewhere encountered pairs. Pursuit flights were almost entirely restricted to territorial males chasing intruders from the territory. There was no step-wise reversal of intensity of hostility as pair bond attachments waned but rather a gradual cessation of hostility prior to pair bond dissolution.

The spatial displacement of one pair by another provided a further measure of seasonal change in hostility. A pair was considered displaced when the male and female left the immediate area of encounter and were not subsequently challenged by the original chaser. Pairs on the communal area were not usually displaced far and frequently a change in trajectory by one or both interacting pairs resulted in no further hostility. Typically the displaced pair swam, rather than flew, away without resistance or hostile display.

By the first week in April pairs on the communal area threatened other pairs within 9 m but rarely those further away. During the second week in April when ice had left the marsh, most pairs remained 30-45 m apart. It was rare for the male of one pair to attempt to displace another pair which was more than 45 to 60 m from his female. Pairs beyond 90 m were never attacked on the communal area. This was true for both pairs which had not yet established territories and for pairs which had territories elsewhere.

Figure 3 shows that encounters occurred first on the communal area and remained relatively constant in frequently until pairs established territories. Then, most encounters occurred on territories and the frequency increased. Comparison of the displacement and pursuit flight curves illustrates that the pursuit flight performed by paired territorial males was the most effective mechanism to displace intruders from territories.

Pursuit Flights

Most pursuit flights involved a known territorial male chasing an intruding pair thusincluding three birds altogether. Only twice were males which defended contiguous territories involved as the sole participants. Only eight pursuit flights originated on the communal area and are not included in the ensuing description derived from 132 pursuit flights involving intruding pairs not holding territories in the study area and a known paired territorial male as the chaser.

Most intruding pairs landed on an occupied pond before being approached by the territorial male. Persistent pairs that continued to return after being chased were frequently chased again before they could land. Females of intruding pairs always landed on territories before their mates. While on the water, a resident male attempted to approach a female whose mate defended her on only two occasions by swimming toward a resident male. When the female's mate was between her and the chaser, the chasing resident simply swam around or jumped over the mate to get to the female. Only once did a chaser peck at an intruding male. The chaser usually swam toward the female, particularly if she was at the edge of his territory and either jumped at or rushed at her when within 6 to 9 m. The female almost always flew before he reached her but on five occasions a female did not immediately fly and a chaser grabbed at her back.

Once in the air the female of a pair was always the subject of pursuit. This was obvious in 48 (36%) encounters where a female's mate remained on the water during the entire chase or lagged at least 9 m behind. Even when her mate was close to her he was always the third bird in a pursuit flight. Only once was a mate observed to grab at a chaser in flight and even then the chaser did not shift his attention from the female. Since a chased female's mate always, if belatedly, follows her, the chaser also indirectly displaces intruding males by chasing females.

When in flight a pursuing male only rarely approached close enough to make contact with a female and, even then, made no obvious attempt to do so. Although a female's mate only occasionally called (rab-rab) during pursuit flights, a pursuer frequently did so while chasing and when he returned to his territory. After pursuits a chaser usually entered his home pond via the same trajectory and occasionally flew around his territory calling (rab-rab) as noted by Dwyer (1974) for gadwalls (A. strepera) and Seymour (1974B) for shovelers (A. clypeata). When intruders remained near a territory the territorial male often sat there alertly after a pursuit flight.

Inciting was observed only three times and involved females which returned to a territory despite repeated chasing by the resident. Persistent quacking by a female occurred during nine (7%) flights; seven of which involved three different females known to be pre-laying birds. Although Repulsion behaviour(Lorenz 1941-1971) by a female was not observed in these flights, during 1976 both Repulsion posture and associated call was observed in two flights. In both cases, the mate of the chasing male and the pursued female were incubating eggs. In one case the pair bond between the pursued female and her mate was no longer intact.

Flights were considered long (>25 s) or short (1-25 s) based on the median of 132 flights which fell in the 21-25 s interval. A chaser invariably chased until intruders left his territory but had to chase returning females again in 30 (23%) encounters. In six of these, chasers made four chases before intruders failed to return. Long flights appeared more to reflect the persistence of females in attempting to land on a territory than attempts by chasers to continue the pursuit. These mainly unmarked females appeared to be exploring ~~for~~ nesting cover and were not there to forage. This conclusion was based not only on the persistence of females to remain near territories but also on observations of females before and after encounters. On 27 occasions females went to other tidal pools after being chased. They did not forage during two hours of observation and, on 12 occasions, females and their mates flew to upland vegetation beside a pond, apparently to search for a nest site. On seven occasions before encounters with territorial males, pairs were observed for 27 to 125 min. During this time the females did not forage and each time flew with their mates into upland vegetation. A further 49 of 61 (81%) encounters on territories, in which an intruding pair was watched for more than five min before an encounter, appeared to involve intruders which were exploring for nest sites and not foraging. Foraging pairs appeared to avoid territories, usually remained on the communal area (Fig. 4) and, when chased by a territorial male, immediately left the vicinity of a territory.

Sometimes females continued onto a territory even after their mates, which had accompanied them on previous attempts, had flown back to the communal area. The male's desertion at this point was ignored by the females, but they left the territory immediately when chased by a defender. The apparent reluctance of intruding males to persist in an area suggests that intruding males may be intimidated by territorial males more than females.

As a result of pursuit flights, intruding males and females were often separated from each other for up to 30 min particularly when the male mated to a chased female did not join the flight immediately or did not accompany the female onto the territory. Since females alone were rarely observed attempting to invade a territory, separation might delay or perhaps completely discourage subsequent attempts by a female to return to a territory.

There did not appear to be an increase in the threshold of response of the chaser with repeated chasing. Some females that repeatedly returned were subsequently chased more vigorously than during initial encounters. There was apparently no quiescent period after pursuits. Males that most frequently encountered intruders appeared to chase intruders more vigorously than males which only occasionally encountered intruders. On returning from pursuit flights males sometimes chased other pairs that had hitherto been tolerated at the periphery of the territory.

A pursuit flight usually ended when the chaser ceased chasing and circled back toward his territory. However six times pursuers landed with chased pairs on the communal area. On three occasions a pursuer sat with his head high within 3 m of a female and within 2 min returned to his territory. But on the other occasions males attempted to mount pursued females who immediately dove beneath the surface of the water. In each encounter the female's mate grabbed at the chaser before he reached the female. Once a pursuer, whose mate was in the egg laying phase of her reproductive cycle, briefly mounted a chased female.

During 1976 paired males were observed in an attempt to determine the frequency of occurrence of attempted rape. As in previous years, a chaser in pursuit flights usually (39 of 42 flights) returned quickly to the territory without landing with the chased female. However, in the other three cases chasers landed with pairs and briefly mounted females before each dove to escape. In one of these encounters, the chaser also attempted to mount the intruding female when she remained on the territory before the pursuit. In the three encounters the chasers returned to their territories, although once a chasing male remained where a chased female had dove for 7 min apparently searching for her. Neither the chaser nor the female's mate which was only 2-3 m away were obviously hostile toward each other.

Despite these observations of attempted rape, it is clear from the way a territorial chaser does not persist after females that he opts to remain with his mate and/or territory instead of attempting to rape strange females. It is unknown whether attempted rape occurs more frequently after pair bond dissolution or when territorial males are away from their territories.

Females appeared to fly after being chased and usually remained for up to 60 min near where they landed after the chase. Regardless of the flight trajectory, all females eventually flew from a territory to the communal area following a chase (Fig. 4).

Table 2 provides a comparison of pursuit flight characteristics analysed according to the following three periods of the female's reproductive cycle: pre-laying (23 flights between establishment of territories which was four or five days prior to the onset of egg laying), laying (89 flights between the laying of the first and last eggs) and incubation (20 flights between the last egg layed by a female and mid-incubation when pair bonds severed and territorial behaviour ceased). It is probable that nine of the pairs included in Table 2 were nesting for the first time that season. The males of these pairs were marked early and the females were among the first birds to begin laying. As previously suggested, many of the pursued females were probably searching for nest sites.

Throughout the territorial period males returned to their territories after pursuits even during the incubation period when their mates were usually at their nests (Table 2). Although evidence below suggests that defense of a territory may be less successful during the later stages of pair bond dissolution, Table 2 suggests that intruders never returned to remain on a territory after pursuits. Birds which returned after pursuits to the vicinity of a territory but not within 90 m of it were considered displaced since birds further than 90 m were seldom chased. This suggests that the pursuit flight is an effective mechanism in the establishment and maintenance of territories.

There was no significant ($p < .05$) difference in flight duration between periods and males never apparently showed reluctance to leave their mates to chase. On three occasions mates of laying females chased intruding pairs immediately after copulation and twice aborted pre-copulatory behaviour to chase. This was in contrast to Gates' (1962) observation that male gadwalls initiated more pursuit flights when their females were there. Dwyer (1974) found pursuit flights in gadwalls were approximately half as long when a male was alone.

Analysis of flights on an hourly basis throughout the day showed that significantly ($p < .05$) more occurred in the hour after sunrise than any other hour. Although there was no significant difference between periods when the day was subjectively separated into three blocks, the highest frequencies were in the morning (0500-1000) and evening (1700-2200) (Table 3). Furthermore, the highest frequency of flights on 30 of 48 days occurred in the morning period.

These findings were not unusual since most flights occurred between territorial pairs and pairs searching for nesting cover. Although nest searching occurred throughout the day, most occurred in the morning. Frequently one persistent female was responsible for several pursuits.

Flight frequency was also analysed weekly for the eleven weeks during 1974 in which individuals within the population behaved territorially (Table 4). These results are representative of the three years in which initial nesting attempts were relatively synchronized for the population. Dwyer (1974), Smith (1968), McKinney (1965) and Seymour (1974B) reported the highest frequency of chasing prior to egg laying in other Anas species. Flight frequency in this population peaked (71% of all flights) during the period when most females were laying. However, in contrast to pre-laying shovelers which were on their territories 15-20 days (Seymour 1974A) before egg laying, black ducks began laying within five days of territory establishment and had proportionately less time to interact with other pairs. In addition, during the general laying period for the population, there were several established territories and also several pairs searching for nest sites which provided high potential for interaction. During incubation frequency of pursuit flights was low probably because, as evidence below suggests, territorial pairs were largely restricted to their territories once egg laying began and did not interact with each other. In addition, there were fewer mobile pairs searching for nests.

Since, as suggested, pursuit flights were due to territorial males chasing pairs searching for nest sites, pursuit flight frequency could be expected to correlate with the number of potential interacting pairs. The simple product of the numbers of territorial and non-territorial pairs was calculated on a weekly basis (Table 4). Comparison of these values with the number of actual pursuit flights observed indicates a strong positive correlation $(r = 0.89, p<0.01)$ between weekly frequencies and the number of possible interactions which is consistent with results reported for the shoveler (Seymour 1974B).

To further determine whether pursuit flight frequency might reflect the number of interacting pairs in an area, frequencies were calculated under different conditions of population density (Table 5). Comparison of two years shows that there were significantly $(p<0.01)$ more flights at higher density. This was particularly $(p<0.001)$ so during the period when most nests and territories were concurrently initiated. However, the black duck populations were relatively low and these results are contrary to Titman's (1973) results for a very dense population of mallards which may suggest that this relationship may not hold under conditions of very high density.

Pursuit flights may have served to advertise the presence of a territorial male in an area. On 19 (14%) occasions chasers circled their ponds before landing when returning after a pursuit. Territorial males sometimes flew, apparently spontaneously, around their ponds in 15-20 s flights particularly if persistent pairs remained nearby. Furthermore, pursuit flights usually ranged far beyond a territory and, except when persistent pairs were involved, appeared to continue after the intruders showed no obvious intention of returning to a territory. These tendencies appear to reinforce the chaser's dominance in an area where pairs might be exploring for nest sites.

Paired females were chased by unpaired males as well as by paired males. The relative occurrence of four types of flights which arose during the courtship activities of unpaired males during 1974 are described in Table 6 and below. Long flights that occurred during social display usually began when males crowded around a female. She would jump into the air when one or more of the males rushed at her. However, on other occasions a female gave pre-flight signals typical of the Anatini (McKinney 1970) and the group became ready for flight. Short flights occurred when a female jumped up, was followed by several males and all birds landed together. Other flights which resembled Spring Courtship Flights of the mallard (Dzubin 1957), were of long duration and although most ranged far, each passed over the origin of the flight several times. Only two flights left the estuary. Males almost always remained with a chased pair after a flight. Of the flights above (27+88), 63% appeared to occur as a result of displaying males pressing around the female.

Another type of flight involved single males which had been with a pair and remained with the pair when it flew. Sometimes a territorial pursuit flight was joined by one or two males which sometimes remained with the pair after the pursuit.

Only 18 flights, included in the second category of Table 6, could be characterized as prolonged, vigorous flights resembling "attempted rape flights" (Dzubin 1957; Lebret 1961) similar to those of the mallard. In general there was no apparent attempted rape by unpaired males. Although it was impossible to know the status of all males in flights, no marked territorial males were observed in flights instigated by unpaired males.

Territory Selection

Pairs used the communal area 30-40 days prior to the establishment of territories. Although inclement weather periodically forced interruptions of feeding, as noted by Wright (1954), these interruptions were brief and probably not a factor in the delay between arrival and establishment of territories. Territories were established only after snow had been gone from nesting cover for three or four weeks and, on the average, eight days after ponds were free of ice. Despite this, pairs continued to use the communal area to forage and did not spend a major portion of their time in ponds at the periphery of the marsh until four or five days before the onset of egg laying.

The general location of a territory was believed to have been determined by the females and corresponded to the section of marsh edge or pond from which she initiated "exploratory flights" into nesting cover (cf Smith 1968). When a female remained in an area her mate did also and his interactions with conspecifics subsequently determined the limits of the territory. Females sometimes explored several areas before localizing their activity. A male always accompanied his female when she deserted a location even after having defended it for two or three days. This corresponds to Hochbaum's (1944) description of territory establishment.

Although a territory is usually associated with a water area near the nest, as noted by Dzubin (1955) for the blue-winged teal (A. discors) and by Stotts and Davis (1960) for black ducks, nests in this study were beside ponds in only four of 17 cases. However, in each case the nest was in the area that was influenced by the territorial activity of the male since females searching for nest sites initiated exploratory flights from ponds and not from the communal area. Territorial males prevented such females from using ponds hence preventing them from exploring for nesting cover over a considerable area around the pond.

The pond *per se* was apparently the most assiduously defended feature (cf Emlen 1957) of a territory and its boundary approximated the physical limits of the pond. Sometimes, when a male was in the marsh adjacent to a pond, he chased other pairs but interactions were less frequently (17% of 23 encounters) observed and less vigorous beyond the limits of the pond. This occurred despite the fact that pursuit flights extended up to 250 m past a pond and 100-125 m into areas where other pairs were usually tolerated. Males returning from pursuit flights frequently encountered other pairs foraging in the marsh within 30 m of their ponds. Males did not usually chase these birds although they occasionally landed near such a pair and stayed briefly (<60 s), before returning to their ponds. On other occasions territorial males chased foraging pairs from near their ponds even after they had been tolerated for 30 min or more. Pairs which had been chased previously, particularly if they had just been chased, were usually pursued when they landed within 30 m of the pond. Further suggesting that the pond was the focal point of defense, males invariably (265 h observation randomized as to direction of sun and wind) had their heads or eyes oriented toward the water enabling rapid detection of intruders which typically (95% of 140 encounters) attempted to land on a pond and not in the vegetation surrounding it.

While on a defended pond males were visually isolated from pairs on the marsh. Males investigated recordings of persistent quacking and decrescendo calls produced in the vegetation around their territories and in the adjacent marsh.

There was no evidence to indicate that there was variation in the area defended according to time of day or stage of breeding prior to pair bond dissolution as Dzubin (1955) found for mallards and blue-winged teal. Males abruptly deserted their territories during incubation with no gradual shrinkage occurring in the size of a defended area. Territorial males did not incorporate other ponds or sections of the marsh into their territories when they were deserted by neighbours. Neighbouring pairs apparently avoided each other's territories after initial boundary delineation and most (>70%) of approximately 80 encounters between neighbours occurred in four or five days when pairs were establishing territories.

It was difficult to show site attachment by pairs which defended portions of the marsh edge. However, these pairs appeared to be less localized, used the communal area more, and the males apparently remained in the area only during the laying period of their females. In addition, few pursuit flights by these males were observed. Boundaries here were never well defined probably bacause of the lack of physical features. Daily fluctuations in the tide changed the pattern of vegetation and frequently visual isolation from other pairs was impossible for several hundred metres. Females of these pairs nested inland but returned to the marsh to feed.

Territory Utilization

Males were found on their territories approximately 27-32 days and females approximately 45 days. Territories of seven pairs were established five days prior to laying of the first egg (pre-laying period) and the laying period was estimated to be 10-12 days. Males remained on the territories for approximately 15 days during incubation similar to what others have found (Coulter and Miller 1968; Reed 1970; Stotts and Davis 1960).

Table 7 indicates the time spent on their territories during the three periods by seven pairs during 395 h of observation. Members of a pair were typically together on a territory during pre-laying but, as expected, during laying and particularly during incubation the female was observed less often. A male, was almost always on his territory during the pre-laying and laying periods when the maximum frequency of copulation was observed. During laying males usually remained on their territories when their mates were at the nest. Males spent less time on territories during incubation but were most often there during the morning and less frequently during the evening, times when females were most likely to be off their nests. Prolonged periods of absence from a territory by a male preceded pair bond dissolution. During incubation males spent more time on the communal area and consorted with other males, even former territorial rivals. For two or three days before two neighbouring males deserted their territories, one male frequently joined the other on his pond and both flew together to the communal area. When not on a territory birds were usually on the communal area (Table 7). During 12 h of observation of territorial males off their territories, foraging and loafing were the main activities and these males did not join females which were sometimes nearby.

Pairs apparently used only portions of ponds (Fig. 1). Each of two pairs watched for 61 h during the entire reproductive period was almost always (96, 97%) on its pond (1.8, 3.9 ha) but used only 0.16 and 0.85 ha respectively (Fig. 1). There was no change in the pattern of use with time whether each male was with his mate or alone. The females used the same locations after pair bond dissolution, took their newly hatched and mobile broods to the pond briefly, then went to the communal area and were rarely observed on their territories again. Only one female remained on a 3.9 ha pond with her brood until they fledged. Pairs in general used remarkably small portions of ponds and subsequent residents usually used the same general areas.

Although only a portion of a pond was used, the resident male apparently defended the entire pond. Both males referred to in Figure 1 chased pairs which landed in an area of approximately 4.0 ha comprising primarily the pond but also part of the adjacent marsh. This was apparently the maximum area defended by males on the study area.

Activity Schedules

The relative occurrence of the three activities (foraging, loafing, hostility) was determined for both males and females of pairs while on the communal area and on their territories. Data concerning occurrence of these activities was based on continuous periods of observation. A bout of activity was scored as foraging for the time birds were preoccupied with this activity. For example, brief interruptions to preen or rest were not recorded as such but rather the whole bout was scored as foraging.

Loafing, which included sleeping, resting, preening, etc. was similarily scored. Rushing at, chasing and fighting with other black ducks accounted for only approximately 20% of the observed hostility. Included in the hostility calculations was the amount of time that a male or female of a pair was prevented from either loafing or foraging because of the aggressive activities, or even presence of nearby pairs. For example, males frequently suspended foraging and remained alert when other pairs were nearby and this was considered hostility.

Figure 5 indicates the frequency of occurrence of these activities by pre-territorial pairs observed on the communal area and by the members of seven pairs on their territories during the three reproductive periods. Both males and females foraged almost continuously while on the communal area. Initially pairs foraged throughout the day but a peak of voracious foraging occurred during the three hours after dawn. A lower peak occurred in the two hours before dark. Foraging during peak times was sometimes interrupted by loafing for up to 15 min and after the morning foraging peak pairs usually loafed up to 60 min before foraging again. Although birds were not observed at night, observation at dawn and dusk suggested that foraging terminated before dark and began again at dawn especially early in the season when birds foraged on the bottom and appeared to locate food visually. This observation remains tentative since Swanson and Sargeant (1972) and Tamisier (1974) report nighttime feeding by ducks. Territorial pairs foraged when on the communal area and returned to their territories to loaf. Foraging remained the predominant activity of a female when on her territory. Although during laying and incubation she spent proportionally more time away from her pond in nest oriented activities. A male on the other hand, foraged less and loafed more when on his territory than during the pre-territorial period. During incubation males apparently foraged more on the communal area than on their territories. Males whose mates were at the nest were watched for 38 h while on their territories. These males fed significantly ($p<0.05$) less when their females were with them. A male often began to forage when his mate returned from her nest although he frequently only accompanied her and remained alert as noted by Dzubin (1957) for mallards. Male and female involvement in foraging activity was not significantly different while the pair was on the communal area but, on a territory, a male foraged significantly less than a female during each period, particularly during incubation (Fig. 5).

Analysis of foraging rates by individuals on a minute by minute basis revealed further differences in the actual amount of time devoted to foraging. Individuals of foraging pairs observed for 402 h on the communal area and on territories, fed primarily (77%) by dipping head and neck under the surface and by tipping up (21%), but not by filtering. Fast and slow rates were subjectively determined for both dipping and tipping. Fast tempo for dipping was head up 0.5 s or less and head submerged 3 s or more and slow tempo was head up 1.5 s or more and submerged 2 s or less. Fast tempo tipping was 12 or more tips per minute with the head submerged for 4 s each tip and slow tempo was 10 tips or less per min with had submerged for 4 s. During a minute of fast tempo dipping the minimum duration that the head was submerged was 51.2 s, while during a minute of slow tempo dipping the minimum duration submerged was 35.2 s. Similarly during a minute of fast tempo tipping the minimum duration that the head was submerged was 48 s and during slow tempo 40 s submerged. Comparison of rates between males and females of pairs for both the communal area and on their territories showed that the female most often (>90%) foraged at fast tempo on both areas while males foraged at fast tempo approximately 70% as much as the females during the pre-territorial period on the communal area. Similarly on their territories males foraged approximately 60% as much as females during laying, and approximately 20% as much during incubation.

Considering rate and total duration of foraging when a pair was together, it was estimated that a female fed 35-40% more than a male on the communal area prior to egg laying. When a pair was together on their territory during pre-laying and laying a female foraged 50-60% more than a male.

It is possible that the male assists the female in locating food. On the communal area when no conspecifics were nearby male and female often searched for food 5-10 m apart thereby increasing the probability of locating food. Usually the birds moved rapidly until food was found and then the bird that found the food was immediately joined by the other. A male feeding on his territory when his mate returned from her nest was typically joined by the female who was able to begin feeding immediately.

When foraging together the male was usually more alert than the female as Swanson, Meyer and Serie (1974) found for the blue-winged teal. When on a territory and particularly when on the communal area the male often looked about before submerging his head and, when other pairs were nearby, sometimes foraged with only his bill submerged but eyes exposed. Males usually suspended foraging completely, at least initially, when other pairs or predators were encountered. Although a female was almost always (95% of 123 observations) the first to fly when a predator approached, her mate was apparently usually the first to detect the predator. As predators approached a male usually called in barely audible "raab" notes and made flight intention movements. Often his female continued to forage but with only her bill submerged.

Feeding appeared to be a priority for a female when she returned to her territory from her nest. Despite pre-copulatory display by their mates, females began to forage immediately on 20 of 23 observations. Twice males attempted to copulate with females. In both cases the female was joined by her mate when she landed approximately 10 m away from him. He swam to her dipping his bill in the water and then began pre-copulatory Head-pumping. The female did not display and swam away from the male when he attempted to mount her. There was only one attempt made in each case. Usually (15 of 18 observations) copulation occurred after bouts of foraging. One possible attempted forced copulation of a female by her mate occurred when the male returned after chasing a pair. The male twice grasped at the nape of the female and attempted to mount her without preliminary display. The female swam away and after another attempt to mount her the male began foraging beside her.

Figure 5 shows that throughout the breeding season, while male and female of a pair were together, the male was involved in hostility with other pairs significantly ($p<0.05$) more than the female. A foraging female was not usually interupted by another pair unless overt hostility developed between her mate and the pair. Hostility by males was observed throughout the season but there was no significant difference between periods.

Territorial Behaviour by Males

Although a male associates a site with a female and would not be there if she used another area, some evidence suggests that the physical site holds special significance for him while his pair bond is strong. The amount of time spent on territories by males, particularly during pre-laying and laying has been noted (Table 7). Evidence indicates that pursuit flights lead to spatial displacement of intruders, whether a chaser is alone on his territory or with his female, and are primarily initiated from territories. Males left their mates to chase other pairs when on a territory but not when on the communal area and chasers always returned to their territories after pursuits. Despite the presence of his mate, intruding males appeared intimidated when on territories and never gained sufficient advantage to remain on or displace the resident from a territory.

Indeed intruding males usually appeared to be on a territory only because they followed their females. In eight cases the intruding male was alone on a territory with the resident female while his mate was being chased but did not approach the resident female. Two such males were previously observed chasing females of other pairs elsewhere and twice chased other pairs immediately after being chased from a territory. On four occasions intruding males threatened a territorial chaser only after they had landed together on the communal area.

Prior attachment to a site appeared important in the defense of a territory. Males which returned to a territory from the communal area and found an intruding pair invariably displaced it despite the fact that on two occasions the intruding male had chased another pair from the pond in the absence of the resident. Three times a male that was chased with his mate from a territory became the chaser when on his own territory. However, neighbouring males appeared to recognize each other and after initial encounters the birds rarely trespassed on each others' territories.

Not all intruders elicited the same response from a territorial male. Contrary to Wright's (1954) observations, marked unpaired males were not chased, although territorial males initially threatened and sometimes attacked them.

Even when males vigorously displayed to the resident female there was no apparent attempt by her mate to displace them from the pond. On 12 occasions when unpaired males displayed to a female on her territory, her mate left her for up to 2 min to chase an intruding female and did not chase the males when he returned.

Unaccompanied paired males from neighbouring territories were not usually attacked unless the resident female rushed at them and/or Incited vigorously. Rather, the resident male usually followed the intruder about the pond, at times making little rushes at him, until he left. Neighbouring males were tolerated when the resident's pair bond was advanced and on four occasions a resident female rushed at an intruding male without Inciting in an apparent attempt to displace him herself.

There was some evidence that males whose pair bonds were advanced were less successful in defending territories. On two occasions involving different birds, an intruding pair persistently returned after being chased from a pond and, after approximately three days from the first encounter seen, this pair was observed on the pond more than the resident male. In both cases the female of the resident male had been incubating for at least 10 days when the first encounter occurred. Subsequently the resident male left his territory and the new male chased other pairs from the pond. In each case the former resident male was neither observed on the pond nor with his mate again suggesting that during late incubation unsuccessful encounters with persistent pairs may hasten the departure of a male from both his territory and mate.

CONCLUSIONS

Probably many factors are important in the evolution of territorial behaviour in a particular habitat. Indeed the proximate selection pressures may be different for male and female. Ultimately territorial behaviour must enhance the reproductive output of both members of a pair and the success of a male is tied to that of his female. The male, which in this study defended the female at least four weeks prior to egg laying, had a considerable investment of time and energy in the female. He did not defend a territory until after his mate began to use a particular pond intensively but rather accompanied her everywhere. Once territorial he spent most of his time on their territory which was a focal point for both the male and female to locate each other after separation. The male was almost always on his territory during the pre-laying and laying periods when copulatory activity is presumably most critical to successful insemination. The male also accompanied the female whenever she left their territory presumably to minimize the chances of other males raping her.

Although a male may defend a territory and remain attentive to one female to maximize his chances of inseminating her, as a consequence of territorial activity, both he and the female enjoyed relative seclusion from other conspecifics and perhaps also predators. Territories provided seclusion from unpaired males and predators which primarily frequented the communal area, and from pairs which were chased away by territorial males. Seclusion provided females with a greater opportunity for undisturbed foraging, copulation, exploration of nesting cover and other activities critical to breeding success. Since the location of nests was related to territories, nest spacing which could be critical to the reproductive success of a pair, also occurred as a consequence of territorial behaviour. Ponds apparently were preferred for territories because males could most effectively defend a well defined area and thereby be assured of the maximum possible time with the female.

The onset of egg laying in birds may be influenced by the date at which the female is able to find enough food to form eggs (cf Perrins 1970). In this study establishment of territories corresponded with a shift in the activity of the female from almost continuous foraging on the communal area to nest oriented activity on the territory. Pairs foraged at least 3 to 4 weeks on the communal area before establishing territories 4 to 5 days prior to the onset of laying.

Krapu (1974B)suggested that the availability of aquatic invertebrates is a major proximate factor influencing the onset of laying in pintails (A. acuta). If this is so for black ducks then one might expect a longer pre-laying tenure of the territory unless day by day feeding during laying, which occurs primarily on the territory, is critical to egg production and maintenance of the female. Krapu (1974A)and Swanson et al (1974) found that invertebrate consumption in females was highest during egg laying. This suggests the possibility that defense of ponds provides the female with an advantage in feeding during the critical, but relatively short, laying period. Broods, which are generally hatched when food appears abundant, usually spend little time on the territory suggesting that it is not critical to their development.

The activities of the paired male probably contribute to the eventual reproductive success of his mate long before the territory is established. Protection of the paired female against predators, conspecific unpaired and paired males on the communal area (cf Condor 1949; Dzubin 1955; Koskimies and Routamo 1953) likely provides the female with more undisturbed foraging time than if she had been alone. This association may be particularly important if, as suggested, development of ova is linked to the ability to obtain food on the breeding ground.

Except for aspects of utilization and size of territories, description of territorial behaviour in this population is reminiscent of the shoveler. However, it would be misleading to suggest that the social system of the black duck is similar to that of the shoveler. Characteristics like pair bond tenure, lack of hostility between males, frequency of occurrence of attempted rape and details of pursuit flights suggest a social system more similar to the mallard.

LITERATURE CITED

Bartonek, J.C. and C.W. Dane. 1964. Numbered nasal discs for waterfowl. J. Wildl. Manage. 28(4): 588-692.

Condor, P.J. 1949. Individual distance. Ibis 91: 649-655.

Coulter, M.W. and W.R. Miller. 1968. Nesting biology of black ducks and mallards in northern New England. Vermont Fish and Game Bulletin No. 68-2. 74 pp.

Dwyer, T.J. 1974. Social behavior of breeding gadwalls in North Dakota. Auk 91(2): 375-386.

Dzubin, A. 1955. Some evidence of home range in waterfowl. Trans. 20th N. Amer. Wildl. Conf.: 278-298.

Dzubin, A. 1957. Pairing display and spring and summer flights of the mallard. Blue Jay, XV(1): 10-13.

Emlen, J.T. Jr. 1957. Defended area? A critique of the territory concept and of conventional thinking. Ibis 99: 352.

Gates, J.M. 1962. Breeding biology of the gadwall in northern Utah. Wilson Bull. 74: 43-67.

Hochbaum, H.A. 1944. The canvasback on a prairie marsh. The Wildl. Manage. Inst., Wash., D.C. and the Stackpole Co., Harrisburg, Pa. 2nd ed., 1959. 207 pp.

Koskimies, J. and E. Routamo. 1953. Zur Fortpflanzungsbiologie der Samtente Melanitta f. fusca (L.). I. Allgemeine Nistokologie. Papers on Game Research, 10.

Krapu, G.L. 1974A. Feeding ecology of pintail hens during reproduction. Auk 91(2): 278-290.

Krapu, G.L. 1974B. Foods of breeding pintails in North Dakota. J. Wildl. Manage. 38(3): 408-417.

Lebret, T. 1961. The pair formation in the annual cycle of the mallard (Anas platyrhynchos L.). Ardea, 49: 97-158.

Lorenz, K. 1941-1971. Comparative studies of the motor patterns of Anatinae. In: Studies in Animal and Human Behaviour, Vol. 2, Methuen, London. Pp. 14-113 (translation by R. Martin of "Vergleichendre Bewegungsstudien an Anatinen" J.F. Orn. 79, 1941).

McKinney, F. 1965. Spacing and chasing in breeding ducks. Wildfowl Trust 16th Ann. Rept. pp. 92-106.

McKinney, F. 1970. Display of four species of blue-winged ducks. Living Bird, 9: 26-64.

Mendall, H.L. 1958. The ring-necked duck in the Northeast. Univ. of Main Bull. 60(16). 317 p.

Nixon, S.W. and C.A. Oviatt. 1973. Ecology of a New England salt marsh. Ecological Monographs 43(4): 463-498.

Perrins, C.M. 1970. The timing of birds' breeding season. Ibis 112: 242-255.

Reed, A. 1970. The breeding ecology of the black duck in the St. Lawrence estuary. Ph.D. thesis, Laval Univ. Quebec City.

Seymour, N.R. 1974A. Territorial behaviour of wild shovelers at Delta, Manitoba. Wildfowl Trust 25th Ann. Rept. pp. 49-55.

Seymour, N.R. 1974B. Aerial pursuit flights in the shoveler. Can. J. Zool. 52(12): 1473-1480.

Smith, R.I. 1968. The social aspects of reproductive behavior in the pintail. Auk 85(3): 381-396.

Stotts, V.D. and D.E. Davis. 1960. The black duck in the Chesapeake Bay of Maryland: breeding behavior and biology. Chesapeake Science 1: 127-154.

Swanson, G.A. and A.B. Sargeant. 1972. Observations of nighttime feeding behavior of ducks. J. Wildl. Manage. 36(3): 959-961.

Swanson, G.A., M.I. Meyer and J.R. Serie. 1974. Feeding ecology of breeding blue-winged teals. J. Wildl. Manage. 38(3). 396-407.

Tamisier, A. 1974. Etho-ecological studies of teal wintering in the Camargue (Rhone Delta, France). Wildfowl Trust 25th Ann. Rept. pp. 123-133.

Titman, R.D. 1973. The role of the pursuit flight in the breeding biology of the mallard. Ph.D. thesis, University of New Brunswick, Fredericton. 201 pp.

Wright, B.S. 1954. High tide and an east wind. Stackpole Co., Harrisburg and Wildl. Manage. Inst., Wash., D.C. 162 pp.

Table 1. Results of 122 encounters between two pairs of black ducks in which an intruding pair attempted to supplant another pair previously present at a foraging location. Encounters occurred on the communal area when ice restricted availability of foraging locations.

Behaviour	Number	Percent
Hostility between males		
Threat	103	84
Chase	84	68
Fight	7	6
Females chased by male of other pair	27	26
Response of female to chaser		
Inciting	15	12
Inciting and rush at male	9	7
Previously present pair supplanted	32	31

Table 2. Characteristics of 132 pursuit flights involving 12 marked territorial male black ducks and intruding pairs during the 1973 and 1974 breeding season in Antigonish estuary, Nova Scotia.

Characteristic	Pre-laying		Laying		Incubation	
	number	percent	number	percent	number	percent
Total flights	23		89		20	
Pursuer with mate prior to flight	23	100	67	75	8	40
Pursuer straight trajectory	21	88	41	46	15	75
Pursuits short duration (1-25s)	21	88	43	48	5	25
Pursuer back to territory after pursuit	23	100	88	98	19	95
Pursued bird(s) ultimately landed in vicinity but not within 90 m of territory after pursuit (all others landed at least 270 m from territory)	10	46	28	32	2	11

Table 3. Frequency (pursuit flights per hour) of 156 pursuit flights, during three daily periods, measured over the entire breeding season in 1974.

Daily period	Hours observed	Flight frequency per hour
0500-1000 h	232	0.49
1000-1700 h	48	0.25
1700-2200 h	34	0.64

Table 4. Frequencies of pursuit flights by territorial males related to the product of the average number of territorial and non-territorial pairs of black ducks during 1974 at Antigonish estuary, Nova Scotia.

Week	Approx. period	Frequency per 10 hour period	Number of pairs on study area (av./week)	Product of territorial and non-territorial pairs	Frequency during three periods (av.)
18-24 Mar.	Prelaying	0	23	0	
25-31 Mar.	Prelaying	0	18	0	2.3 (prelaying)
1-7 Apr.	Prelaying	3	10	16	
8-14 Apr.	Prelaying	2.5	16	39	
15-21 Apr.	Laying	10	16	60	
22-28 Apr.	Laying	12	15	56	8.9 (laying)
29 Apr. - 5 May	Laying	5.5	14	48	
6-12 May	Incubation	2	11	28	
13-19 May	Incubation	2	10	18	
20-26 May	Incubation	3	8	12	2.4 (incubation)
27 May - 2 June	Incubation	0	6	5	
3-9 June	Incubation	0	5	0	

Table 5. Comparison of black duck pursuit flight frequencies between years with low (1973) and higher (1974) densities of territorial and non-territorial pairs at Antigonish estuary, N.S.

Year	Hours Observed	Index of potential interacting pairs (territorial x non-territorial pairs)	Frequencies in flights per hour per pair during whole breeding season	Frequencies of flights per hour per pair during peak nest and territory initiation
1973	216	5 x 4 = 20	0.017	0.016
1974	314	8 x 6 = 48	0.034	0.064

Table 6. Characteristics of pursuit flights in which marked and unmarked males joined paired black ducks during 1972, 73, 74 at Antigonish estuary, N.S.

Description	Number of flights	Mean number of males involved	Range in numbers of males	Duration(s)		Approx. range in height (m)	Approx. distance travelled from origin, range (m)	Unpaired males returned with pair after flight
				av.	range			
Female flew in short hops (<20s) to avoid males	27	12	3-22	12	4.20	4.5-9	15-180	27 (100%)
Long flights by female to avoid males	88	12	3-23	128	28-5 min.	9-120	180-800	86 (97%)
Male flew with pair	34	1	1-3	-	-	-	-	-
Male joined a territorial pursuit flight	12	1	1-2	24	28-120	-	-	4 (33%)

Table 7. Time in hours spent on territories by territorial males during the entire territorial period. Composite data for seven marked pairs obtained during 395 h of observation during 1973, 74 at Antigonish estuary, N.S.

Period	Hours of observation	Male on territory, alone or with his female	Pair or male on communal area when not on territory	Location of pair or male unknown
Pre-laying	130	118h (91%)	8 (6%)	4 (3%)
Laying	151	127h (84%)	18 (12%)	6 (4%)
Incubation	114	77h (68%)	23 (20%)	14 (12%)
Three periods	395	322h (82%)	49 (12%)	24 (6%)

Figure 1. Approximate boundaries and percentage use by resident pairs of portions of two territories observed for a total of 61 h, a sketch of the study area at Antigonish estuary Nova Scotia (inset) showing the approximate boundaries of six territories. Boundary delineation based on hostile encounters with other pairs.

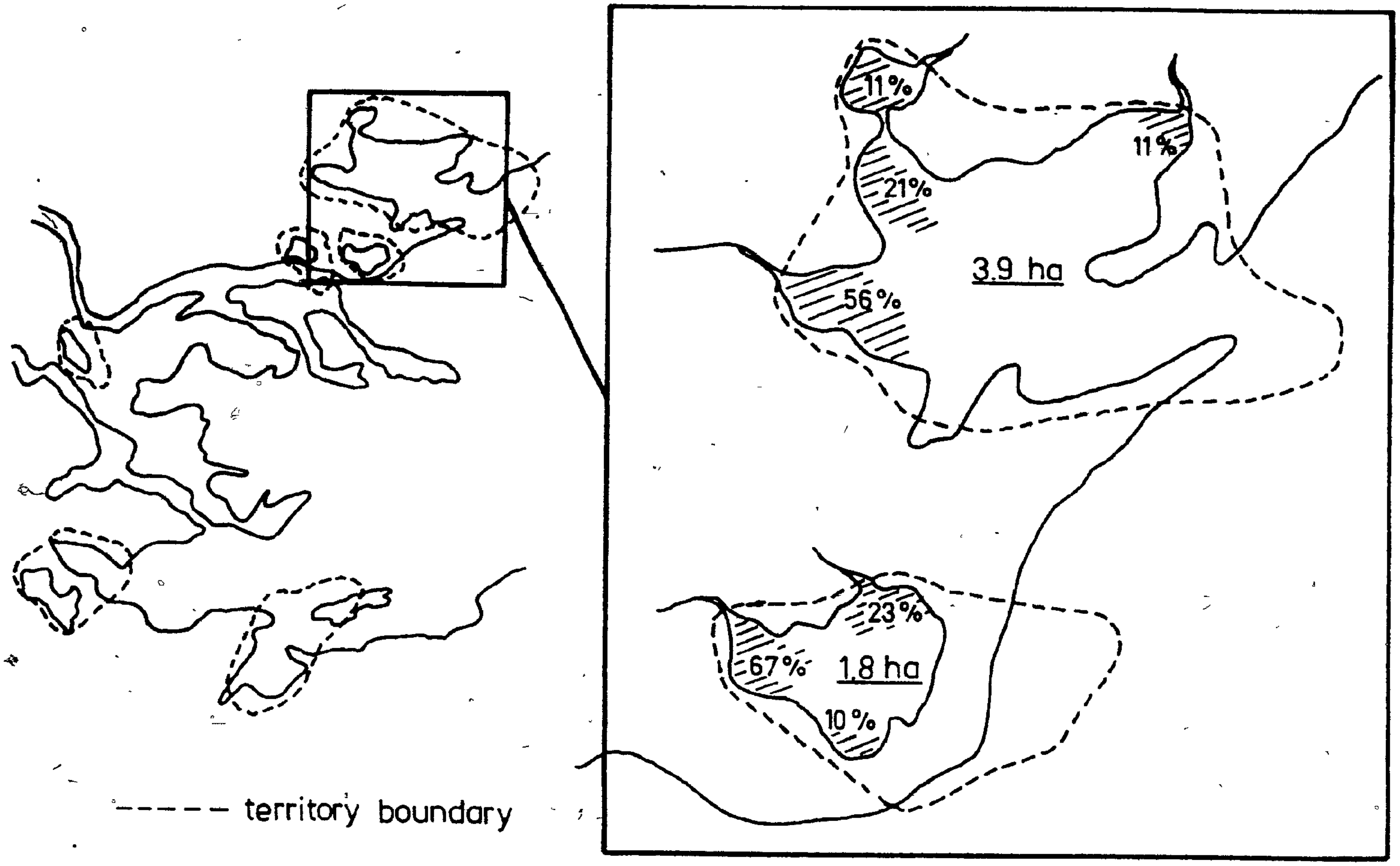

11%
11%
21%
56%
3.9 ha
23%
67%
1.8 ha
10%
territory boundary

Figure 2. Change over the breeding season in the occurrence of four forms of male hostility during 336 encounters between pairs at Antigonish estuary, Nova Scotia. Each display is plotted as a percentage of total displays observed during one day.

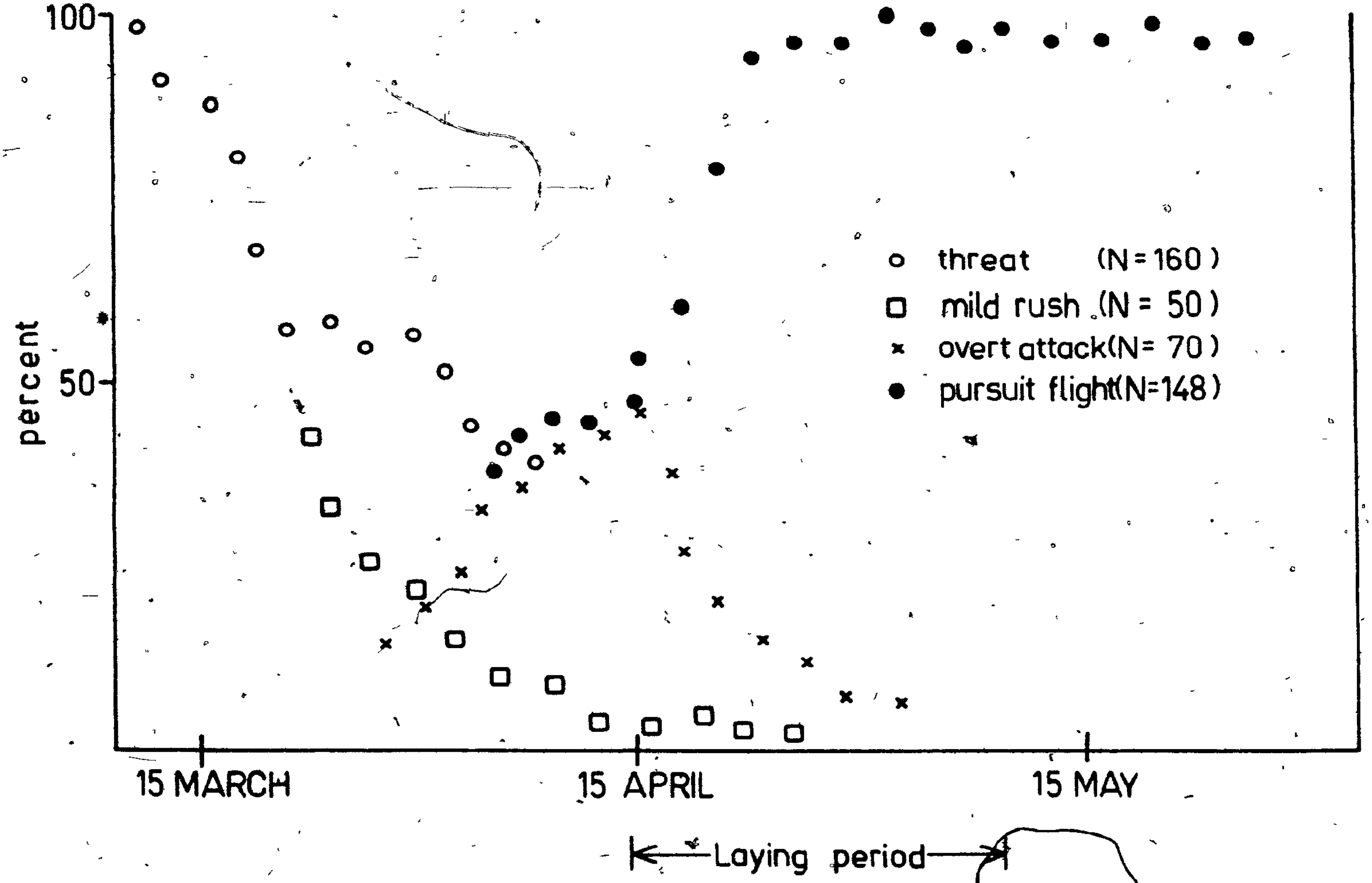

100
50
percent
15 MARCH
15 APRIL
15 MAY
Laying period
○ threat (N = 160)
□ mild rush (N = 50)
× overt attack (N = 70)
● pursuit flight (N = 148)

Figure 3. Changes in the location (communal area or territory) and frequency of occurrence of 402 hostile encounters between pairs during the breeding season. Also changes in the percentage occurrence of 156 pursuit flights and in the occurrence of pairs displaced 90 m or more from the location of 176 encounters between pairs. All data from Antigonish estuary, Nova Scotia, in 1974.

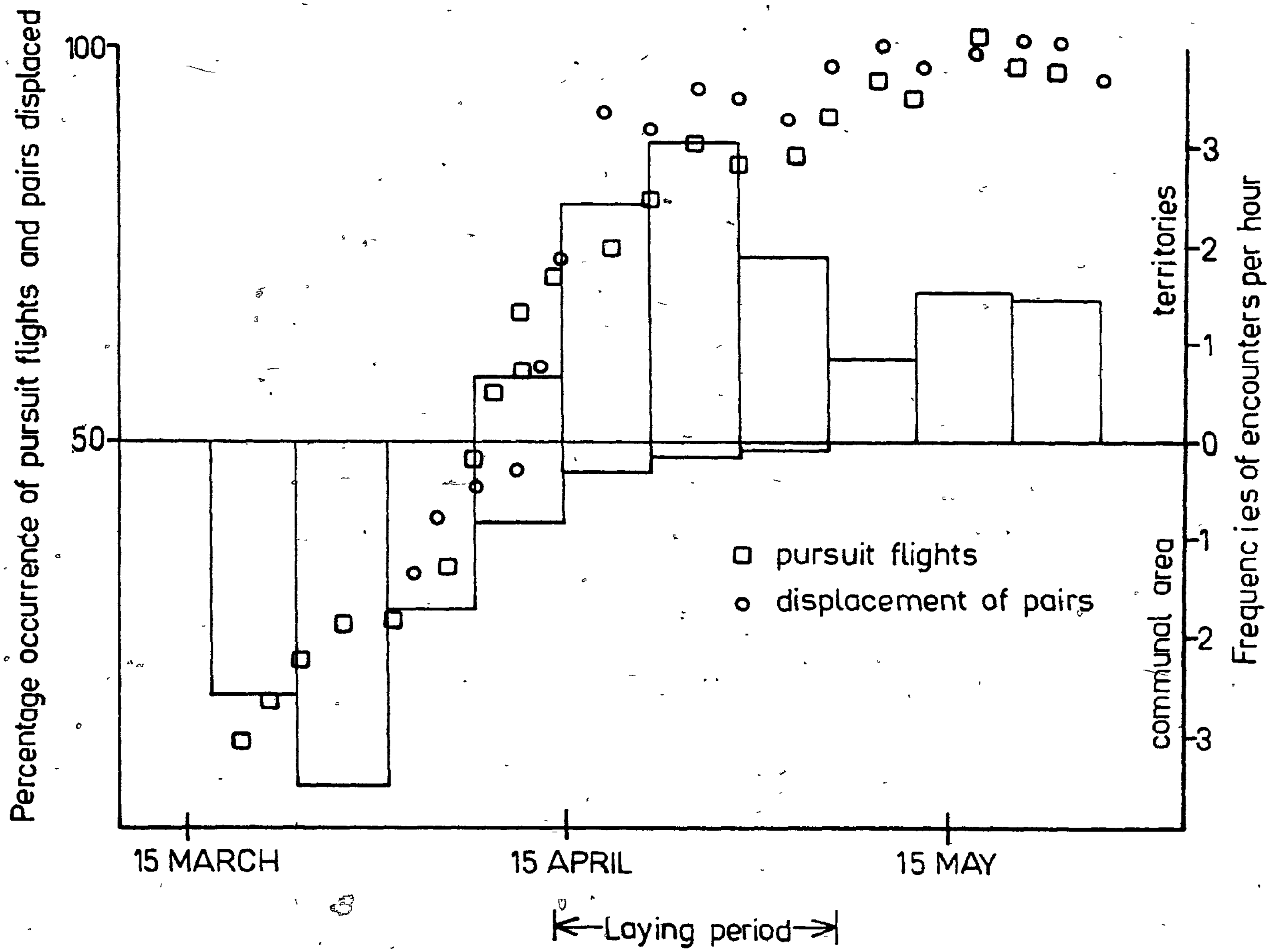
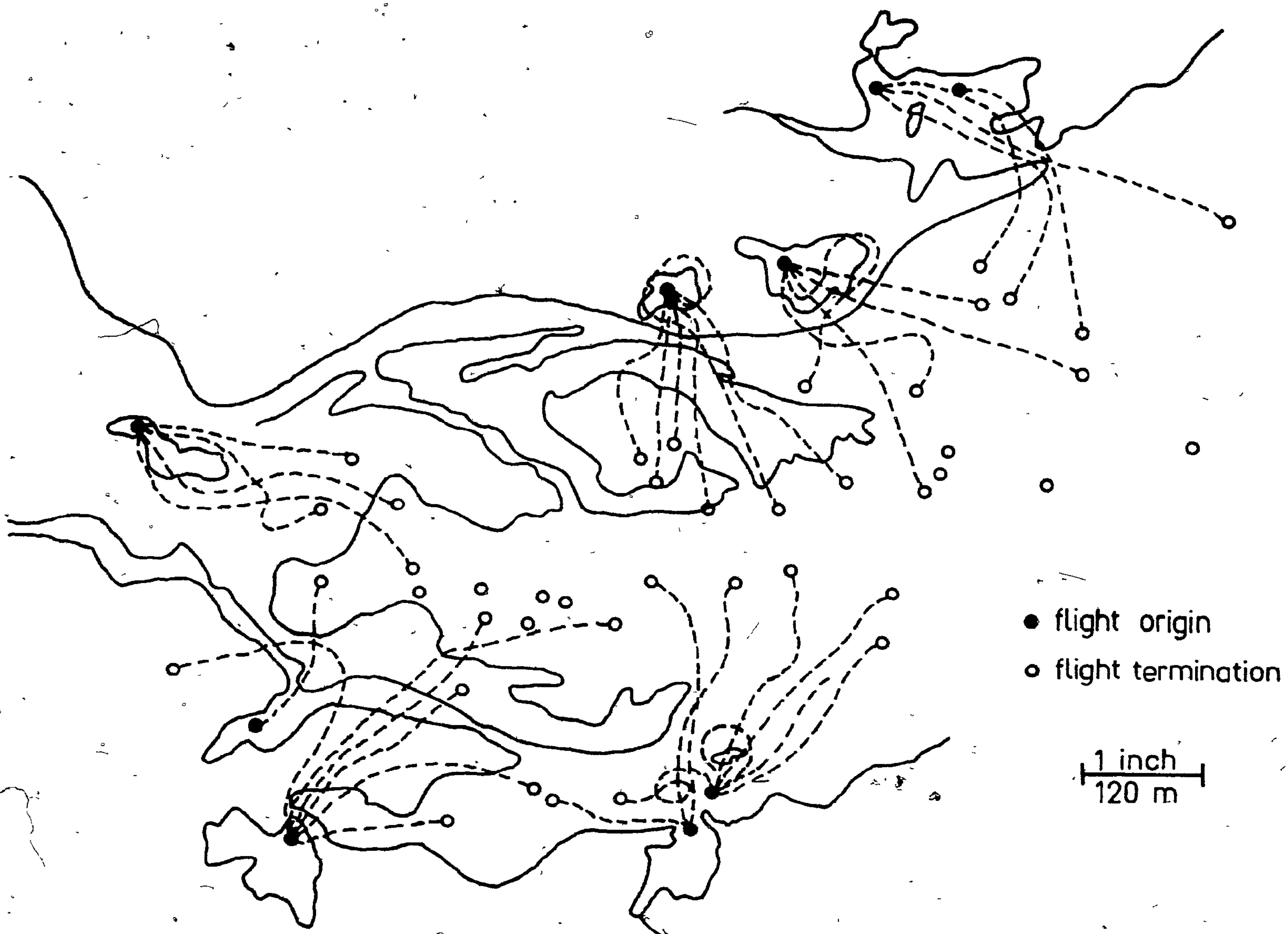
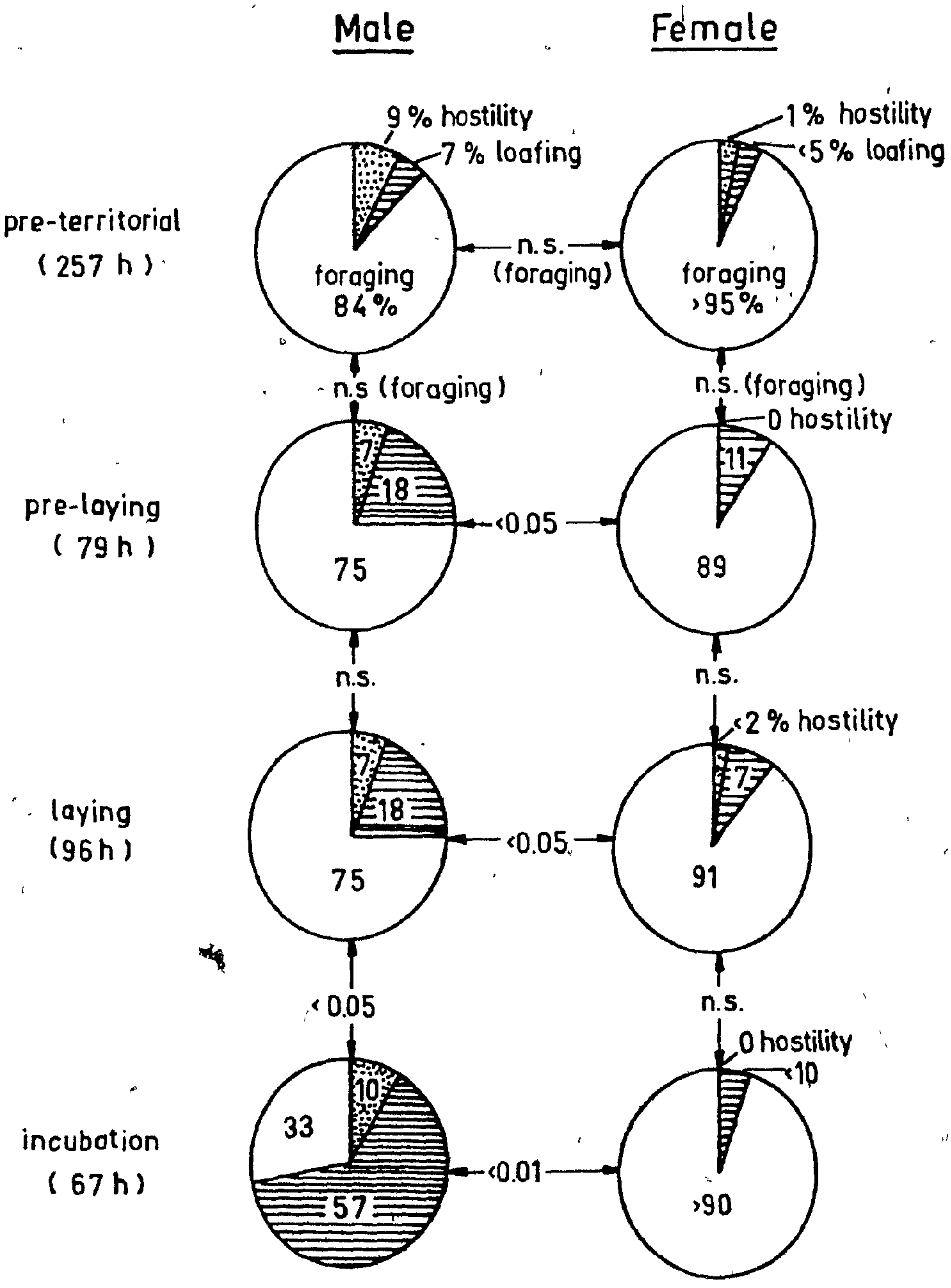

Percentage occurrence of pursuit flights and pairs displaced
100
50
15 MARCH
15 APRIL
15 MAY
←Laying period→
territories
communal area
Frequenc ies of encounters per hour
3
2
1
0
1
2
3
□ pursuit flights
○ displacement of pairs

Figure 4. The approximate point of origin on territories (75 flights) and termination on the communal area (44) of pursuit flights by territorial males with complete trajectories for 36 flights (1973) at Antigonish, N.S.



● flight origin
○ flight termination
1 inch
120 m

Figure 5. Percentage occurrence of three activities of pairs while males and females were together during the pre-territorial and territorial (pre-laying, laying, incubation) periods. Based on bouts of continuous observation during 1973 and 1974 at Antigonish estuary, Nova Scotia.


Male
Female
pre-territorial
(257 h)
9 % hostility
7 % loafing
foraging
84 %
n.s.
(foraging)
1 % hostility
<5 % loafing
foraging
>95 %
n.s (foraging)
n.s. (foraging)
pre-laying
(79 h)
7
18
75
<0.05
0 hostility
11
89
n.s.
n.s.
laying
(96 h)
7
18
75
<0.05
<2 % hostility
7
91
<0.05
n.s.
incubation
(67 h)
10
33
57
<0.01
0 hostility
<10
>90

The reproductively oriented behaviour of unpaired males during the breeding season is a component of the social system of ducks. The behaviour of unpaired male ducks, particularly interactions between these males and pairs, has been largely ignored in the literature.

Details of the behaviour of unpaired male black ducks further elucidates aspects of the social structure of this species. This behaviour is not included in the first manuscript, dealing with territoriality, because the daily and seasonal activities of unpaired males need not involve interactions with paired birds. In addition, the behaviour of these males is interpretted in terms of benefits incurred by the unpaired male and not the pair.

BEHAVIOUR OF UNPAIRED MALE BLACK DUCKS DURING THE BREEDING SEASON

ABSTRACT

The behaviour of wild unpaired male Black Ducks, *Anas rubripes* was studied on a tidal marsh in eastern Nova Scotia, Canada. Interactions between males and pairs were studied during the breeding season. There were no unpaired females. Much of the data were derived from observations of seventeen marked males. Males actively displayed to females from late March until late May. Groups of unpaired males interacted most often with pairs yet interactions between single unpaired males and pairs also occurred. Most encounters occurred on the central marsh area and not on breeding territories at the periphery.

Changes in daily and seasonal frequencies of foraging, loafing and reproductively oriented activities were determined. In March encounters between groups of males and pairs consistently resulted in social display by the males. This activity decreased in mid April and ceased by late May. Single males rarely displayed but remained near pairs. The median duration of an association between a group and pair was in the 61-90 min interval and for a single male and a pair it was in the 91-120 min interval. However, on four occasions a single male remained on a territory with a pair for at least three days.

The reaction of paired males to unpaired males changed during the season. There was no reaction early but then threat and more overt hostility developed rapidly and continued until after unpaired males ceased active display in late May. Paired males remained close to their mates and did not engage in long chases after unpaired males. Territorial males appeared to tolerate single unpaired males on their territories. The likely significance of unpaired males in the breeding biology of the black duck is discussed.

BEHAVIOUR OF UNPAIRED MALE BLACK DUCKS DURING THE BREEDING SEASON

INTRODUCTION

Little is known about the behaviour of unpaired male ducks of the genus Anas during the breeding season. This paper describes the daily and weekly activity of unpaired male black ducks (A. rubripes) throughout the breeding season and interactions of these males with conspecific males and pairs. In addition, the possible influence of unpaired males on the activities of breeding pairs is discussed.

The study area was an undisturbed 170 ha Spartina marsh at the upper end of a tidal estuary in Antigonish County, Nova Scotia. The central part of the marsh was used by the ducks as a communal area and paired males established territories in tidal pools which were primarily at the marsh edge (Seymour in prep). The marsh was free of ice two weeks or more before inland waters and was used by migrants and residents which wintered in the lower estuary.

Several vantage points allowed virtually complete surveillance of the marsh and frequently many birds could be observed simultaneously. Numbers and locations of birds were estimated each year (1972-1974) from counts made from 15 March to 31 May. Counts during the last two weeks of March were made at three hour intervals (dawn to dusk) every two days. During April and May counts were made at two hour intervals on three or four days each week. A grid of wooden poles placed approximately 100 m apart was used to locate and follow the movement of birds. These grids each covered approximately 2 ha and were located on six of the most frequently used parts of the marsh.

During 1973, 17 unpaired males were captured in poultry wire traps which were baited with captive female black ducks. Captured birds were marked with nasal saddles (Bartonek and Dane 1964) and released. Groups and single unpaired males, both alone and associated with pairs, were observed continuously from 30 min to 7 h for a total of 569 h from 15 March until 15 June in 1973 and 1974.

To facilitate observation of males, females held in cages were placed in strategic locations in the marsh to attract males. Additional detail on the study area and breeding population can be found elsewhere (Seymour in prep).

RESULTS

Unpaired males apparently remained on the marsh and, except for the first two weeks in April when migrants were in evidence, counts revealed a relatively consistant weekly average of 128 (range 114-132) for 1973 and 112 (range 102-118) for 1974. In early June however, numbers increased as presumably post-breeding birds joined these males.

Unpaired males and pairs were together in flocks before pairs became intolerant toward other conspecifics. Even then, unpaired males remained together and from approximately 15 March to 10 April, 1974, they usually (87% of 138 h of observation) stayed in a 0.80 ha portion of the marsh. On 72 occasions during this period males left this area to follow pairs but returned within 15 min. After 10 April the large flock consisted of smaller groups (Table 1) which used more of the marsh. Despite this, males still used the main area more (67% of 628 sightings, 15 March to 15 June) than any of four areas of high use. More extensive use of the marsh corresponded with an increase in the frequency of unpaired males which joined pairs that were now less tolerant of conspecifics. The average size of groups of males associated with pairs varied with time (Table 1) but seldom contained more than 12 individuals. Most associations (81% of 180 sightings) involved groups of more than two males but 19% involved single males. Observations of marked birds within groups suggested that groups remained relatively intact. Individuals that left a group usually returned and frequently the whole group joined a pair as a unit.

From late March until mid-April males accompanied most pairs that used the communal area and most males joined pairs when they were accessible (Table 1).

Usually (98% of 438 observations) associations involving groups of males were seen on the communal area and not on territories. However, 27% of 102 observations of single males with pairs occurred on territories.

Grouped and single males often joined a pair as soon as it landed and remained with it for a considerable period of time (Table 2), frequently until it left the estuary. No groups apparently persisted throughout the day with a pair as did some single males. On four occasions a male remained with a territorial pair for at least three consecutive days.

The activity of unpaired males was divided into foraging, loafing and reproductively oriented activity. A bout of activity was scored as foraging for the time an individual was preoccupied with this activity. For example, brief interruptions to preen or rest were not recorded as such but rather the whole bout was scored as foraging. Loafing, which consisted primarily of sleeping, was similarly scored. A bout of reproductively oriented activity was measured from the time and individual male or group of males joined a pair until they separated. For groups this activity consisted primarily of social display toward the paired female which was apparently never a willing participant.

Figure 1 details the changes in the relative occurrence of the three activities in groups of males. Foraging decreased throughout the season. Loafing was always a major activity but increased dramatically after reproductively oriented activity subsided at a time when food was probably plentiful. Reproductive behaviour began suddenly during the last week of March and remained a major activity for eight weeks, until the last week of May. Group social display (Figure 2) was observed most frequently during the first two weeks in April. Prior to this, groups of males associated with pairs but did not display. Decoy ~~females~~ which were placed in areas frequently used by males were visited only rarely after mid-May and social display ceased entirely in early June, despite the presence of pairs. Single males only periodically engaged in obvious reprodutively oriented activity for brief periods and usually performed the same activity as the pair. During 48 h of observation only 8% of the activity of unpaired males was obvious sexual behaviour. After mid-May these males were less frequently seen with pairs.

Changes in the relative occurrence of the three activities throughout the day are outlined in Figure 3 for the five continuous weeks during 1974 when groups of males most frequently displayed. There was an early morning and a lower evening peak of foraging and a mid-day peak of loafing. Reproductive activity, which depended on pairs being nearby, increased after morning foraging and remained relatively high until approximately 13:00 h. There was a lesser peak in the evening.

Unpaired males influenced the activity of pairs more markedly as the season advanced. During March pairs did not avoid males or significantly alter their activities in response to unpaired males. By the first week in April, males associated with pairs for as long as 90 min but did not vigorously display to paired females. Pairs avoided males then but their activity was not generally interrupted. During the second week of April males crowded around females when displaying and persistently followed them everywhere in the marsh frequently interrupting the activities of the paired birds. It was particularly difficult for pairs to forage during social display by males.

Interactions Between Unpaired Males and Pairs

In March encounters between groups of males and pairs consistently resulted in social display except for some hostility at feeding places. Whether on the communal area or on a territory, males appeared unconcerned by the presence of a paired male and displayed to his female. Any form of resistence to paired males was rare. Usually males ignored threat postures by a paired male and simply swam away when attacked. Unpaired males quickly returned to within 1 m of a female after being chased, often before her mate. Males usually joined any nearby pair but often stayed with certain females longer and courted them more vigorously than others. Males quickly joined females which performed Persistent Quacking (Dzubin 1957) or precopulatory behaviour. It appeared that groups of males preferred to display to females without mates since there were continuously groups with decoy females that did not leave them to join nearby pairs. Males joined foraging pairs in 87% of 337 encounters observed and loafing pairs in the remainder.

Although groups were often associated with pairs for several hours, males did not usually display continuously. Social display was most intense immediately after males joined pairs. Table 3 shows the change in frequency of male displays during a typical 25 min bout involving 10 males. Only obvious male displays, subjectively measured, were recorded but almost invariably the entire repertoire of displays as described by Lorenz (1941) for the mallard (A. platyrhynchos) was seen during each bout. The wing flap which Johnsgard (1960) says is characteristic of early stages of courtship was frequently observed. Most bouts lasted 25-95 min with intervals of 19-55 min between bouts of displays. Males loafed or foraged near the pair between bouts of display. Sometimes all display had ceased within the first 12 min of an association and did not resume despite the group remaining nearby.

Usually the number of males decreased after the first 5 min, particularly when several males were involved. Occasionally those that left joined other pairs. Bouts were sometimes extended by newcomers which displayed vigorously on arrival and appeared to stimulate resumption of social display by other males. A renewal of the most vigorous display always occurred (27 observations) when females landed after making short (<20S) flights presumably to elude displaying males. Flight by a female often appeared to be the signal for inactive males to join in or to resume active social display. Males frequently left one pair to join another which had just landed or taken flight. On 11 of 14 occasions pairs flushed by a bald eagle (Haliaeetus leucocephalus) were joined by formerly inactive males that pursued the female in flight and displayed to her upon landing. Similarly, on 17 occasions a pair was joined by a new group within 15 min after it had eluded an earlier group.

Two to five males within a group frequently displayed, often at the same time, while others apparently neither displayed nor joined in flights. Jump-flights were identical to those described for the mallard (Lebret 1958). Several males performed Jump-flights one after the other or almost simultaneously. Sometimes only one male Jumped. Males which lagged behind a group often flew in flights resembling Jump-flights but landed several feet behind the female suggesting that such a flight was simply made to rejoin the group. Continuous male vocalization ("raab" notes) was usual during social display.

Single males responded to pairs differently than did groups. Social display was recorded during only 7 of 102 observations of single males with pairs. Usually a male remained within 3 m of a pair and followed them whether on a territory or on the communal area. However, on three occasions involving a male that had been with a pair for at least two days, the male remained on his territory when the resident pair flew to the communal area and rejoined them when they returned. Sometimes when a territorial male threatened other pairs, the associated unpaired male also held his head high in apparent threat posture and on seven occasions remained with the paired female while her mate chased intruders. When this occurred the unpaired male remained alert until the paired male returned. Hostility between paired males and unpaired males was rare (<10% of encounters). However, fighting occurred on three occasions when a male which had been associated with a pair for at least two hours swam close to the female despite threat postures by her mate. Fighting was never observed between paired males and groups.

Unpaired males did not apparently attempt to rape females. This was so throughout the year even though males often came into contact with females during social display. Similarly, rape was not observed when groups or single unpaired males briefly found themselves alone with a female on her territory.

Response of Females to Unpaired Males

Throughout the breeding season paired females usually (71% of 232 encounters) responded to groups by Inciting (cf Lorenz 1941) and then swimming close beside or more often behind her mate. Repulsion posture (cf Lorenz 1941) was observed infrequently (<5%) and involved only females which were in the laying or incubation phases of the reproductive cycle. When males persisted the female usually followed her mate with her head pulled back and head and neck feathers depressed. At such times she appeared much smaller than her mate. Social display appeared to facilitate the occurrence of Inciting as Weidmann and Darley (1971) found for the mallard. Paired females Incited throughout bouts of displays, often as frequently as 18 times during 25 min, sometimes rushing at a male and then immediately rejoining her mate. Often females tended to Incite and chase one particular male although he appeared to behave in the same manner as the others. When males pressed around a female she either remained extremely close to her mate or took flight. The female usually foraged during lulls in display activity however she was often displaced from where she had been feeding by the activity of the males.

Although females Incited when they initially encountered single males, they usually stopped Inciting within approximately 20 min unless the male displayed or continued to approach her. After 20 - 30 min females tended to ignore single males which, unlike groups, apparently only disrupted their activity periodically and briefly (Table 4).

Four unpaired females that were released on the study area associated with individual males within five hours of release. These females oriented to their "new mates" and Incited and rushed at displaying males. The "new mates" threatened and chased their former associates and appeared to try to lead the female away from them the same way that males with long standing pair bonds did. The females and at least one of the newly paired males, which was marked, left the marsh within two days of release. This suggests that unpaired males will remain with females given the opportunity.

Response of Paired Males to Unpaired Males

The form and intensity of hostile response by paired males to groups of males changed over the breeding season (Figure 4). Early paired males either did not react to males or did so only after 17 - 92 min of Inciting by their females. Later paired males threatened when they first encountered males and only occasionally thrust their bills and rushed (mild rush) toward them. As males became more attentive to their mates, they made vigorous 4 to 6 m rushes (overt attack) over the water with bill open and neck outstretched. The chaser often pecked at the other male. Although the unpaired male usually jumped into the air to elude him, the pursuer never took flight but returned immediately to his mate. Overt attack was often directed toward one or two specific individuals in a group. One paired male attacked one individual in a group of 10 in 16 of 21 chases during a 15 min bout of social display. The male frequently appeared to ignore other males closer to his mate in order to chase specific males. This response was repeatedly seen during the breeding season. By the time overt attack was common, a paired male reacted as soon as or before his mate Incited. A paired male sometimes left his mate to attack males up to 6 m away. However, during intense display a paired male chased only males 1.5 - 2 m from his mate, with head and neck feathers erect, and appeared to try to lead the female away from the group. Paired males usually made no attempt to forage when groups were nearby (see Table 4) or, unlike their mates, during lulls in display activity.

Before hostility among pairs had developed, formerly compatable paired males frequently threatened and rushed at each other after interacting with unpaired males. On 18 occasions a group of males joined first one and then another pair that had foraged and loafed within 15 m of each other for more than two hours before the encounters. In each case the paired male had threatened and attacked the unpaired males beforehand. After the unpaired males left the two paired males threatened and chased each other until the pairs separated and remained 200 - 300 m apart. Frequently this same response occurred when single unpaired males visited nearby pairs.

Males encountering groups of unpaired males did not react with the same intensity of hostility on a territory as they did on the communal area. Paired males often did not chase or threaten unpaired males after an initial encounter and did not apparently lead their females away from the males. On two occasions a male slept while his mate, which was foraging, was courted. The paired male became alert only when his mate periodically Incited. On 12 occasions males left their mates with groups of males for up to 2 min while chasing intruding pairs.

Paired males became alert when first joined by single unpaired males. However, unless the unpaired male displayed or the female continued to Incite vigorously the paired male performed threat displays which ceased within 7 - 12 min. The most intense hostility was usually not more than following behind the unpaired male and occasionally rushing at him. On 19 occasions an unpaired male was tolerated within 3 m of a female within 20 min of joining the pair. In long term associations the paired and unpaired males frequently sat less than 1 m apart while the female foraged 6 to 9 m away.

Other Interactions Involving Unpaired Males

Males loafed and foraged together when not associated with pairs. However, when with pairs formerly compatible males threatened and chased each other and sometimes fought (Table 3). Weidmann and Darley (1971) found an increase in the frequency and intensity of overt aggression between unpaired male mallards after a female was introduced to their enclosure. In four cases two males were repeatedly seen together throughout the breeding season. Only one of these males was ever observed to display, although the other followed close behind him during social display and other activity.

One of three male Mallards joined a group of courting black ducks on 12 occasions. When on the water these birds performed the same repertoire of social displays as the black ducks and were often synchronized with the black ducks. Mallards joined 18 flights which arose during social display. Male pintails (_A. acuta_) joined displaying groups on the water on 8 occasions. They performed Grunt Whistles, were usually at the periphery of a group and did not join fights.

DISCUSSION

Evidence suggests that the activities of unpaired males may have a detrimental influence on the ability of pairs to reproduce successfully. Most encounters between pairs and unpaired males occurred on the communal area before most females had begun egg laying. Most (87%) encounters were with foraging pairs. Despite the high probability of being joined by males, pairs continued to use favoured foraging locations which were also the locations where unpaired males concentrated.

Since pairs foraged on the communal area until only a few days before egg laying, it is likely that successful foraging here could be critical to the female's ability to develop ova. Anything inhibiting the foraging activity of females at this time could potentially affect her reproductive effort. Evidence (Table 4) suggests that unpaired males did inhibit and sometimes prevent females from foraging. Seymour (in prep) suggested that adequate food in this population may have influenced the date of egg laying. It is possible that continued interruption of foraging by unpaired males could potentially retard egg laying for some females. This might be particularly so in the case of later nesting birds which, at times of high pair density, might be excluded from alternate foraging locations by territorial males.

Harrassment of pairs by unpaired males may have contributed to the dispersal of pairs which led to the establishment of territories. Interactions between the mobile unpaired males and pairs were often followed by increased hostility among even formerly compatible pairs. Dispersal of pairs began about the time that unpaired males began to associate with pairs.

Unpaired males may also have had subtle influences on pairs. Forced pair bond copulations were sometimes seen when, after a brief separation, a male returned to his mate and found an unpaired male there. On two such occasions the male landed beside his mate, and without preliminary display, grabbed her by the nape and mounted her, despite her attempts to swim away. In both cases copulation appeared successful and the pair subsequently remained together.

Single males that were tolerated by pairs, particularly territorial pairs, may have benefited the pairs. Although they consumed some of the food on the territory, they often located food for the pair. In addition these males were usually alert and could provide aid in detecting predators. These males may have helped to maintain a territory since they usually stayed with a female when her mate chased intruding pairs and may have provided an additional deterrent against further or other intrusion.

Hochbaum (1944) speculated that males which had associated with pairs may subsequently compete more successfully for a mate. The benefit to the male may be immediate since the female may recognize him and become familiar with him, especially during long associations. This may give the male a competitive advantage if she later requires another mate. The immediate presence and availability of a single male may be important in a female's choice of a new mate. Since unpaired males apparently did not attempt to rape females this seems to be the most probable means by which an unpaired male may leave progeny during the same breeding season. It would yield a direct return for the sometimes considerable time a male invests remaining close to a female. Conversely it appears that the alternate strategy of remaining in a group and testing apparently firm pair bonds through display, would be less successful unless females ignored single males and went to groups of males when searching for a new mate. Observations revealed that some males employed both strategies and this was probably so for all males.

Despite the apparent ability of unpaired males in this population to form pair bonds with newly introduced females, it is unlikely that they competed successfully for already paired females. Although unpaired males may be able to reproduce by bonding with abandoned re-nesting females, it seems likely that the main benefit to the unpaired male in associating with females was in experience gained.

LITERATURE CITED

Bartonek, J.C. and Dane, C.W. 1964. Numbered nasal discs for waterfowl. J. Wildl. Mgmt, 28: 688-692.

Dzubin, A. 1957. Pairing display and spring and summer flights of the mallard. Blue Jay, XV(1): 10-13.

Hochbaum, H.A. 1944. The Canvasback on a Prairie Marsh. Amer. Wildl. Inst., Washington, D.C. 207 pp.

Johnsgard, P.A. 1960. Pair-formation mechanisms in *Anas* (Anatidae) and related genera. Ibis, 102: 616-618.

Lebret, T. 1958. The "Jump-flight" of the mallard, *Anas platyrhynchos* L., the teal, *A. crecca* L. and the shoveler, *Spatula clypeata* L. Ardea, 46: 68-72.

Lorenz, K. 1941-1971. Comparative studies of the motor patterns of Anatidae. In: Studies in Animal and Human Behaviour, Vol. 2. Methuen, London. Pp. 14-113 (translation by R. Martin of "Vergleichende Bewegungsstudien Anatinen". J.F. Orn. 79, 1941).

Weidmann, W. and Darley, J. 1971. The role of the female in the social display of mallards. Anim. Behaviour, 19: 287-298.

Table 1. Group size and disposition of unpaired males and paired black ducks in Antigonish Harbour, Nova Scotia, during the breeding season, based on 628 sightings of unpaired males and 766 sightings of pairs during 1974.

period	mean size of groups of unpaired males not with pairs	mean size of groups seen with pairs	range in size of group with pairs	percent of pairs accompanied by one or more unpaired males	percent of unpaired males associated with pairs
11-17 March	23	2	2-3	22	8
18-24	25	3	2-5	48	45
25-31	15	12	8-15	66	74
1-7 April	15	12.7	4-20	83	84
8-14	18	12.3	5-28	78	82
15-21	16	7.0	4-14	14	24
22-28	18	7.2	4-15	9	18
29-5 May	15	7.6	4-15	11	27
6-12	19	6.9	4-14	2	8
13-19	22	4.2	4-10	2	9
20-26	28	0	0	0	0

Table 2. Duration of association of one or more unpaired males with paired black ducks, based on 254 h of observation during the four peak weeks of display activity (1973 & 1974).

number of unpaired males	Duration of association in minutes									apparent all day association
	<15	16-30	31-45	46-60	61-90	91-120	121-180	180-240	>240	
2 or more (n = 62)	4 (6%)	4 (6%)	6 (10%)	8 (13%)	16 (26%)	12 (21%)	4 (6%)	4 (6%)	4 (6%)	0
one (n = 66)	16 (24%)	2 (3%)	4 (6%)	4 (6%)	6 (9%)	10 (15%)	4 (6%)	6 (9%)	16 (24%)	12

Table 3. Frequencies of displays by unpaired males and response by pairs of black ducks during the first 25 min of a bout of display activity based on 42 observations of groups of 10 males in which each male participated throughout, at Antigonish, Nova Scotia in 1973 and 1974.

Time interval	Grunt whistles (av.number for 10 males)	Head-up Tail-up (Av.)	Wing Flap (Av.)	Female Incite (Av.)	Jump Flight (Av.)	Unpaired male chasing unpaired males (Av.)	Paired male chasing unpaired males (Av.)
0- 5 min	17	5	19	9	2	21	5
6-10 min	6	<1	6	1	1	13	4
11-15 min	4	0	3	1	0	3	4
16-20 min	11	1	9	1	0	12	5
21-25 min	15	4	14	2	0	20	5

Table 4. Percent occurrence of foraging and hostility by pairs associated with unpaired male black ducks during extremes of reproductively oriented activity on the communal area. Numbers based on observation periods of 60 min in which social display or inactivity dominated behaviour.

activity of pair	response of pair to display activity by a group of 5-10 unpaired males (N = 108)		response of pair to a group of 5-10 unpaired males, associated but not displaying (N = 62)		response of pair to display activity by one unpaired male (N = 4)		response of pair to one unpaired male, associated but not displaying (N = 42)	
	female	male	female	male	female	male	female	male
foraging	9(15%)	0(0%)	52(87%)	48(80%)	26(43%)	6(10%)	60(100%)	60(100%)
female Inciting	7(12%)		2(3%)		6(10%)		0	
female following mate, flying or otherwise evading males	44(73%)		6(10%)		28(47%)		0	
male threat, chase or remain alert		17(28%)		6(10%)		22(37%)		0
male leading female or otherwise evading males		43(72%)		6(10%)		32(53%)		0

Figure 1. Percentage occurrence of three activities (foraging, loafing, social display) throughout the day by groups of unpaired male black ducks based on 448 sightings during the 12 week breeding season (1974).

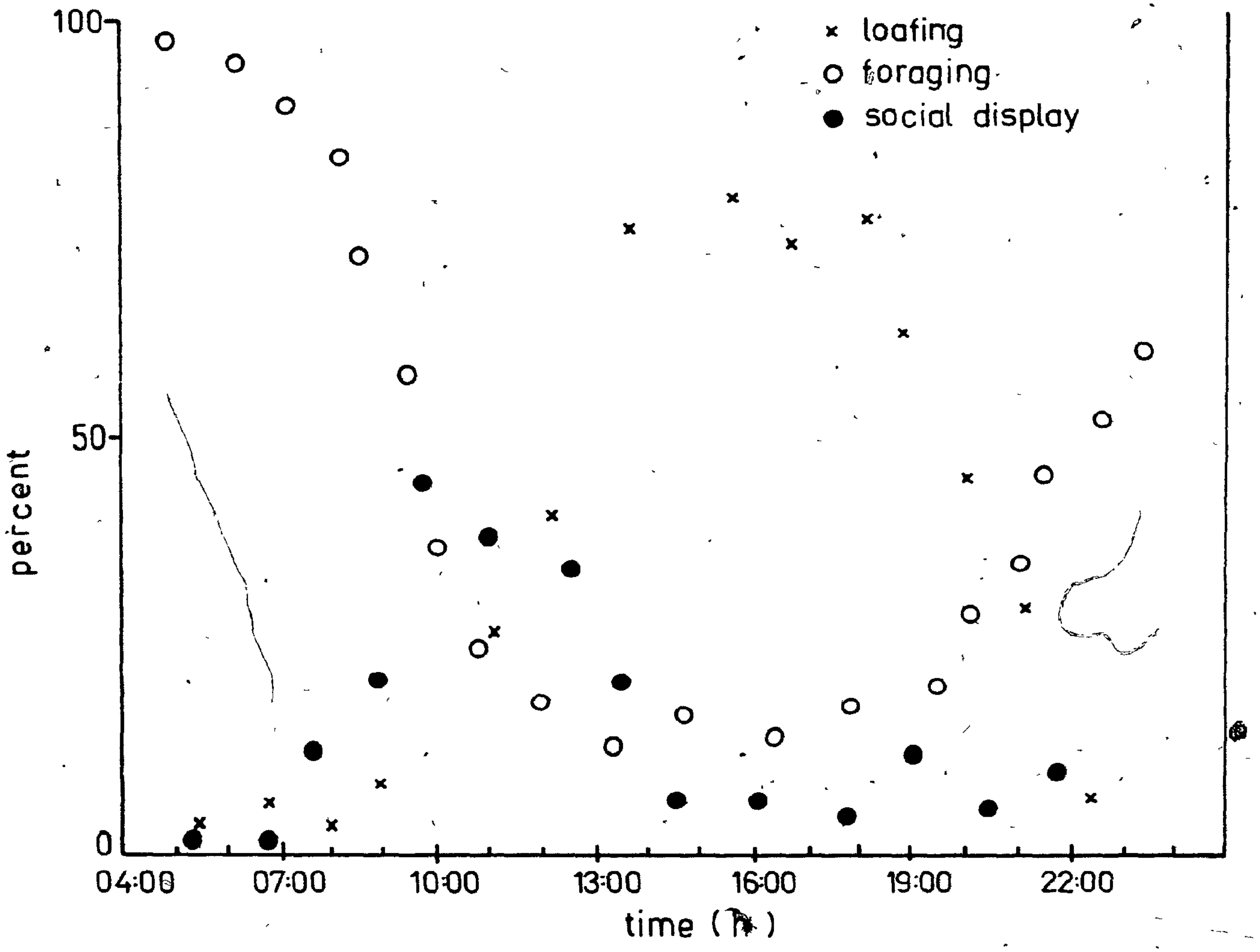

loafing
foraging
social display
100
50
0
percent
04:00
07:00
10:00
13:00
16:00
19:00
22:00
time (h)

Figure 2. Frequency of occurrence of group social display by black ducks, based on 180 encounters during the entire period when social display was observed (1974).

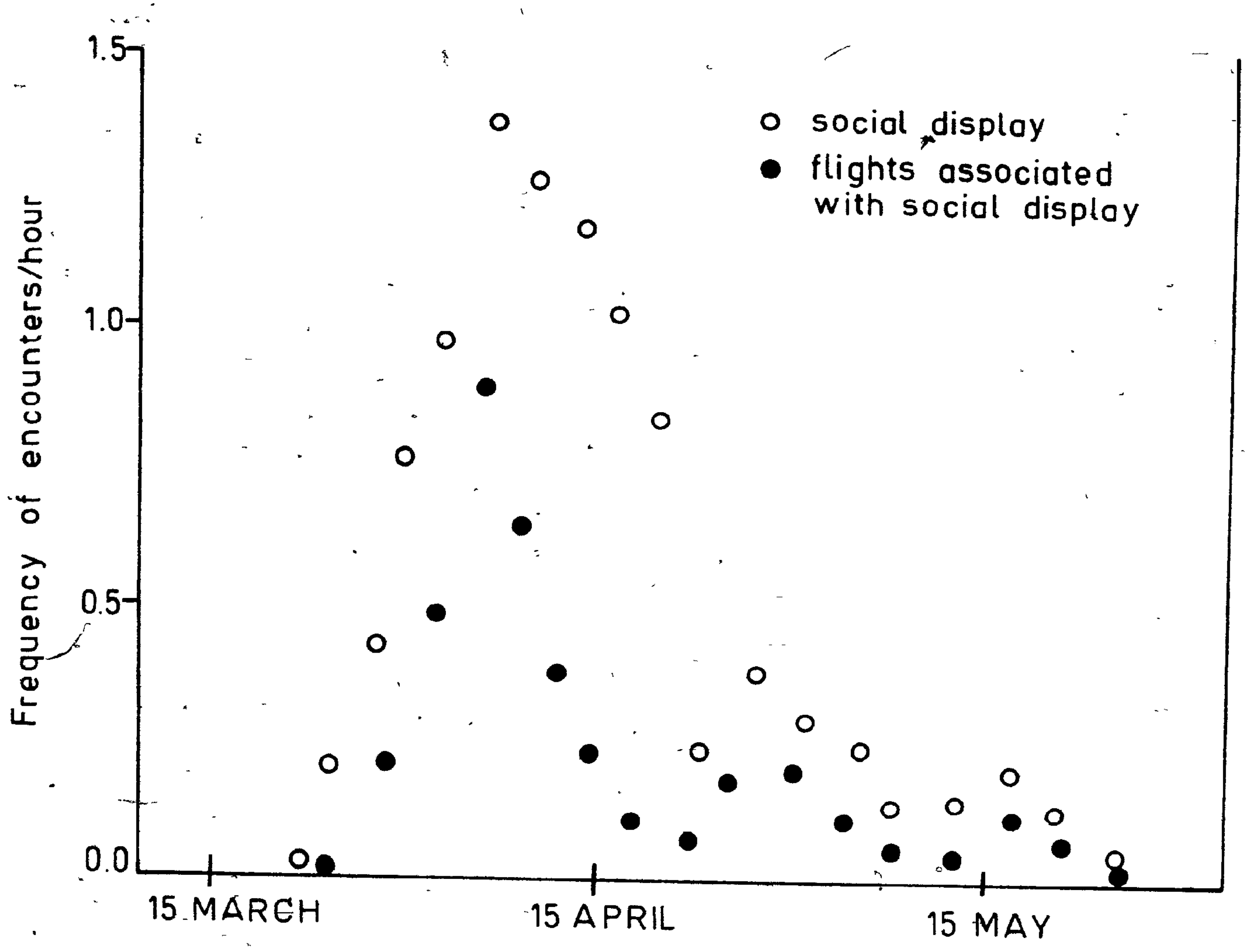
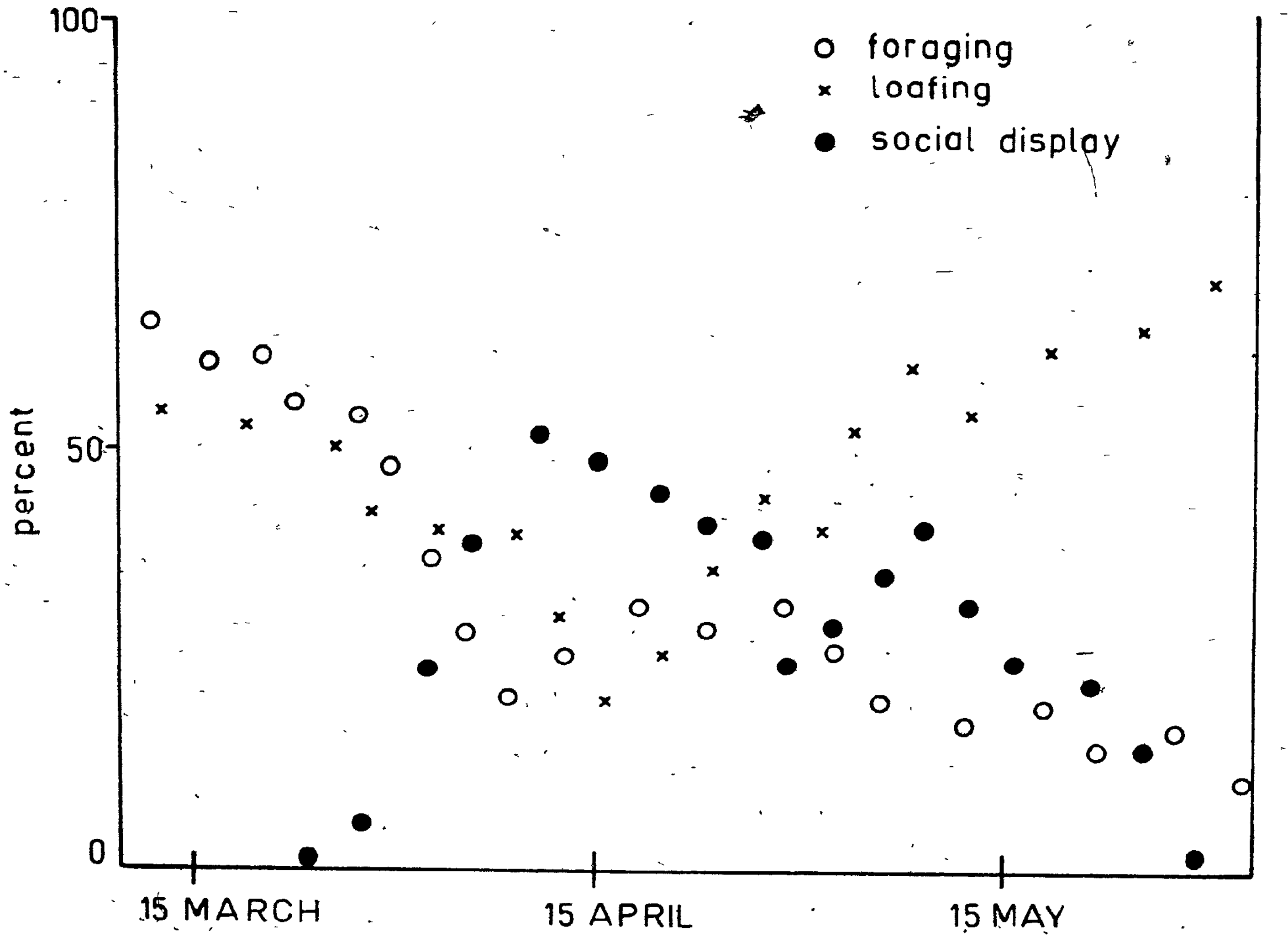
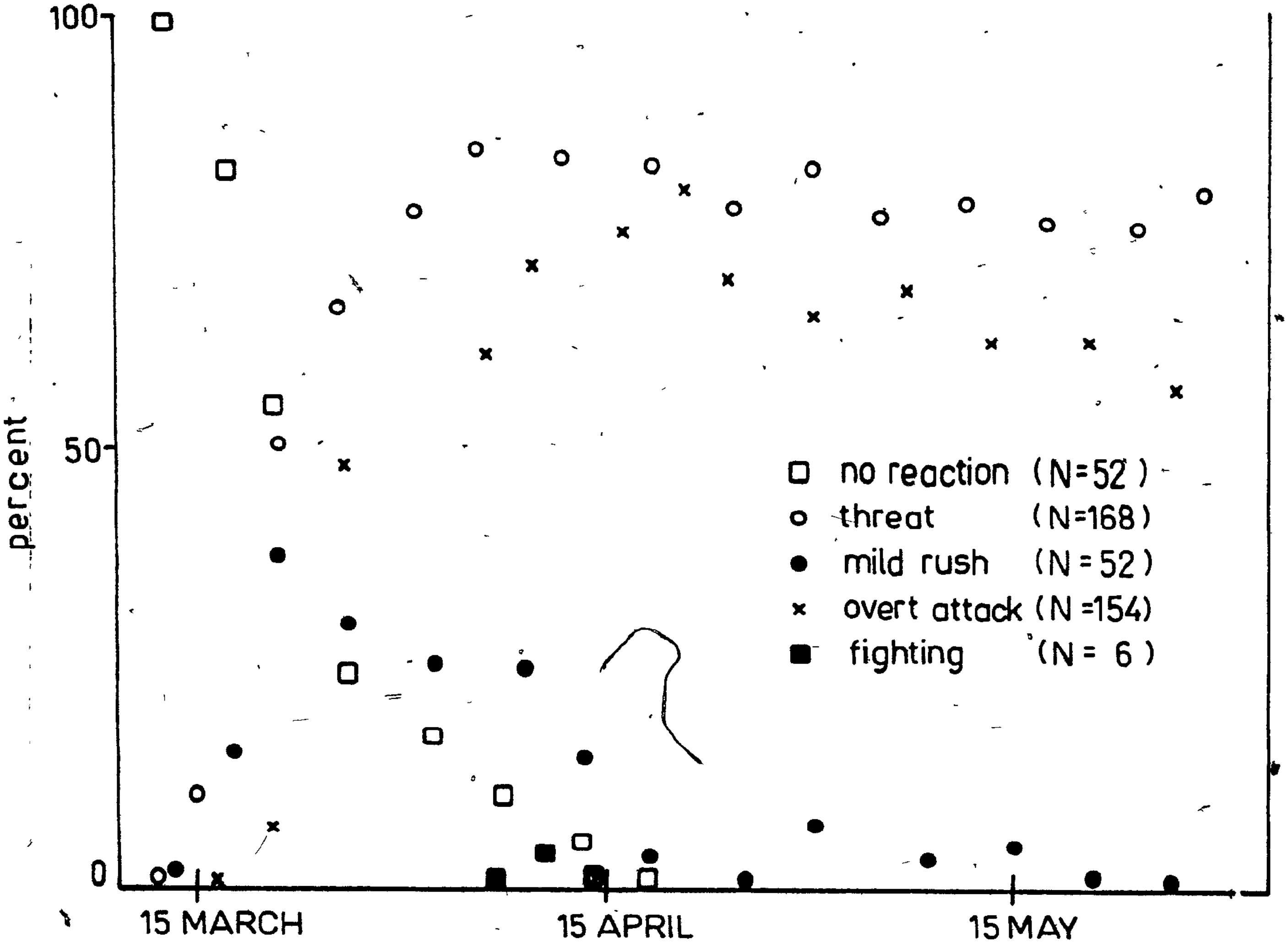

1.5
1.0
0.5
0.0
Frequency of encounters/hour
15 MARCH
15 APRIL
15 MAY
○ social display
● flights associated with social display

Figure 3. Percentage occurrence of three activities (foraging, loafing, social display) of groups of unpaired male black ducks during daylight hours. Based on 116 h of observation during the four peak weeks of social display (1974).



100
50
0
percent
15 MARCH
15 APRIL
15 MAY
○ foraging
× loafing
● social display

Figure 4. Change in the relative occurrence of paired male response toward groups of unpaired male black ducks based on observations of 232 encounters during the entire breeding season (1974).


100
50
0
percent
15 MARCH
15 APRIL
15 MAY
□ no reaction (N=52)
○ threat (N=168)
● mild rush (N=52)
× overt attack (N=154)
■ fighting (N= 6)

Some of the information on pursuit flights presented in the first manuscript of this thesis is also used in the third manuscript. The pursuit flight is a behaviour pattern common to most species in the genus Anas and is probably the major mechanism functioning in the dispersal of pairs on the breeding grounds. It is an important aspect of the social systems of the five species discussed in the third manuscript and further elucidates aspects of the social system of each species.

In the third manuscript the social system of the black duck is compared with four other species. The objective of this manuscript is to place the black duck into perspective within the genus and compare it with other better known species.

PURSUIT FLIGHTS BY FIVE SPECIES OF ANAS DUCKS

ABSTRACT

Observations of pursuit flights by five species of ducks in the genus Anas were made in Manitoba and Nova Scotia. Data were obtained from both marked and unmarked birds. Pintail pursuit flights were significantly different from those of the other species. Pursuit flights by this species suggested lack of site attachment, a poorly developed pair-bond and an oportunistic breeding strategy. Attempted rape of strange females by paired males suggested that purusits by pintails are probably mainly sexually motivated.

Pursuit flights in black ducks and mallards suggested that the pair-bond was well developed, at least until mid-incubation when males deserted territories and mates.

The gadwall and particularly the shoveler represent two species that are in direct contrast to the pintail. Pursuit flights by these species function primarily in the establishment and maintenance of territories. These birds have a well developed pair-bond and paired males protect females from conspecifics well into the incubation period.

PURSUIT FLIGHTS BY FIVE SPECIES OF *ANAS* DUCKS

INTRODUCTION

Species within the genus *Anas* have evolved different breeding strategies in response to different selection pressures. The pursuit flight is common to several species although McKinney (1965) says the function and motivation of the chaser, whether primarily aggressive or sexual, are controversial topics. McKinney (1973) stressed the importance of comparing the behaviour and ecology of related species in elucidating details of specific breeding strategies.

This paper compares characteristics of pursuit flights by the pintail (*A. acuta*), mallard (*A. platyrhynchos*), black duck (*A. rubripes*), gadwall (*A. strepera*) and the shoveler (*A. clypeata*) and attempts to relate this behaviour to the degree of development of the pair-bond and to the general breeding strategy of each species, similar to McKinney's (1973) treatment for the pintail and shoveler. The function of pursuit flights is discussed.

Pursuit flights by five species were observed during intensive investigations of the breeding biology of the mallard, black duck and shoveler from 1968 to 1976. All species except the black duck were observed primarily in the "pothole country" of southwestern Manitoba. This area consisted of mainly agricultural land dotted with small ponds which ranged from 0.04 to 4.86 ha. Additional description can be found in papers by Evans, Hawkins and Marshall (1952) and Kiel, Hawkins and Perret (1972). Observations were also made along a roadside ditch and adjacent flooded meadow near the Delta Marsh, Manitoba. Black duck observations were made in 170 ha cordgrass marsh in a tidal estuary in eastern Nova Scotia. Permanent ponds occurred at the periphery of the marsh and ranged in size from 0.61 to 3.9 ha.

Results for shovelers, black ducks and mallards were derived principally from observations of birds marked with nasal saddles (Bartonek and Dane 1964). Pintails and gadwalls were not marked although it was sometimes possible to determine the identity of certain birds.

Nests found during searches in representative study locations enabled an estimate to be made of the general reproductive stage of the population. It was possible to determine when the peak of laying began in these populations.

RESULTS

The characteristics of pursuit flights are described in Table 1 and reported in greater detail in the following paragraphs. Results in Table 1 are based on pursuit flights which for the most part were seen in their entirety.

Although the status of all birds could not be determined, most pursuit flights appeared to involve paired males as chasers and not unpaired males. The status of the chased birds in these species was only rarely known but it appeared that most chased birds were males and females of pairs. Data are least reliable for pintail pursuit flights.

Shoveler and black duck pursuit flights originated almost exclusively from a chaser's territory and occurred when a pair flew near or landed on a territory. Mallard pursuit flights originated primarily from "activity centers" (cf Dzubin 1955) as did gadwall flights. Titman (1973) for mallards and Dwyer (1974) for gadwalls both use the term activity center instead of territory but an activity center is a place where a male spends considerable time during the laying and incubation periods and waits for his mate. This area is analagous to the territory. Pursuit flights in the wide-ranging pintail originated from various places in the habitat although some paired males spent much of the laying period on certain ponds and most pursuit flights by these males originated there.

Although most pursuit flights involved one pursuer and a pair, there were pursuit flights involving more than one chaser. These were most frequently observed in pintails and the chasers were often in small groups of males before a pursuit. Often a long ranging pursuit flight picked up chasers which were believed to be males waiting for females. These males sometimes quickly stopped chasing and returned to where they had been before the flight. However, sometimes they continued chasing and did not return immediately. In gadwalls and shovelers, pursuit flights with more than one chaser usually involved pairs which flew over several territories and were chased by each territorial male.

Shoveler and gadwall males frequently chased other males. A chased male was most often a neighbouring territorial male in shoveler pursuits and this was so for at least some gadwall pursuits. Territorial male shovelers did not chase unpaired males in pursuit flights but this information is lacking for gadwalls. Hostility between males was pronounced in these two species and the mate of a chased female often threatened or flew at the chaser during pursuits. Sometimes the chaser shifted his attention from female to male. When this happened the chaser usually ceased chasing after a few seconds.

In black ducks and mallards, there was little apparent hostility between males during pursuit flights. There was never any defense of a female when a black duck male encountered a territorial male on his territory. However, hostility between males was sometimes observed after a chase when the three birds landed together off a territory. Defense of the mate by shoveler and gadwall males appeared to occur whenever another male was encountered.

In general though, a pursuit flight was directed toward the female of a pair. The female was usually the first bird in the flight followed by the chaser. This was sometimes difficult to determine in shovelers and gadwall because of the way the female's mate often flew between her and the chaser. In pintails and black ducks, and to a large extent in mallards, it was obvious that the chase was directed toward the female. It was particularly obvious when the beginning of flights were seen since the chaser apparently ignored the female's mate as he tried to get to the female.

Although a male showed no apparent reluctance to leave his mate to chase, these males usually returned quickly to their mates. There was no significant difference in the duration of pursuit flights among shovelers, gadwalls and black ducks although some flights by mallards lasted longer when a male was alone and waiting for his mate. Pintail males which left their mates to chase returned after pursuit flights of average duration in 32 of 37 pursuits. It is probable that in all species a male with a female is reluctant to leave her for an extended time.

Probably the duration of a pursuit flight reflects both the persistence of a male to remain in an area and the willingness of the chaser to continue the pursuit. In shovelers, gadwalls and black ducks most flights longer than the average occurred when an intruding female remained in the region of the chaser's territory. This appeared true also for mallards but several long pintail pursuit flights involved females that flew directly away from the origin of the chase.

The average duration of pursuit flights by shovelers, gadwalls and black ducks reflects the fact that most chasers returned quickly to their mates and/or territories. The figure for gadwall pursuits is probably somewhat high since many of the pursuit flights observed were between chasers and persistent females which often returned to a territory and were chased again. The average pintail flight was longer than any by the other species and, at times, appeared to reflect the willingness of the male to continue chasing. A pursued female often flew in an erratic trajectory which covered several land miles in an apparent attempt to escape her chaser(s). Although some chasers persisted for a long time pintail pursuits were characterized by males joining a pursuit flight along its trajectory and then leaving, sometimes before getting close to the female. This had the effect of prolonging the flight for the female who sometimes, in an apparent attempt to avoid the chaser(s), landed in dense vegetation not normally used by pintails. Pintail females also were occasionally observed to land on ponds, dive immediately, surface in vegetation at the periphery of the pond and remain there until after the males had left.

Although it appeared certain that most females wanted to escape the pursuer(s) some of the pintail flights may have involved a "teasing" female (cf Sowls 1955). Particularly later in the season when most females were incubating or attempting to re-nest, pursuit flights involving a female without her mate were seen. On two separate occasions such flights occurred when a female was observed throughout an entire day with a group of males. The pursuit flights associated with this situation were less erratic than other pursuits and often continued longer.

The stage of the reproductive cycle of the chaser's mate may have influenced the willingness of the male to chase. McKinney (1965) says that prolonged, vigorous flights associated with rape (cf Lebret 1961) may occur when the chaser's pair-bond is weak. Although comparison of duration and frequency of flights throughout the year provided no evidence of this in black ducks, shovelers and gadwalls, analysis of the large mallard sample revealed a definite trend toward longer flights later in the season. Results on the pintail were inconclusive but it did not appear that pursuit flights changed throughout the season and observations of rape occurred throughout.

Pursuit flights usually originated on the territory or "activity center" of the chaser. The chaser and pair were considered to have returned to the origin if they came back to within 0.4 ha of where the chaser was prior to the flight. This area was chosen because intruders within that area around a male were usually chased by him. The chaser and chased bird(s) were observed to determine where they went after a pursuit flight. Chasing pintail males often remained with the chased female, or, at least, did not return to where they were prior to the chase. This was particularly so when the chaser(s) was in a group prior to the chase. This suggests that male pintails have no strong attachment to a physical site beyond the time that their mates are there. In the other species, whether the female was with the male or not, there was a high rate of return to the region of the origin suggesting that the site had some specific significance for the male if only through association with the female.

Chased birds did not usually return to the origin in mallards, black ducks and shovelers. This suggests that pursuit flights discouraged pairs from trying to remain in the area. Chased pintail pairs did return after pursuit flights and, although there were exceptions, they appeared to be tolerated, probably reflecting a lack of territorial behaviour. Among gadwalls, many pursuit flights involved pairs which were establishing territories at the same time. Several pairs eventually established contiguous territories which were within the critical 0.4 ha area due largely to physical discontinuities which provided visual isolation between pairs. Despite seemingly contrary evidence, the pursuit flight in this species appears to be a successful mechanism for displacing intruding pairs.

Successful rape was rarely observed in any species but it occurred most often in pintails. It was difficult to determine when males attempted to rape a female unless there was some obvious manifestation such as mounting or grabbing at the nape of her neck. It seems that if a female chooses to escape she can usually do so by flying and it appears virtually impossible for a male to catch her unless she becomes exhausted. It was difficult to anticipate attempted rape during a pursuit flight, however, it was observed when the chaser and female were together on the water prior to and after flights (Table 1). Although shoveler, gadwall and to a lesser extent mallard males attempted to prevent the chaser from reaching the female, it seemed obvious that the chaser was attempting to get to the female. Pintail males rarely defended their mates and, at least while on the territory of the chaser, the intruding black duck male did not defend his mate.

Male shovelers and gadwalls pecked at an intruding female but it was impossible to determine whether they were grasping at her in an attempt to mount her. Obvious attempted rape in these species was rare. Similarly in black ducks and mallards obvious attempted rape was rare but this tendency was apparent in some males. Most obvious attempted rapes observed were by pintails. Lack of defense of the female by her mate and the persistence of the chaser made female pintails more susceptible to rape. However, it is probable that for all species the chaser would rape a female more frequently than the figures suggest if it were not so logistically difficult to do so. These figures probably do reflect the relative incidence of attempted rape in these species.

Lack (1968) suggested that casual chases in which rape is seen are perhaps initiated by surplus males without mates. Although there were surplus males in each species, there was no evidence to support this. Intensive observations of unpaired male black ducks (Seymour in prep) and shovelers (Seymour in prep) suggest that attempted rape by unpaired males is rare.

DISCUSSION

Although males of most Anas species form pair-bonds and copulate primarily with one female, there would be a potential reproductive advantage to the male in raping other females unless this jeopardized his chances to inseminate his mate or was detrimental to her reproductive success. Lack (1968) says it is surprising to find that monogamy is the rule in many ducks since only the female incubates and cares for the young. It might be expected that promiscuity would be developed and, although Lack (1968) says promiscuity has evolved in a few ducks, presumably in most Anas species the ephemeral pair-bond between male and female is a more successful reproductive mechanism for both. There are more males than females in most populations hence it is probably advantageous for a male to accompany one female and perhaps defend a territory to provide seclusion from conspecifics.

However the tendency to rape strange females is probably developed to some extent in all species despite the existence of a more or less well developed pair-bond. Table 2 provides a comparative measure of the degree of development of the pair-bond in the five species considered in this study. Although the development of apparently strong pair-bonds sometimes occurs among pintail, attempted rape of strange females by paired males is relatively common.

This is in contrast to the shoveler which has a strong pair-bond and shows relatively little tendency to rape.

These contrasting behaviour patterns in shovelers and pintails reflect the general social system of both species as discussed by McKinney (1973). The paired pintail male, which does not defend a territory and associates with other males, has less time and energy invested in one female. His committment to a female probably does not continue much past her laying phase. McKinney (1973) suggests that the pintail is an opportunistic breeder and takes advantage of good breeding conditions when available. Pintails use temporary ponds and begin nesting soon after arrival on the breeding grounds (Smith 1968). Protection by the male of the female, which appears ready to lay eggs soon after arrival, seems less critical in this species than in others. Promiscuity or at least a well developed tendency to search for and rape strange females appears more practical in this species.

In contrast, the shoveler male invests considerable time in one female by accompanying her in the pre-laying period and by defending a territory. The pair-bond, and territorial behaviour continue well into incubation. Even after the male has left, evidence (Seymour 1974) suggests that other conspecifics avoid his former territory. The shoveler is not opportunistic and is tied to rigid food requirements. It is probable that a female cannot lay eggs before having spent a considerable time foraging after arrival on the breeding grounds. Her breeding success is probably closely tied to the success of her mate in protecting her throughout the entire tenure of the pair-bond. For the male to make this committment to the female, the pair-bond would have to be strong to ensure that only he inseminates her. Males would not have time or probably the opportunity to make this committment to more than one female. The tendency to rape other females then must be suppressed in favour of remaining with or near his mate. Certainly promiscuity implies mobility and this is not possible for the shoveler which defends a particular physical site.

The pursuit flight provides a basis for comparison of the five species in this study (Table 1). The gadwall appears more closely aligned with the shoveler than with the other species, particularly the pintail. Although the black duck and mallard were observed in different habitats, characteristics of their pursuit flights are broadly similar and both species fall between the pintail and gadwall-shoveler extremes.

Comparison of the social systems of these species (cf McKinney 1973) further supports the alignment suggested above (Table 2). Although there are differences in degree, the gadwall is similar to the shoveler in all parameters. Similarly the social systems of the black duck and mallard are closely aligned to each other and both appear closer to the gadwall and shoveler than to the pintail.

Although the motivation of the chaser is unclear, it seems possible that, in all species, the chaser would rape the female if the opportunity is presented. However, in all species except the pintail the chaser, at least during the laying and early incubation periods when he is attentive to his mate, opts to remain with or near her. The tendency to rape in species other than the pintail appears modified by the tendency to remain with or near the female.

Regardless of the motivation of the chaser, pursuit flights must ultimately have functional significance to the chaser, his mate and to the reproductive success of the pair. Although a chaser may produce more offspring if he rapes a female during the laying period, the pursuit flight functions in an immediate sense, to discourage intruders from remaining near a chaser and hence spaces breeding pairs. The pursuit flight in all species, with the possible exception of the pintail, is the main mechanism in the establishment and maintenance of territories or activity centers. Pursuit flight activity can provide seclusion for the pair from other conspecifics and thereby potentially increase the reproductive success of both the male and female.

To benefit the chased female rape would have to occur when the female requires insemination. Re-nesting females may not have time to choose another mate and rape could be beneficial. However, with the possible exception of the pintail, it is more likely that most pursuit flights are damaging to the female because they disrupt her breeding activities. It appears probable that pursuit flights though spectacular when observed, occur relatively infrequently once spacing has occurred. Pursuit flights involving laying or incubating females are probably rare because these birds are usually secretive and females of territorial species remain on their territories.

LITERATURE CITED

Bartonek, J.C. and C.W. Dane. 1964. Numbered nasal discs for waterfowl. J. Wildl. Manage. 28(4): 588-692.

Dwyer, T.J. 1974. Social behavior of breeding gadwalls in North Dakota. Auk 91(2): 375-386.

Dzubin, A. 1955. Some evidence of home range in waterfowl. Trans. 20th N. Amer. Wildl. Conf.: 278-298.

Evans, C.D., A.S. Hawkins, and W.H. Marshall. 1952. Movements of waterfowl broods in Manitoba. U.S.D.I. Fish and Wildlife Service Spec. Sci. Rep.: Wildlife No. 16. 47 pp.

Kiel, W.H., Jr., A.S. Hawkins, and N.G. Perret. 1972. Waterfowl habitat trends in the aspen parkland of Manitoba. Canadian Wildlife Service Report Series No. 18: 63 pp.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co. Ltd., London. 409 pp.

Lebret, T. 1961. The pair formation in the annual cycle of the Mallard, Anas platyrhynchos L. Ardea 49: 97-158.

McKinney, F. 1965. Spacing and chasing in breeding ducks. Wildfowl Trust 16th Ann. Rept. 92-106.

McKinney, F. 1973. Ecoethological aspects of reproduction. Pp. 6-21 in Breeding biology of birds (D.S. Farner, Ed.). Washington, D.C.

Seymour, N.R. 1974. Aerial pursuit flights in the shoveler. Can. J. Zool. 52(12): 1473-1480.

Seymour, N.R. Behaviour of unpaired male shovelers during the breeding season. In preparation.

Seymour, N.R. Behaviour of unpaired male black ducks during the breeding season. In preparation.

Smith, R.I. 1968. The social aspects of reproductive behavior in the pintail. Auk 85(3): 381-396.

Sowls, L.K. 1955. Prairie ducks. Wildlife Mgmt. Inst., Washington, D.C.

Titman, R.D. 1973. The role of the pursuit flight in the breeding biology of the mallard. Ph.D. thesis, University of New Brunswick, Fredericton. pp 201.

Table 1. Comparison of pursuit flight characteristics in five species of *Anas* ducks.

Characteristic	Pintail	Mallard	Black Duck	Gadwall	Shoveler
Involved a chased pair	106(66.2%)	1051(74.8%)	204(96.1%)	324(75.5%)	146(54.9%)
Involved in a chased male	0(0%)	22(1.6%)	2(1.0%)	22(9.8%)	95(35.1%)
More than one chaser	53(33.1%)	275(19.6%)	6(2.9%)	77(17.8%)	12(4.5%)
Female of pair object of pursuit	160(100%)	365(80.4%)	203(99%)	365(87.9%)	173(90.1%)
Aggression between males in flight	0(0%)	15(1.5%)	2(1.2%)	40(18.9%)	67(42%)
Average duration(s)	96 S (69 flights)	59S (985 flights)	32S (168 flights)	37S (169 flights)	15S (160 flights)
Duration ≤ 30 s	22(31.8%)	517(52.6%)	88(61.4%)	203(76.9%)	136(72.7%)
Duration >120 s	13(18.8%)	94(9.6%)	11(7.7%)	11(4.2%)	11(5.8%)
Chaser returned to within 0.4 ha of his location before flight	33(54.9%)	260(82%)	155(92.3%)	175(93.1%)	174(96.1%)
Chased pair did not return to within 0.4 ha of chasers original location	32(44.3%)	255(81%)	138(82.1%)	105(57.4%)	151(84.4%)
Obvious attempted rape of chased female	12(19.4%)	19(3.2%)	6(2.9%)	10(0.7%)	2(0.9%)

Table 2. Characteristics of social systems and measures of pair-bond strength of five species of *Anas* ducks.

Characteristic	Pintail	Mallard	Black Duck	Gadwall	Shoveler
Measure of pair-bond strength					
paired male hostile toward other paired males when near his female	X (rare)	XX	XX	XXX	XXX
paired male hostile toward unpaired males when near his female	0 (absent)	X	X	XX	XX
paired male returns to female rapidly after pursuit flight	XX	XXX (usual)	XXX	XXX	XXX
paired male protects female when other males attempt to rape her	X	XX	XX	XXX	XXX (vigorous)
paired male associates with other males before pair-bond broken	XXX (frequent)	XX	XX	X	X
pair-bond breaks during incubation	first week	second week	second week	second week	third or fourth week
Social system					
size of home range during breeding	XXX (large)	XX	XX	X	X
male on territory or restricted "activity center" during laying and incubation	X	XXX (usual)	XXX	XXX	XXX
when nest initiated after arrival on breeding grounds	X (early)	X	XX	XXX	XXX

OVERALL SUMMARY AND CONCLUSIONS

A population of Black Ducks, Anas rubripes, was studied during the 1972, 1973 and 1974 breeding seasons on a tidal marsh at Antigonish estuary, Nova Scotia. Additional information was obtained during June of 1976. The objectives of the study were to elucidate aspects of the breeding biology of paired birds and to investigate the behaviour of unpaired males.

Observations of wild marked birds provided a qualitative and quantitative description of hostile interactions between pairs throughout the breeding season. Interactions occurred first on the communal part of the marsh and later on territories. Changes in the form and intensity of hostility led to the spatial displacement of pairs. The pursuit flight by males was the main mechanism in the establishment and maintenance of territories.

Territories corresponded to tidal ponds (0.61-3.9 ha) at the marsh periphery and were established only after pairs were on the marsh 30-40 days. Territories were established approximately five days before egg laying began and females were responsible for choice of locations. Females spent approximately 45 days on their territories and males stayed 27-32 days. Males remained almost continuously on their territories during the pre-laying and laying periods but left both their females and their territories during mid-incubation.

The activity of males and females of pairs was analysed and frequencies of foraging, loafing and hostility were compared. Pairs, and particularly females, foraged almost continuously during the pre-territorial period. When pairs were together prior to laying, females fed 35-40% more than males. Similarly on territories females fed 50-60% more. Hostility by territorial males toward intruding pairs provided seclusion for the resident pair.

Most of the data on unpaired males was derived from observations of seventeen marked birds. Males actively displayed to females from late March until late May. Most interactions involved groups of males but sometimes one male accompanied a pair. Most encounters occurred on the marsh and not on territories at the periphery.

The behaviour of the males was divided into foraging, loafing and reproductively oriented activities. Changes in the daily and seasonal frequencies of these activities were determined. In March encounters between groups of males and pairs consistently resulted in display activity by the males. This activity decreased in mid April and ceased by late May. Single males rarely courted but remained near pairs. The median duration of an association between a group and pair was in the 61-90 min interval and in the 91-120 min interval for encounters between a single male and a pair. However, on four occasions a single male remained on a territory with a pair for at least three days.

Females responded to unpaired males by Inciting and remaining close to her mate. Males interrupted the activity of females primarily at the outset of an encounter.

The reaction of paired males to unpaired males changed during the season. There was no reaction early but then threat and more overt hostility developed rapidly and continued until after unpaired males ceased active courtship in late May. Paired males remained close to their mates and did not engage in long chases after unpaired males. Territorial males appeared to tolerate unpaired males on territories.

Observations of pursuit flights of five species of ducks in the genus *Anas* were made in Manitoba and Nova Scotia. Data was obtained from both marked and unmarked birds. Pintail, *A. acuta*, flights were significantly different from those of the other species. Flights in this species suggested lack of site attachment, a poorly developed pair bond and a generally opportunistic breeding strategy. Attempted rape of strange females by paired males suggested that pursuits in Pintails are probably mainly sexually motivated.

The Mallard, *A. platyrhynchos*, and closely related Black Duck employ similar breeding strategies although they differ in detail. Variations probably reflect, to some degree, differences in habitat. Pursuit flights in these species suggested that the pair bond was well developed, at least until mid-incubation when males deserted territories and mates.

The Gadwall, *A. strepera*, and particularly the Shoveler, *A. clypeata*, represent two species that are in direct contrast to the Pintail. Pursuit flights of these species function primarily in the establishment and maintenance of territories. These birds have a well developed pair-bond and paired males protect females from conspecifics well into the incubation period.