THE UNIVERSITY OF MANITOBA

TERRITORIAL BEHAVIOUR OF THE SHOVELER, *ANAS CLYPEATA*, AT DELTA, MANITOBA

by

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ABSTRACT

A population of northern shovelers, Anas clypeata, was studied at Delta, Manitoba, to determine if behavioural mechanisms contributed to the spacing of breeding pairs.

Further evidence supporting the contention that the Shoveler is a territorial species was obtained. Aggression of territorial drakes was localized about a loafing bar and defended boundaries existed between adjacent territories.

The aerial pursuit flight was also shown to deter other shoveler pairs from establishing in the pursuer's territory. In 94.1 per cent of pursuit flights, the pursued bird(s) left the chaser's territory.

Pursuit flight frequency reflected the density of pairs in the area studied. Flight frequency was the highest during pre-laying then decreased when incubation began. A subsequent increase in frequency coincided with an influx of presumably re-nesting pairs into the study area from elsewhere in the marsh.

Flights were associated with aggression, rarely with rape, suggesting that aggression, rather than sex, was the primary motivation.

ACKNOWLEDGEMENT

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TABLE OF CONTENTS

List of Figures

LIST OF TABLES

GENERAL INTRODUCTION

Territory is typically used to refer to a "defended area" (Mayr, 1935: Noble, 1939; Nice, 1941; Hinde, 1956; Brown, 1969). Territorial behaviour may function to limit avian populations (Brown, 1969) by spacing breeding pairs such that some pairs fail to reproduce.

In waterfowl, the status of territory is less clear. The Northern Shoveler, Anas clypeata, is considered by Hochbaum (1944), McKinney (1965, 1967), Siegfried (pers. comm.) and others to be a territorial species however other authors, Hori (1963), disagree. Quatitative data concerning the territorial behaviour of this species is lacking for wild populations.

In ducks, a striking behaviour pattern thought to be associated with territorial defense is the so-called "Pursuit flight" that apparently functions to space breeding pairs over the habitat in time and space (Hochbaum, 1944). In the case of territorial species, like the Shoveler, these flights presumably function in the establishment and maintenance of the territory.

The broad objectives of my study were to determine the degree to which territorial behaviour was developed in a wild population of shovelers and how the establishment

a wild population of shovelers and how the establishment and maintenance of the territory was affected by various behaviour especially aerial pursuit flights. Specifically, I wished to obtain quantitative information on the extent to which a localized defended area was used and also on the frequencies and types of hostile behaviour associated with the defense of such areas. In addition, I wanted to determine the relative importance of the male and female, and also of habitat factors, in determing the choice of the location of the territory. Detailed analyses of pursuit flights were then conducted to test the hypothesis that they function in the establishment and maintenance of territories, to measure their effectiveness as a spacing machanism. In addition the motivation of flights was considered by determining the incidence of apparently sexually motivated as opposed to aggressively motivated flights.

PART I

TERRITORIAL BEHAVIOUR

OF THE SHOVELER,

ANAS CLYPEATA,

AT DELTA, MANITOBA.

Territorial behaviour has been documented for many vertebrate species, especially birds. Territory typically refers to a "defended area", e.g. Mayr (1935), Noble, (1939), Nice, (1941), Tinbergen (1939), Hinde (1956), Brown (1969). Although minor objections have been raised (e.g. Pitelka, 1959), this common usage is adhered to throughout this study.

The status of territory in ducks is less clear than in most other birds such as the passerines. Hochbaum (1944) considered it to be present in all dabbling ducks. In subsequent studies however, Sowls (1955), Dzubin (1955) and Lebret (1961) concluded that the concept is not always applicable to all ducks.

In the Shoveler (Anas clypeata) published accounts are conflicting. Hori (1963), for example, concluded from his studies of wild shovelers in North Kent, England, that the Shoveler is non-territorial. Poston (1968), who studied a low density breeding population of shovelers on potholes near Strathmore, Alberta, also found little evidence for territorial behaviour. However, McKinney (1967), in agreement with Hochbaum (1944) and Sowls (1955), presented evidence, based mainly on intensive studies of captive birds, that territorial behaviour can be well developed in this species.

Although there is thus strong evidence that territorial behaviour, in its classical sense, is exhibited by at least some shoveler populations, detailed and quantitative data relating to this behaviour in wild, non-captive shoveler

populations is lacking. The major object of my study was to investigate the behaviour of the individuals of a wild population of shovelers, to obtain quantitative date on the extent to which the defended area is used and also on the frequencies and types of hostile behaviour that presumably function to keep any such defended area exclusive. I also attempted to determine the extent to which a pair is restricted to the defended area, as opposed to the remaining undefined portion of their home range. The relative importance of the male or female, and of habitat factors, in determining the choice of the territory, was also investigated.

Earlier studies by Hochbaum (1944) and Sowls (1955), as well as my own preliminary observations conducted in 1969, indicated that territorial behaviour was well developed in the shoveler populations breeding in the roadside ditches near Delta, Manitoba. This habitat also provided excellent opportunities for unobstructed viewing of behavioural interactions, hence this population was selected for intensive observation.

Materials and Methods

Study Area

The study area was a 1.9 km. long roadside ditch and portions of adjacent meadows beginning 2.4 km. south of Delta, Manitoba. The general features of the area in 1970 were essentially unchanged from a description given by Sowls (1955),

who previously observed and reported on waterfowl using the area. I observed the area from 20 April until 5 July, 1970. This 12 week period encompassed all known shoveler breeding activity on the area.

The ditch and adjacent east meadow was a continuous body of water during the first eight weeks of observation. The water area of the meadow decreased progressively, however, from approximately 26.8 hectares during week one to a small wet area adjacent to the ditch of approximately 0.4 hectares during week eight. The ditch proper, which became distinct from the drying meadow during week nine, contained water throughout the summer.

Vegetation on the flooded meadow began to emerge during week five and covered much of the meadow by week seven. Except for a 0.2 km. portion at the north end, the ditch, which ranged from 10 to 20 metres in width, was never clogged with vegetation, although emergent vegetation (Typha sp., Scirpus sp. and Phragmites sp.) did appear in discontinuous patches along the sides of the ditch throughout the summer. The 1.9 km. of ditch included in the study area was discontinuous, being broken by four small dykes across it.

Methods

Males were trapped by placing a hand-reared captive female in a clover trap of the design described by Lincoln and Baldwin (1929). These birds were marked with nasal discs (Bartonek and Dane, 1964) of white vinyl with black letter-

ing and released at the trap site. Mated males using a portion of the ditch were caught by placing the trap at the male's major loafing bar, unmated males were captured in the adjacent meadow. Seventeen males in total were caught, marked and released. In addition three females were caught, on their nests, with the use of a long handled net. These also were marked and released.

The ditch was observed for parts of the daylight hours for five or six days each week for 12 weeks. Observations were made from three vantage points, each of which overlooked the entire study area. A car was used as a blind to observe the area at the northern and southern limits of the study area while a 6 metre observation tower was used near the centre of the area. From these positions, the nasal saddles of stationary colour-marked birds could be readily identified with a 15x telescope. Laths were located at 30 metre intervals north, south, east and west of the major loafing bars of drakes under observation. These laths were usually extended to 135 metre from the loafing bar enabling me to determine approximately where the drake was relative to the loafing bar. In the meadow, laths were placed at 90 metre intervals to enable me to estimate the point where a defending male terminated pursuit.

A schedule for monitoring the numbers of ducks, particularly shovelers, was instituted on 20 April. The first count was normally made at dawn (approx. 05:00) and lasted for 30 minutes. Subsequent counts of the same duration were

done at two-hour intervals, the last count being at dusk (approx. 22:00). This schedule was followed for either four or five days each week, except weeks one and 12 when the schedule was reduced to three days.

Weekly aerial transects of the marsh were made from 6 May to 13 July and intensive checks of the water areas at the periphery of the marsh were made every two weeks from 1 May to 1 July to determine where shoveler territories occurred.

Data collected in this study were analysed and the statistical significance of the results were tested by the chi-square test (Siegel, 1956) and the Rank Correlation test (Siegel, op. cit.) where applicable.

Results

Breeding chronology

Breeding activity of shovelers on the study area spanned a twelve week period from 20 April to 5 July,1970. Groups of firmly paired shovelers began to use the flooded east meadow, adjacent to the ditch, during week one. These pairs were non-aggressive (McKinney 1967), upon arrival. Poston (1968) also found that paired shoveler males in Alberta showed little hostility towards other paired males for a period just after arrival.

Most pairs fed almost continuously throughout the day, with males showing little hostility towards other pairs until week two, when male threat display increased in occurrence. A "moving territory", (Dzubin, 1955), in which the male defended the mobile female, appeared to best describe the situation at that time. Such groups of pairs completely dissolved into discreet pairs during week three.

Unmated males arrived during week two. They courted and chased mated females and made "jump flights" as described by Lebret (1961) and McKinney (1970). Pairs were harassed by from one to seven males. Simultaneously, mated males showed an increase in aggression towards other males. During week three 12 of 19 (63.2%) pairs under observation began searching for nest-sites on the ditch. Unmated males remained on the flooded meadow at that time, rarely harassing pairs using the ditch.

Fig. 1 indicates the weekly number of pairs on the study area that were considered "territorial" and "non-territorial" on the basis of evidence presented below. There were 12 different resident pairs on the study area over the 12 weeks, the last pair having been established during week 10. Non-territorial pairs, which appeared to consist mainly of pairs searching for suitable breeding areas, were present on the study area for variable periods ranging from two days to three weeks. The increased numbers of non-territorial pairs in weeks eight, nine and 10 (Fig. 1), reflect an influx of pairs into the study area. During weeks 10 and 11, all but one nest that had been present on the study area was destroyed by predators and most pairs left the area. No new territories were subsequently established.

Aggressive Behaviour and Territorial Defense

Evidence that breeding shovelers on the study area were territorial was derived primarily from direct observations of localized aggressive behaviour of nine paired males. Additional supporting evidence was provided by observations of "ritualized flighting" (McKinney 1967) that was primarily localized at the apparent boundaries of areas defended by neighbouring males.

Aggressive Behaviour

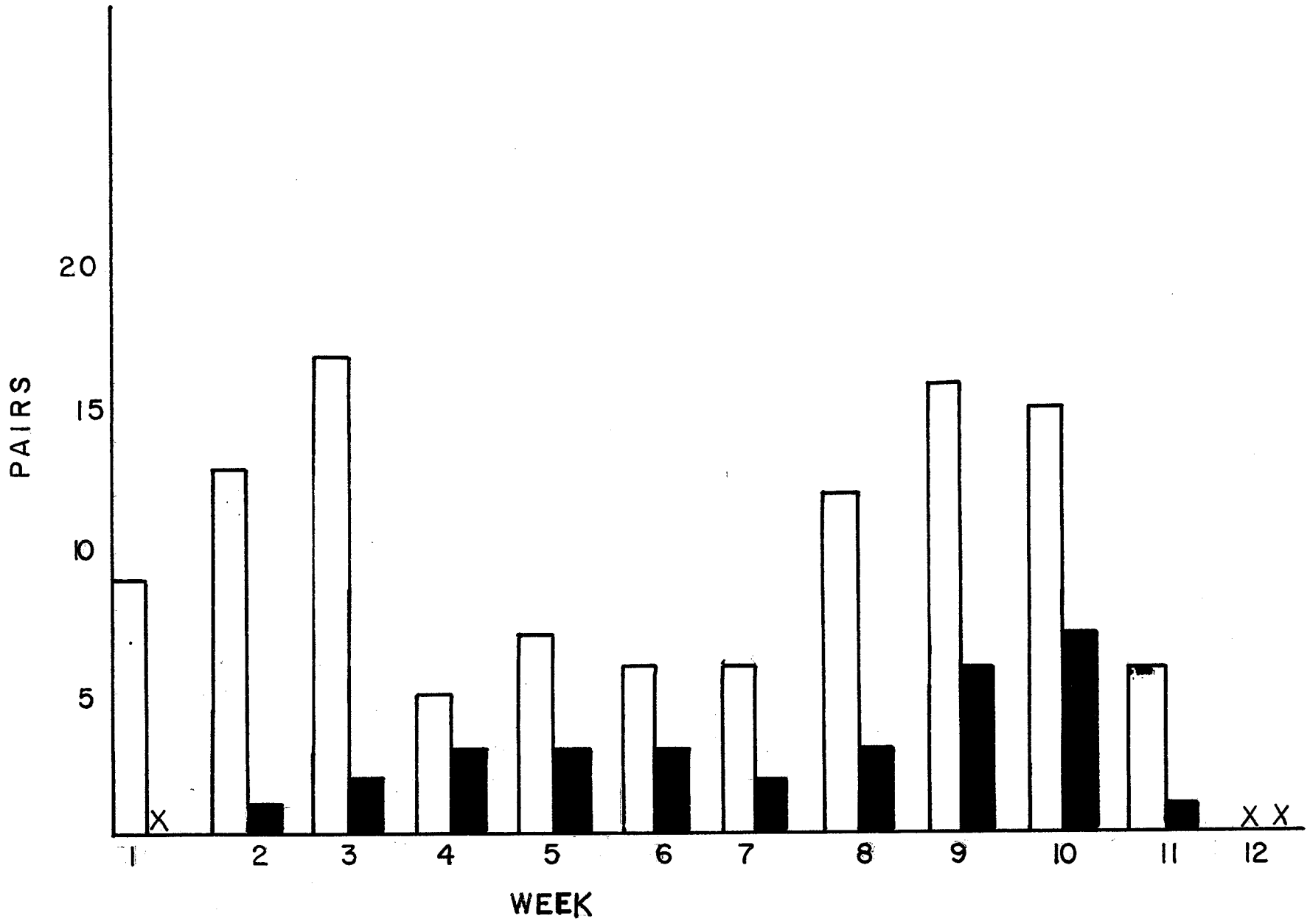
In addition to "ritualized fighting", to be described below, aggression in shoveler males is manifested by "hostile

Figure 1. Territorial and non-territorial pairs on the study area, 20 Apr. - 5 July, 1970.


non-territorial pairs


territorial pairs


no pairs


PAIRS
20
15
10
5
X
X X
1
2
3
4
5
6
7
8
9
10
11
12
WEEK

pumping", "threat display","chasing", and"three-bird flights" (McKinney 1967,1970). I refer throughout to "three-bird flights", as pursuit flights.

"Hostile pumping" and associated call (McKinney,1970) was elicited in a resident male when an intruder approached the defended area. "Hostile pumping" was followed by "chasing", and often pursuit flights, when intruders did not immediately leave the area. "Hostile pumping" and calling was also noted, in the apparent absence of other shovelers, when the male returned to the defended area, after pursuing intruders, or after feeding off the defended area. At these times, he typically sat in the ditch near the loafing bar (a component of the territory described by Hochbaum(1944), Sowls (1955), Dzubin (1955) and others) for 5 to 10 minutes or longer then went to the loafing bar. "Hostile pumping" was also seen when a male approached a neighbouring defended area whether or not the resident male was there. This suggests that the area alone associated with a territorial shoveler male may on occasion elicit threat display by a neighbour.

"Chasing" involved primarily unmated males as chased birds. It consisted of a territorial chaser rushing over the water at the other male with his neck outstretched and bill, often open, pointed at the other male. As McKinney (1970) states, the bill is typically held slightly upward at this time. The birds being chased showed little hostility toward the chaser and usually left the area quickly.

Whether pursuit flights are to be considered territ-

orial defense or in some other functional category is equivocal (Hochbaum, 1944; Sowls, 1955; Dzubin, 1955; Lebret, 1961; McKinney, 1965; Hori, 1963). In the shoveler, as will be discussed in a subsequent section (Part 11 of this thesis), they do appear in part to function in driving away intruders, and hence seem relevant to territorial defense.

Localization of Aggression

Aggressive interactions were highly localized, occurring mainly in the vicinity of the loafing bar. Fig. 2 indicates the frequency of aggressive behaviour, except for pursuit flights (see Part 11), of resident males during the laying and incubation periods. Intervals are measured from the loafing bar. There were significantly more hostile encounters close to the loafing bar (0-100 foot interval). both for the composite data, ($x^2 = 88$, $P < .001$) and for an additional single male ($x^2 = 212$, $P < .001$).

Almost all (95%) hostile displays occurred either at the loafing bar or in the ditch as opposed to the adjacent meadows, suggesting that the water area rather than the meadow area was being defended. Prior to pursuit flights, the pursuer was usually on or in the ditch near the loafing bar. After 264 (99.2%) flights encompassing the entire reproductive period of all pairs on the study area, the pursuer returned to the territory, which further indicates that aggression was centered around the territory. Also, in the case of pursuing males whose mates were at the nest-site,

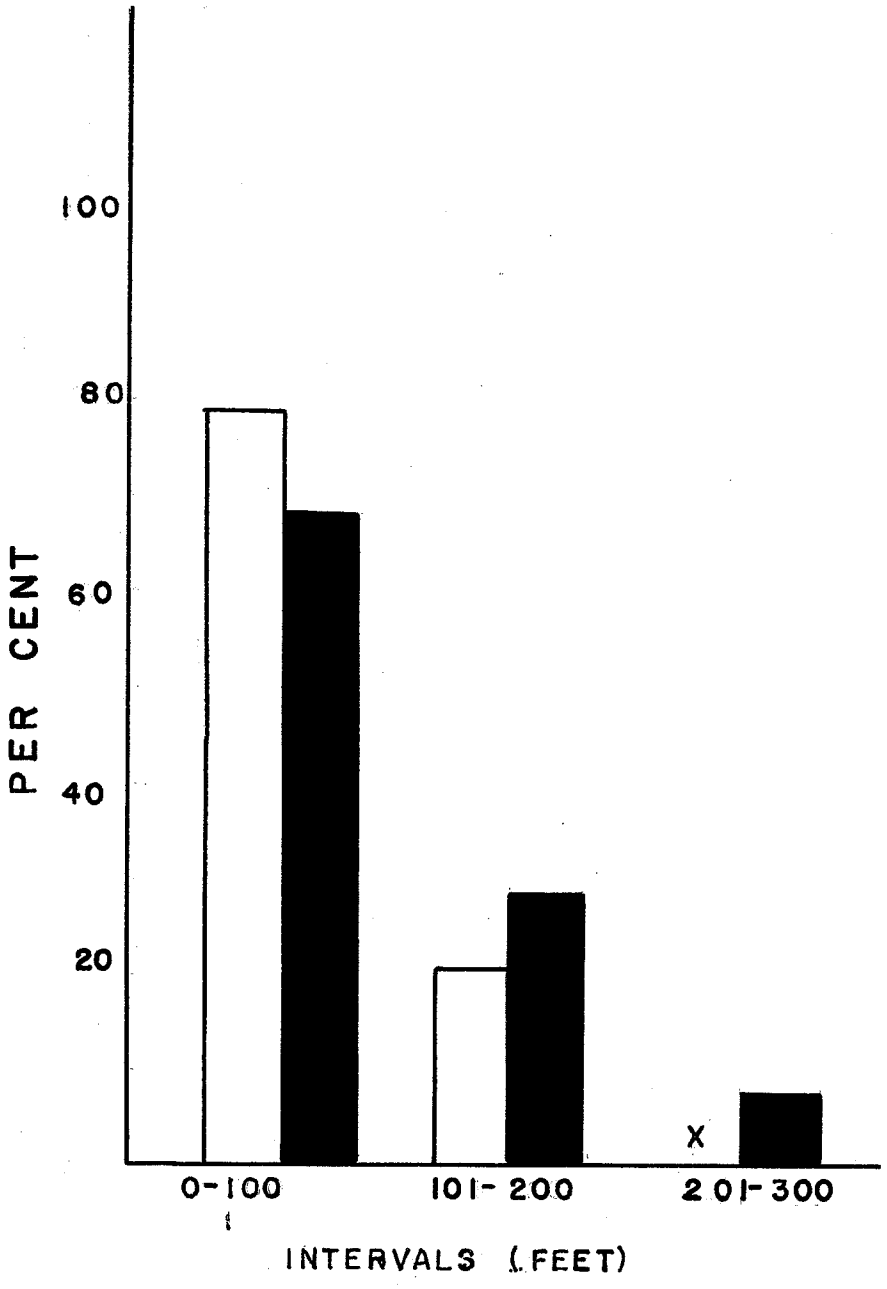
Figure 2. Distance of aggressive interactions from the loafing during laying and incubation, composite of 9 marked males, including 144 aggressive interaction observed over 12 weeks.

210 responses for one additional male, represented alone, are also shown. For the 10 males, 81% of encounters involved intruders which did not hold territories on the study area (non-territorial)

□ data from one separate drake, $x^2 = 212$, $P < .001$

■ data from 9 drakes, $x^2 = 88$, $P < .001$

X no observations of aggression


100
80
60
40
20
PER CENT
X
0-100
101-200
201-300
INTERVALS (FEET)

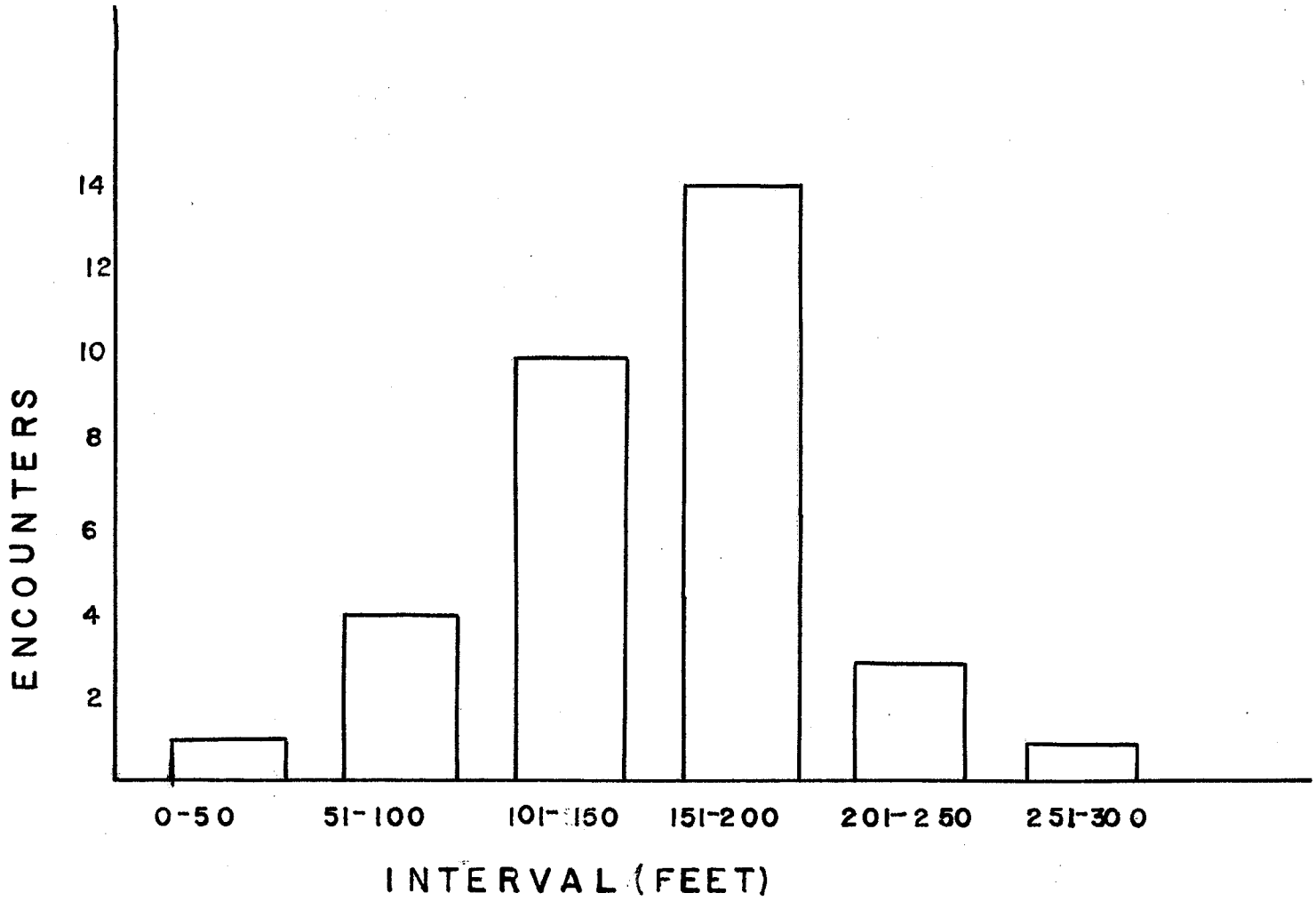
males returned to the territory on 188 (95.5%) occasions, suggesting that the behaviour of the male is related to the physical site also and not just the position of the female.

Interactions at territorial boundaries

Hinde (1966) indicated that, "along the boundary between territories is a narrow no-man's land where prolonged skirmishes take place and actual combat is rare, such skirmishes being practically limited to the boundary region". "Ritualized fighting", which appears to be an example of such skirmishes, was used by McKinney (1967) to indicate the location of shoveler territorial boundaries. I therefore examined the locations of "ritualized fighting" to aid in determining boundaries of territories at Delta. As indicated in Fig. 3, most "ritualized fighting" occurred in the area of 151-200 feet from the loafing bar ($x^2 = 25.7$, $P < .001$).

Males utilizing contiguous areas appeared to adhere to common boundaries. Males were seen sitting relatively inactive for as long as 60 minutes within 3 to 6 metres of each other, each bird on its own territory. "Hostile pumping" and occasionally "ritualized fighting" did occur at this time, but primarily when one male approached closely to the other or crossed the common boundary. Such interactions by males whose females were laying or incubating eggs typically occurred after the male accompanied the female to the nest-site and returned to the ditch at which time these drakes swam or flew towards the neighbouring drake, thus

Figure 3. Distance of boundary conflicts from the loafing bar, based on five marked males (33 observations), during pre-laying, laying and incubation.


ENCOUNTERS
14
12
10
8
6
4
2
0-50
51-100
101-150
151-200
201-250
251-300
INTERVAL (FEET)

indicating an aggressive awareness.

Intensive observations (96 hours) of four neighbouring males which established territories at approximately the same time, provided additional information about territorial boundaries. The territories of these males (A-D) are illustrated in Fig. 4. Dashed lines, in Fig. 4, represent the limit of the area intensively used and defended by each of the males while on the study area during the pre-laying period. Although it is difficult to define exactly the location of boundaries where actual conflicts were not seen, the dashed lines can be taken as delineating approximately the actual territories on the basis of disputes that were seen (dots in Fig. 4) combined with the almost exclusive use by the resident male of the remaining area within the dashed lines. Most encounters at the northern boundary of the territory of male A and southern boundary of the territory of male B involved unmarked males presumably attempting to establish territories. Most encounters occurred on the ditch as opposed to the adjacent meadows primarily because most intruders landed on the ditch and the resident male could most readily observe the water area from his vantage point on the loafing bar. Male A did not apparently violate the territory of male B for several days after pair B deserted the territory and even then A did not incorporate this territory into his.

Pursuit flight endings are also included in Fig. 4. They indicate that pursuits typically ended near, but outside of the area as defined by boundary conflicts per se.

Figure 4. Territories of four marked shoveler males, which existed simultaneously.

Scale:

o loafing bar

x nest

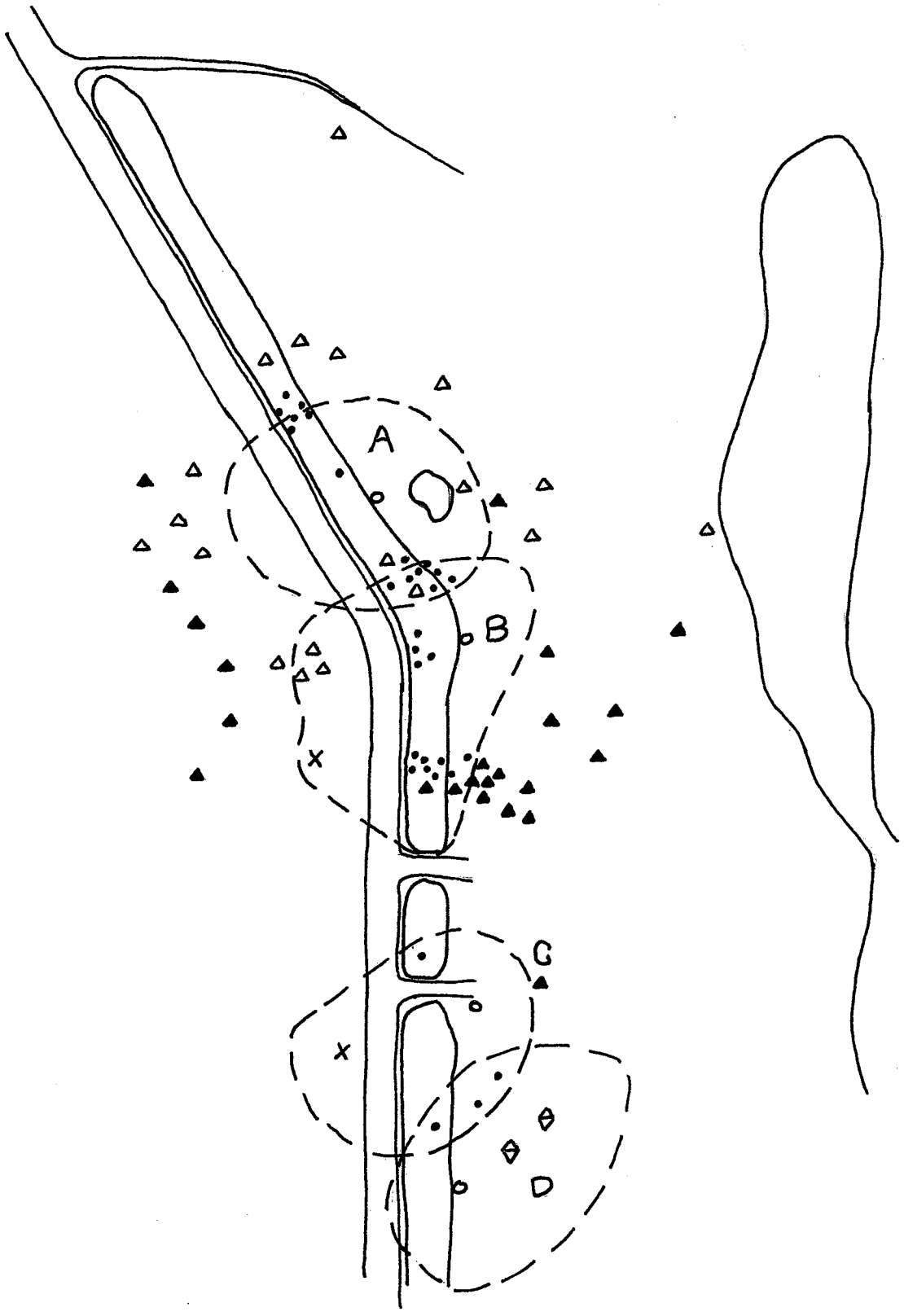
• boundary conflict

---maximum area used

△ End of pursuit, drake A

▲ End of pursuit flight, drake B

◈ End of pursuit flight, drake D


A
B
C
D
x
x

Pursuit flight behaviour, involving males A and B as the interactants, provided further evidence that neighbouring males, recognize and observe a common boundary between their abutting territories. Thus, these flights typically involved reversal of roles, the pursuer becoming the pursued bird when crossing above the boundary line in the ditch (cf. Hinde, 1966).

Selection of the territory

Although the male is responsible for essentially all the aggressive acts that contribute to the establishment and defense of a shoveler territory, there is observational evidence that in this species, like other dabbling ducks, the female is mainly responsible for determining where the territory will be situated (Hochbaum, 1955; Dzubin, 1955; Sowls, 1955). Because of the problems inherent in assigning a definite role to one member of the pair when they are free to move about together, an experiment was devised which involved shifting a trapped bird.

Methods

A captive unmated female shoveler, captured in the wild and held over for one year, was placed in a trap to decoy unmated males using the flooded east meadow during the period weeks two and 12. Three trapping sites on the meadow were used (referred to below as sites A, B, and C). The

female was placed at site A for four days to determine whether males would be attracted to her and further to discover whether one male would become dominate over the others and establish a territory. Consequently, the female was removed from the study area to determine if one particular male (male 1), which had become dominant over other males at site A, would remain in and defend the area, in the absence of the female. After two days absence, the female was placed at site B, which was 65 metres east of site A, to determine if male 1 would desert site A to follow the female. Two days later I again shifted the female, to site C, 150 metres north of site B. Male 1 was visually isolated from the female on site C, hence this shift made it possible to determine if drake 1 would follow the female even though initially visually isolated from her. After two days I shifted the female back to site B to determine if another male (male 2), which had been dominant at site C, would follow the female and be dominant over male 1 when both were present at site B. The female was then removed from the study area, terminating the experiment. The duration of the experiment was from 27 May to 10 June, 1970. Behaviour of these birds was observed for a total of 27 hours. In addition, hourly checks (06:00-21:00) of the three sites were made for 10 days of this period. Males referred to above as male 1 and 2 were caught, marked and released on the study area.

Results

Within one day of placing the female at site A, male 1 became dominant in the area, chasing and pecking other males, which subsequently tended to avoid him. By the second day, male 1 could approach the female and not be threatened or pecked by her. The female reacted to other males, whose numbers varied from one to seven, by inciting posture and avoidance response as they approached the trap. Thus, a pair-bond appeared to have been formed between male 1 and the female. Male 1 then remained with the female, until she was removed from the study area four days later. After the female was removed, male 1 remained at site A until the female was returned to the study area two days later. During the female's absence, male 1 threatened, chased and made pursuit flights after virtually all unmated males and pairs which entered the area.

When the female was returned to the study area at site B, male 1 found her within 2 hours, and deserted site A to join her. He immediately began to chase several males from near the trap and assumed dominance in the area. As before, male 1 continued to chase intruders at site B even after the female was removed to visually - isolated site C two days later.

At site C, male 2 became dominant over other shoveler males, although the female threatened and avoided him. After 36 hours, male 1 then found the female at site C, but was prevented from approaching closer than 6 metres by male

2, who maintained his dominance over all males, including male 1. While the female was at site C, male 1 would typically remain five to 30 minutes at that site, then return to site B, where he continued to chase other shovelers. Both male 1 and 2 chased other males while at site C but male 2 remained dominant over male 1.

Male 1 found the female 30 minutes after I returned her to site B from site C. Male 2 found her the next day, but at site B he was prevented from approaching close to her by male 1, who remained dominant there over all males until the female was removed from the study area two days later.

Conclusion

This experiment showed that the unmated decoy female attracted unmated males, one of which assumed dominance, in an area, over the others. The area defended was thus initially determined by the female. However, once established, a territorial male may go on defending an area, although presumably not indefinitely, in the absence of the female. This suggests that once defended, the area comes to have some special significance for the male even in the absence of the female. The dominant position of male 1 at site B, and of male 2 at site C, both in the presence of the same female, also provides further evidence that once selected, the site may be of significance for influencing the male's aggressive and territorial behaviour. Despite the development of such attachments, however the behaviour of male 1

who deserted the defended area B to follow the female to site C, clearly shows that the female still remains the crucial factor in determining the location of the territory.

Territory size

As noted previously, defense was primarily of the water area and not the adjacent meadows. Estimates of these territories, although difficult to obtain due to the lack of rigidly defined boundaries, were obtained by measuring the maximum area defended. It is important to note that the territory is actually only a very restricted portion of the total home range used by the pair (Dzubin, 1955). This is illustrated by territorial males which may go far outside the territory on pursuit flights, as described in Part 11 of this thesis.

As shown in Fig. 2, all defense during the laying and incubation periods occurred within 90 metres of the loafing bar, thus making the maximum effective size of the territory approximately 9.2 hectares (table 1).

Dzubin (1955) observed that the territory may be larger during the early periods of nesting, in the Mallard and Blue-winged Teal (Anas discors). I also found a significant difference ($x^2 = 13.0, P < .001$), in the mean area utilized by 10 pairs of shovelers before and after the onset of egg-laying (Table 1).

Table 1. Comparison of territories between the pre-laying and laying/incubation periods of 10 Shoveler pairs. Difference in mean between the two periods is significant: $X^2 = 13.0$, $P < .001$

	Time	
Measure	Pre-laying (acres)	Laying and incubation (Acres)
mean area	7.3	2.3
median area	8.1	1.6
range in area	3.2-12.4	0.3-3.8
number of territories	10	10

Although territorial males ranged farther from the loafing bar during the 05:00-10:00 period, making it appear that the territory was larger at this time, this presumably reflects the fact that most aggressive interactions occurred at this time, as a result of increased movement of non-territorial pairs. During other daily periods namely 10:00-17:00 and 12:00-22:00, when non-territorial pairs were active, the same phenomenon was observed, again presumably as a result of territorial males encountering more intruders. However observations of actual territorial defense indicated that after the onset of laying, measurements of 10 territories which ranged in size from 0.12 hectares to 1.5 hectares, were not observed to change significantly in size as a function of time of day or breeding chronology, a result also similar to that found by Dzubin (1955) for the two species indicated above. Observation of three males whose mates had viable nests well into incubation, revealed that defense was strong throughout until it ceased abruptly during late incubation. The results above show that an important correlate of territory size is the reproductive status of the female, the territory becoming more restricted after incubation.

There was no statistically significant size difference between four early territories established before 8 June and five late territories established after 8 June despite the fact that the concentration of pairs, both territorial and non-territorial, on the study area, was greater after 8 June. This suggests that territorial males do not

necessarily occupy as large an area as possible when pressure from other pairs is low. I believe the concentration of pairs on the study area was not sufficiently great, however, to determine conclusively whether territory size decreases with an increase of aggressive encounters between incumbents, and non-territorial pairs.

Stability of territories

Evidence that territories of breeding pairs tended to remain stable was provided by observations that major changes did not occur when adjacent territories were abandoned due to nest failure. Stability was maintained despite frequent hostile encounters between incumbents on the study area and other territorial shovelers (19%) which held territories on the study area, and between non-territorial shovelers and these incumbents (18%) (Fig. 2). Poston (1968) similarly noted that once established, shoveler pairs were not replaced by other pairs. Further support for this conclusion is presented in Part II of this thesis where results of pursuit flights by territorial males during laying and incubation are shown. These indicate that 96.5% of flights involving intruding pairs successfully prevented the intruders from either entering or remaining on the territory, while the remaining 3.5% of flights involved pairs which left the territory after a brief (usually <5 min.) stay.

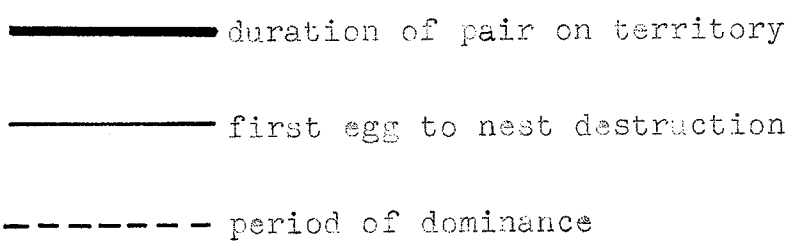
In addition to the above data showing that shovelers at Delta tended to defend particular areas, however, obser-

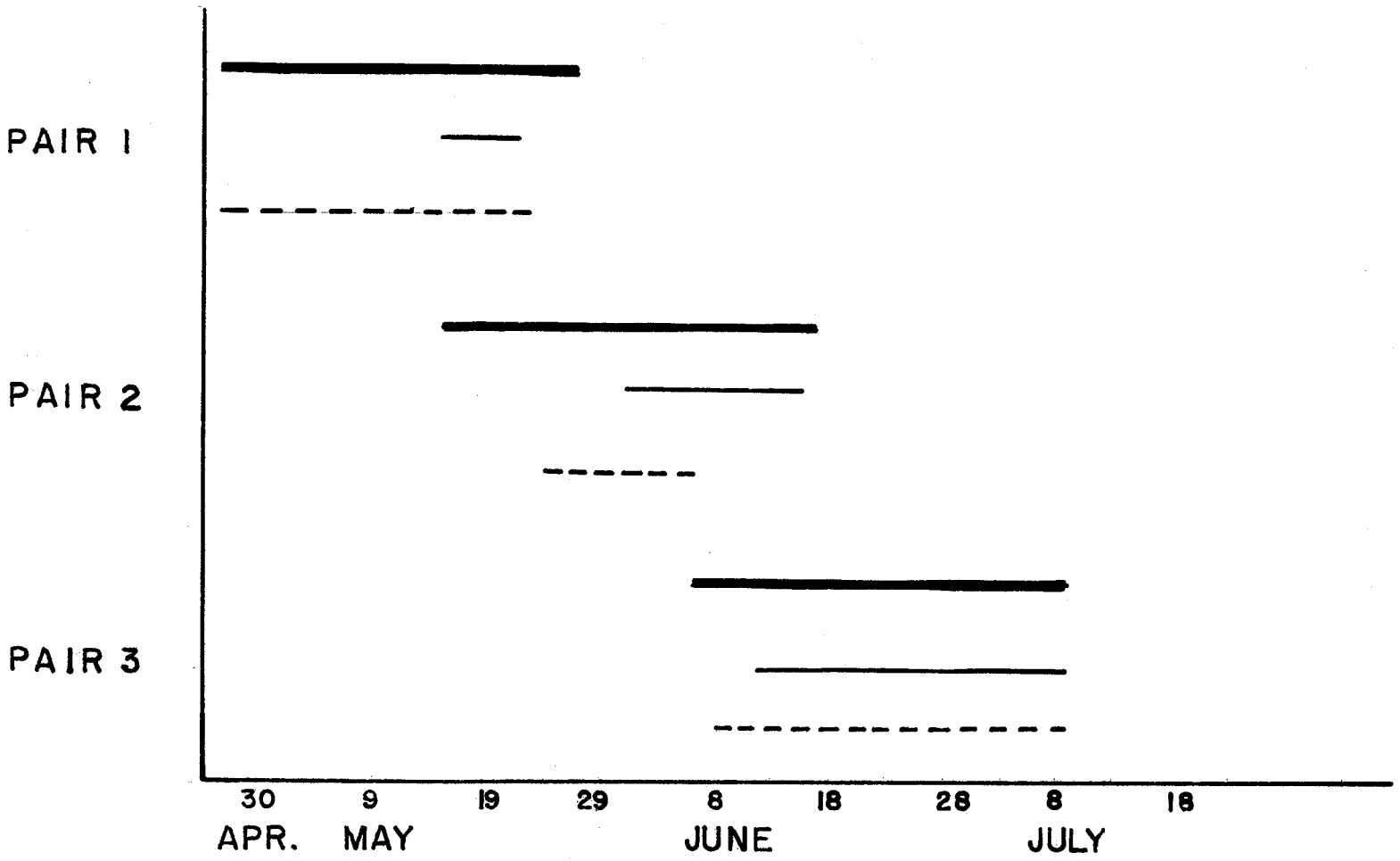
vations were also obtained indicating that such areas were not always occupied exclusively by a given pair throughout an entire breeding season. One striking example of successive usage of a portion of the study ditch during 1970 is illustrated in Fig. 5 where usage by three males referred to as 1-3, according to their chronological order of dominance, is indicated over the season in relation to egg laying and nest losses. The measure of duration on the territory is based on first and last sightings of the male or female of the pair; the duration of dominance of each drake was based on his success in excluding others from the area.

Initially, the area was occupied by male 1 and mate. This pair was dominant through to the time when eggs were laid, at which time the nest was deserted presumably due to egg loss as a result of predation. Male 2, which had been interacting with male 1 at the boundary of the territory for some days, quickly became dominant and took over the major loafing area of male 1 after pair 1 deserted the area following nest destruction.

That dominance may also alter prior to nest loss was indicated by a later change of occupancy of the above territory to male 3. Male 3 assumed dominance over male 2 about 10 days prior to the loss of nest 2 (nest of pair 2), at a time when male 2 was spending greatly decreased time on the territory. At this time (6 June et seq.) male 2 fled from male 3 after encounters, and by 8 June had deserted his loafing bar. He spent the remaining five days of his stay on the territory directly opposite the female's nest, never

Figure 5. Chronology of utilization of the same portion of the ditch by three Shoveler pairs at different times.




PAIR 1
PAIR 2
PAIR 3
30
9
19
29
8
18
28
8
18
APR.
MAY
JUNE
JULY

making a defense of the area, always avoiding drake 3.

The behaviour of females 2 and 3 provided evidence that, in the extended absence of the male, the use of the territory by the female may be severely restricted, if other encroaching males are present. Female 2 did not desert her nest for at least six days after her mate deserted her, but she was extremely secretive when off the nest, staying primarily in the vegetation in the ditch edge, and utilizing only a few square meters of water opposite the nest for feeding. Female 3 also used the territory after her mate deserted her, but loafed and fed within approximately 15 metres of the bar used before her mates departure. This same restricted radius of activity was also noted for the only other two females whose nests were viable when deserted by their mates. These observations suggest that the male is of fundamental importance in maintaining the territory for the female's use.

Except as indicated above, shovelers tended to maintain the territory as an exclusive area. Since this was done largely by intraspecific hostility, the implication is that the male must be on the territory when other shovelers are searching for territorial sites. In agreement with Poston's (1968) work on wild shovelers, I found that pairs did spend much of their daylight hours on the territory. During the pre-laying period, when the territory was being established, 10 pairs spent from 2 to 4 hours on the territory (usually in the period (05:00-19:00). This period coincided closely with the times that other pairs searched for nesting sites.

During late laying and incubation, males of 10 pairs observed spent an average of 73.5% (range 55-90%) of the daylight hours on the territory, thus making use of the area by other pairs virtually impossible.

Territories in relation to habitat

The importance of water for duck species is obvious. On my study area, water, along with the density and pattern of associated vegetation appeared largely to determine where territories were located. The importance of this was illustrated within the study area in that 8(80%) territorial pairs located territories where the ends of the ditch, or a dike crossing the ditch, effectively formed a barrier.

The absence of dense stands of emergent vegetation ringing the edges and covering the surface of water areas appeared to be a prerequisite for territories. Evidence for this was provided by analysis of the 9 aerial transects made over the Delta marsh in 1970. The percentage of territories in four grossly defined habitat types, based on permanence of water and nature of associated vegetation, were; 85 (67%) occurred where sparse or no stands of emergent vegetation ringed or covered the surface of permanent water areas (i.e. the study ditch at Delta), (2) 33 (26%) territories occurred where emergent vegetation ringed but did not cover the surface of permanent water, (3) 13 (7%) occurred where there was temporary sheet water free of significant amount os vegetation but highly susceptible to drying, and (4) no territ-

ories occurred on permanent water covered by emergent vegetation. Thus, as noted by Hochbaum (1944), roadside ditches and farm ponds were primarily frequented by shovelers. In addition, the survey indicated that within Delta marsh, water areas at the periphery of the marsh rather than larger areas of the marsh proper, were used.

Hochbaum (1944) observed that males of dabbling ducks desert territories when drying occurs. In 1970 available suitable habitat at Delta was greatly diminished by the first week of June. Drying of water and growth of vegetation made many areas useless for shovelers. An influx of shoveler pairs occurred, at this time, onto the study ditch which still provided suitable conditions for the establishment of territories. Further evidence that drought conditions may affect territories was provided by observations of one male shoveler, not on the study area who deserted his territory when it became completely dry. This male subsequently re-located 1.6 km. away where his female joined him when off the nest. The above evidence suggests that shovelers have definite water requirements which when lacking may prevent or inhibit the establishment and maintenance of territories.

Another aspect of the habitat that appeared to be an important aspect of shoveler territories was the loafing bar described above. After pairs became localized, one major loafing bar, often a hummock of ground close to the ditch edge, was utilized. Aggressive encounters between residents and intruders were centred at or near the loafing bar (Fig.2)

and observations suggested much of the resident's other activites occurred in this area. To assess the latter possibility locations of resident males relative to the loafing bar and the time spent at these locations were recorded during the laying and incubation period (Fig. 6). Significantly more sightings ($\chi^2 = 631$, $P < .001$) of resident males occurred at less than 30 metres from the loafing bar even though Fig. 3 shows clearly that the territorial boundary disputes occurred most frequently at greater distances. Further, of the 418 (87%) sightings in the 0-30 metre interval, 226 (54%) were right at the loafing bar and an additional 75 (18%) sightings were within 15 metres of it. When not on the loafing bar males often sat in the ditch a mere 1-2 metres away from it.

Using comparisons based on total time spent at various portions of the territory, a similar conclusion emerges. Thus, of 126 hours of observation, significantly more time (93%) ($x^2 = 192$, $P<.001$), was spent in the 0-30 metre interval than elsewhere. This evidence strongly suggests that within the territory the loafing bar forms a focal point in the area in which the male's non-aggressive behaviour is most obvious.

As noted by Hochbaum, (1944), Dzubin (1955), Sowls (1955) and others, females commonly used the same loafing bar as the male, once the pair-bond had broken (Sowls,1955). While on the study area, females used the territory for feeding and loafing, feeding usually within 30 metre of the loafing bar then preening and loafing at or near the loafing

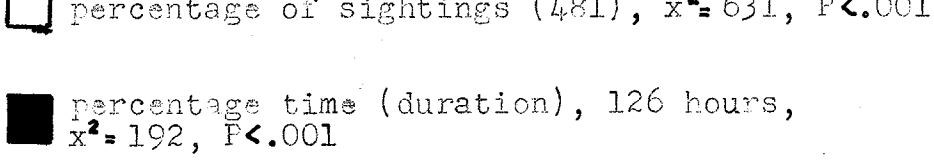
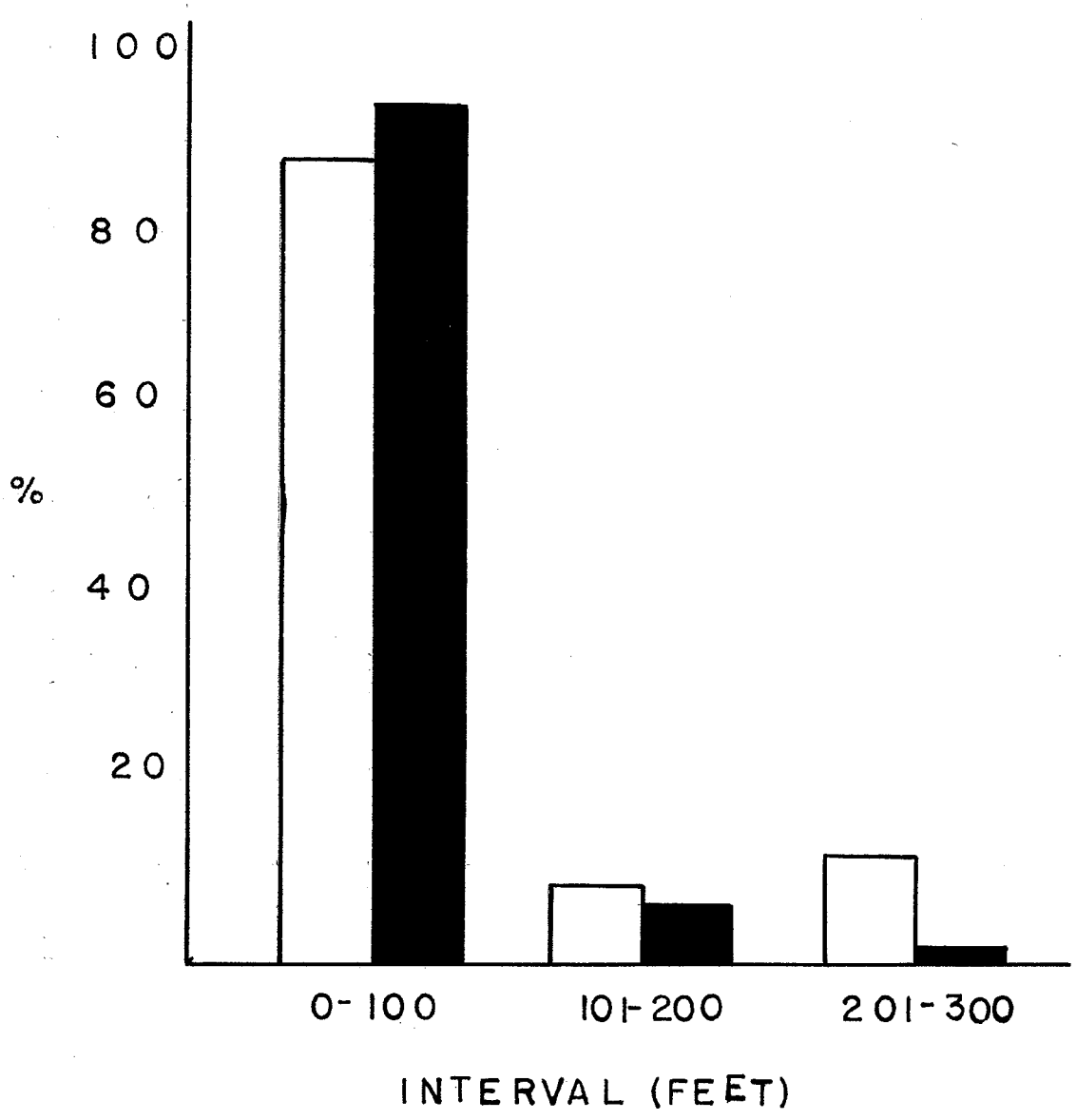


Figure 6. Location of male on territory, relative to loafing bar during the laying and incubation periods, composite of 10 marked males, data gathered over 12 weeks.


100
80
60
%
40
20
0-100
101-200
201-300
INTERVAL (FEET)

bar. These results suggest that, as for the male, the loafing bar is also the focal point of maintenance activities for the female, at least while she is off the nest. It seems likely that the localized activity of the female around the loafing bar even in the absence of her mate functions to keep the female on the territory even though, as Hochbaum (1944) suggested, she may not observe actual territorial boundaries.

Relationship between territory and nests

As noted by McKinney (1967), nesting pairs searched for nests some time before laying the first egg, at a time when territories were established. At Delta, males began defending an area five to 19 days prior to deposition the first egg by the female. The males of four pairs which nested early, prior to 15 May, defended an area for only 6 on average days prior to their females depositing their first eggs (Table II). These late birds, presumably re-nesting pairs, established territories quickly, at a time when suitable habitat was limited, despite the fact that there were several other pairs attempting to establish in the area. This suggests that some pairs are able to establish territories while others cannot, possibly because of the strength of the pair-bond or physiological condition of the female.

The importance of the territory to nest success was shown by the behaviour of two pairs whose males could not establish territories on the ditch due to hostility by in-

Table 11. Duration of time pairs spent in an area prior to nest initiation.

Time	Days to first egg	Average days to first egg
Prior to 8 June (early nesters)		
week 2	19	
3	14	16
4	13	
4	17	
After 8 June (late nesters)		
week 8	5	
8	6	6
8	7	
9	5	

cubent shoveler drakes. The females of these pairs made nest scrapes but did not nest. Both pairs left the area after attempting to establish for three weeks. It seems likely that such delays of nesting, particularly when suitable habitat was dwindling, near to drying, could result in some pairs failing to produce young for that year.

As noted by Poston (1968) and Hochbaum (1944), nests were close to, but not always within, the defended area. Four of nine nests at Delta were outside the area usually defended by the male, an average of 140 metres from the loafing bar. The males did not similarly move, however, suggesting that once the territory was established, they were reluctant to re-establish territories even when females moved far outside the territories to nest. The remaining five nests were within the defended area, an average 42 metres from the loafing bar. The proximity of the nest-site to the loafing bar in the case of the latter five nests appeared to ensure the females a greater measure of protection from strange shoveler males because she was within her mates sphere of protection. In addition, the location of the nest which was determined after the loafing bar was established suggests that females may relate to the male and/or the loafing bar when establishing nest-sites.

Although the territory is heavily utilized by both the male and female while nests are active, it was invariably deserted within three days after nest destruction. Contrary to the observations for shovelers reported by Hochbaum (1944), three pairs whose nests were destroyed during laying deserted

their territories.

Some evidence was obtained that pairs remained together after nest destruction. The strongest evidence for this conclusion was three pairs that remained on the territory for two days after nest loss. Pairs presumably left the area together, although direct proof is lacking. Two such pairs who lost their nests late in the season were, however, seen together within a large group of feeding males, suggesting that the pair-bond was still intact at this time. Further indirect evidence suggesting pairs remained together was provided by the apparent total lack of re-pairing activity in shovelers prior to re-nesting.

Discussion

Since Hochbaum (1944) suggested that territoriality was evident in ducks, several authors (Dzubin, 1955; Sowls, 1955; etc.) have criticized aspects of the concept as applied to ducks while others (Lebret, 1961; Hori, 1963) state that this phenomenon does not occur in the Mallard and Shoveler (Hori, 1963), due primarily to the dearth of evidence for a defended area (McKinney, 1965). However, McKinney (1965) and Siegfried (pers. comm.) state that the concept is valid and widely accepted. In agreement with McKinney's (1965,1967,1970) work on captive shovelers, my observation of localized activity (Fig. 2), including intraspecific hostility (Fig. 6) interactions at territorial boundaries (Fig.3) and exclusiveness of the localized area (Fig. 5), all show

that the Shoveler male may defend an area, which is often contained within reasonably well defined limits (Fig. 4).

Poston (1969) who worked in a prairie pothole habitat where the concentration of breeding pairs was low, found home range sizes of shovelers to be 29.2 hectares, while Gates (1962) who worked in habitat similar to that found on my study area, measured home ranges of not greater than 8 hectares. I measured territory size relative to the loafing bar most frequently utilized by the resident male and found the effective size of the territory to be 0.9 ha. for 10 territories, a figure that more closely resembles Poston's (1969) estimate of 0.6 hectares for the "core area" for two pairs. Comparison of my data with these data for home range size indicates that the territory, where 10 pairs spent 73.5% of the time during late laying and incubation, is a very restricted portion of the total home range. My osbsevations of males leaving territories on pursuits (Part II of this thesis) also agrees with this interpretation. It seems likely that this confined area, which is not readily reduced by aggressive behaviour of intruders (Stability of territories), must be considered the portion of the home range crucial to reproductive success.

Establishment and maintenance of territories

In agreement with the observations of several authors (Hochbaum, 1944; Dzubin, 1955; Sowls, 1955), the experimental results of my study indicated that the female deter-

mined the general location of the territory. However, the final positioning of the territory boundaries were accomplished by the male, whose behaviour actually defined the defended area (Fig. 2,3), often prior to nest-site selection, and usually in the absence of the female.

As stated by Hochbaum (1944), habitat, particularly a suitable location for a loafing bar for the male, appeared to be critical for the establishment of the territory. My results indicate that no drake was without a loafing bar, which was the focal point for both the male and female. Another important aspect of habitat was indicated by the finding that males deserted territories, previously selected by their mate, when drying occurred, a phenomenon also noted for ducks in general by Hochbaum (1944). This suggests that although the female may choose the general location of the territory, the male may subsequently reject the area, if conditions are not suitable. My observations show in addition that when the male leaves such an area, he may go elsewhere to establish the territory even though the female remains on her original nest up to 1.6 km. away. These observations suggest the general hypothesis that the female, accompanied by the male, selects the general area where the territory will be located but males may "veto" a particular area if it is not suitable for the establishment of a territory.

Because the male accompanies the female when she temporarily or permanently leaves the territory, several authors (Lebret, 1961; Hori, 1963) believe that there is no "site-attachment" (Tinbergen, 1957) and still others (McKinney, 1965)

suggest this topic in ducks should be avoided since the possibility usually cannot be excluded that the male is defending a female rather than a site to which he is "attached". As noted above, however, shovelers at Delta did defend an area of the ditch (Fig. 2,3), and both experimental and observational evidence showed they may defend such an area in the absence of the female, whether she is away from the territory at the nest, or completely removed from the area (Selection of the territory). Of possible relevance, also, is experimental evidence (Selection of the territory) indicating that paired males may lose dominance in a strange territory in spite of the fact that their mate is on the strange territory with them, but regain dominance when the pair is back on their own territory. These results suggest that in the Shoveler, at least once a territory is established, the resident male may then relate to the physical site despite the fact that he also often follows the female, and defends her, while off the territory. It should be noted that experimental results (Selection of the territory) also show that the male will not defend the area indefinitely in the absence of the female.

Functional significance of territory

Although Gates (1962) working with the Gadwall and Poston (1968) working with the Shoveler, discounted hostility, a component of territory (Tinbergen, 1957), as a mechanism limiting density of breeding pairs on their study

areas, McKinney (1965) believes that hostility in the form of aerial chasing, as is seen in the Shoveler, serves to produce some degree, of dispersion of pairs (see also Hochbaum, 1944, Sowls, 1955). In agreement with McKinney, my data indicated that shoveler pairs at Delta were spaced both in time, as seen in the nesting delay of non-territorial pairs (Fig. 5), and space (Stability of territories), as a result of territorial behaviour.

Several hypotheses to explain the function of spacing in ducks have arisen. Hochbaum (1944) theorized that pairs are territorial and thus spaced to ensure completion of copulation, while McKinney (1967) suggests that spacing is probably an anti-predator device, as discussed by Errington (1946), (see also Tinbergen, 1939). Hochbaum,McKinney and Ward (Delta Seminar, 1968) also noted the importance of food to breeding ducks as did Geyr (1924) for the Mallard and Siegfried (1965) for the Cape Shoveler.

What then is the functional significance of territoriality and the resulting spacing in the Shoveler? Although territorial behaviour does ensure protection for the female from aggressive males, this may be little more than a consequence of territory, as discussed by Hinde (1956). Spacing to reduce predation (McKinney, 1965) seems reasonable and cannot be ruled out by my data. In addition to these functions, however, it may also be that some resource essential to reproductive success is being defended, thereby justifying the considerable expenditure of energy by the resident male in maintaining the territory. Broods of

dabbling ducks are apparently very mobile (Evans and Black 1955) and presumably may feed little or not at all on the territory. However, the adult female shoveler at Delta fed exclusively on the territory during the late laying, and entire incubation periods (Territories in relation to habitat). This is a time when Ward (1969) says food is most important to female ducks which spend little time off the nest. If this is so, then maintenance of resources for the female would seem to be a reasonable functional explanation for the estended and well developed territorial behaviour of this species.

As suggested above, maintenance of resources on a territory over the incubation period also suggests a possible reason for the extended territorial behaviour and similarly extended pair-bond that has often been noted for the Shoveler (Hochbaum, 1944; Sowls, 1955; McKinney, 1965, 1967; this study). The further possibility that an extended pair-bond and associated territorial behaviour might be especially important to shovelers during the re-nesting period was suggested by the observation that suitable habitat for re-nests was limited. An increase in the number of late nesting pairs was evident (Fig. 1) at a time when general drying occurred, a condition which correlated with an influx of birds onto the study area. Although nesting habitat was plentiful, competition for territory sites was keen and pairs which established territories nested quickly (average 6 days to first egg). The importance of having a territory was shown by the females of two pairs which did not nest presumably

because of their male's inability to establish a territory (Relationship between territory and nests). It thus seems likely that the extended pair-bond, which does not dissolve until relatively late in the season, reduces the need for re-pairing activity, prior to re-nesting, and thus presumably reduces delay in the establishment of territories that are essential in re-nesting.

SUMMARY

Territorial behaviour was studied in a breeding population of the Northern Shoveler at Delta, Manitoba. Wuantitative data on the hostile behaviour associated with the establishment and maintenance of the territory was obtained.

Localized aggression in the form of "chasing," "hostile pumping", "ritualized fighting" and pursuit flights functioned to establish and maintain the territory. "Ritualized fighting" served to approximately define territory boundaries.

The female was responsible for determining the location of the territory, as shown by experiment. The male was responsible for determining the extent of the territory. Once established, the territory may be defended by the drake even in the absence of the female.

Territory size was significantly greater during prelaying than in the period after nest initiation. Territory size did not change as the pair-bond weakened during the incubation period.

Next to water, the leafing bar appeared to be the most crucial habitat factor in determining the location of territories. The loafing bar was the focal point of the

territory for the drake and aggressive behaviour occurred within 90 metres of this location. The loafing bar was also the focal point for the female when off the nest. The female continued to use the loafing bar after pair-bond dissolution.

Once the territory was established and egg laying began, pairs spent an average of 73 per cent of daylight hours on the territory. Pairs which lost nests vacated the territory and territories defended by drakes whose females were advanced into incubation were susceptable to encroachment by other pairs.

Late nesting pairs began egg laying and established territories more quickly than early nesters. Evidence suggests that a pair must have a territory for the nesting attempt to be successful.

LITERATURE CITED

Bartonek, J.C. and C.W. Dane. 1964. Numbered nasal discs for waterfowl. J. Wildl. Mgmt. 28(4): 688-692.

Brown, J.L. 1969. Territorial behaviour and population regulation in birds a review and re-evaluation. Wils. Bull. 81 (3): 293-329.

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

Errington, P. L. 1946. Predation and vertebrate populations, Quart. Rev. Biol., 21:144-177, 221-245.

Evans, C.D. and K.E. Black. 1955. A four-year duck study in the prairie potholes of South Dakota. Special Scientific Report: Wildlife. U.S. Fish and Wildlife Service.

Gates, J. 1962. Breeding biology of the Gadwall in Northern Utah. Wilson Bull. 72: 102-108.

Geyr von Schweppenburg, H. 1924. Zur secualathologie der stockente. Jour. fur Ornith. 72: 102-108.

Hinde, R. 1956. The biological significance of territories of birds. Ibis 98: 340-369.

Hinde, R.A. 1966. Animal Behaviour A Synthesis of Ethology and Comparative Psychology. McGraw, Hill. Toronto.

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

Hori, J. 1963. Three-bird flights in the Mallard. Wildfowl Trust 14th Ann. Rep. : 124-132.

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

Lincoln, F.C. and S.P. Baldwin. 1929. Manual for bird banders. U.S. Dept. Agriculture, Miscellaneous Public. 58: 116.

Mayr, E. 1935. Bernard Altum and the territory theory. Proc. Linn. Soc. N.Y. Nos. 45, 46 : 24-38.

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

McKinney, F. 1967. Breeding behaviour of captive Shovelers. Wildfowl Trust 18th. Ann. Rep. : 108-121.

McKinney, F. 1970. Displays of four species of blue-winged ducks. The Living Bird: 29-64.

Nice, M.M. 1941. The role of territory in bird life. Amer. Midl. Nat. 26: 441-487.

Noble, G.K. 1939. The role of dominance on the social life of birds. Auk 56: 263-273.

Pitelka, F.A. 1959. Numbers and breeding schedule, and territoriality in pectoral sandpipers of Northern Alaska. Condor 61 (4) : 233-264.

Poston, H.J. 1968. Home range and breeding biology of the Shoveler Unpubl. M.S. Thesis. Utah State Univ.

Poston, H.J. 1969. Relationship between the Shoveler and its breeding habitat at Strathmore, Alberta. Saskatoon Wetlands Seminar. Can. Wildl. Serv. Rep. Series. 6: 132-137.

Siegel, S. 1956. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill Co., N.Y.

Siegfried, W.R. 1965. The Cape Shoveler Anas smithii (Hartert) in Southern Africa. Ostrich 36: 155-198.

Sowls, L.K. 1955. Prairie Ducks. Wildlife Management Institute, Washington, D.C.

Tinbergen, N. 1939. Field observations of East Greenland Birds. II. The behaviour of the Snow Bunting (Plectrophenax nivalis subnivalis (Brehm)) in spring. Trans. Linn. Soc. N.Y. 5: 1-94.

Tinbergen, N. 1957. The fujctions of territory. Bird Study 4: 14-27.

Ward, P. 1969. Tenth seminar on the breeding biology of waterfowl. Delta Waterfowl Research Station Seminar Report 10.

PART II

PURSUIT FLIGHTS OF THE SHOVELER, *ANAS CLYPEATA*, AT DELTA, MANITOBA.

Aerial pursuit flights have been described for several Anas species, including mallard, Anas platyrhynchos (Geyr Von Schweppenburg, 1924; Hochbaum, 1944; Gates and Beer, 1956; Dzubin, 1957; Lebret, 1961; Hori, 1963), pintail, A. acuta (Smith, 1963), gadwall, A. strepera (Gates, 1962), the northern shoveler, A. clypeata (Hori, 1963; McKinney, 1965,1970), and the Cape Shoveler, A. smithii (Siegfried, 1965). The investigators involved in these studies have discussed various aspects of these pursuit flights, however the motivation and function of these flights are still uncertain.

Two types of pursuit flight are usually distinguished. These have been described (McKinney 1965) as:

"i) three-bird flights involve pursuit of the female of a pair by a paired male, the female's mate being the third bird in the group. The chases are often brief, the pursuing male returning to his starting point after flying a short distance....

ii) attempted rape flights are prolonged, vigorous chases, involving the pursuit of a female by a number of males. These flights often range far from the original starting place and they have been observed to end in promiscuous rape of the female, after she is forced to the ground."

In the shoveler, quantitative measures of flights in natural populations are lacking, but those observations that have been made (Hori, 1963; McKinney, 1965) including those

of captive populations (McKinney, 1967) indicate that "three-bird flights" are typically vigorous but of short duration, the chasing drake returning quickly to the flight origin. The male of the pursued pair often defends his mate against the pursuer during the flight. Rape of strange females is apparently rare, at least while the pair-bond is strong (McKinney, 1965; 1967). "Attempted rape flights" would thus presumably occur less frequently than "three-bird flights", particularly while the pair-bond is strong.

A major objective of this study was to quantitatively observe flight behaviour and if possible, extend published descriptions of these flights in the Shoveler. Quantitative comparisons of flight behaviour patterns throughout the breeding season was also done, to determine the incidence of "attempted rape flights" and to determine if this incidence varied between the pre-laying, laying, incubation and re-nesting periods.

According to McKinney (1965), "chasing tends to produce some degree of dispersion and ... it has a significant effect on breeding densities". In a companion study (part 1 of this thesis), I have obtained evidence that a degree of dispersion of shovelers may result from territorial defense by the drake involving behavior other than the pursuit flights considered here. These findings cast some doubt on the probable importance of flights in the spacing of this species. In an attempt to clarify this issue, I obtained quantitative measures of whether pursued birds left the area after the pursuit, and whether the pursuer returned to the

territory after the flight.

Evidence from captive shovelers indicates that flight frequency varies with general patterns of daily and seasonal activity (McKinney, 1967). To determine if flight frequency of wild shovelers corresponded with periods of activity in McKinney's captive birds, my data were further analysed according to time of day and breeding season chronology. In addition, the possibility that flight frequency correlated with the number of potential interacting pairs on the study area was also examined.

The study area consisted of a 1.9 km. section of ditch 1.6 km. south of Delta. Details of the area, and the methods used to trap and individually mark 17 drake and three female shovelers are described in part 1 of this thesis. Data used in analysis of flights were gathered primarily by observations of birds whose identity was known from individual markers. A total of 266 pursuit flights were observed in which the pursuing drake was a mated bird defending a territory on the study area. The pursued birds included those that defended areas elsewhere on the study area as well as those that did not defend territories on the study area.

Results

General description of aerial pursuits

The following description is for flights that would be included in the "three-bird flight" category defined above. Unless otherwise stated descriptions are based on my own observations of marked birds. Shoveler aerial pursuit flights typically involved a defending drake and either an intruding pair or lone drake. Rather than introduce another category of flights for those additional pursuits that involved two drakes but no female, I include them in the "three-bird flight" category. Except for the absence of the female, these all-male flights are similar to the typical "three-bird flights", and are most certainly distinct from the "attempted-rape flight".

Pairs landed on territories on 54 occasions and the pursuing (territorial) drake apparently attempted to approach the female each time. While on the territory actual contact in the form of pecking the female's back and tail feathers was seen on only 10 (11%) occasions. The female's mate successfully intercepted the pursuing drake on the remaining 44(89%) occasions and forced a short skirmish before the three birds took to the air, led by the female.

Once in the air, the female usually remained the object of the pursuit. In 93 (58%) flights which involved intruding pairs, the pursuing drake clearly pursued the female. In the 67 (42%) remaining flights I could not determine whether the pursuing drake was chasing the female or her mate, either

because the mate succeeded in staying between the female and pursuing drake or because the pursuing drake actually shifted his attention from the female to her mate.

While in flight the pursuing drake usually pecked at the back and tail feathers of the female. This occurred primarily in flights of longer than 15 seconds duration. Only once, however, was this behavior considered responsible for forcing the female from the air. Even in this instance, the female quickly recovered and flew from the water, after which the pursuit continued without the pursuing drake or her mate settling on the water. The pursuing drake did not display special threat postures while chasing but rather his head and neck were outstretched as seen in normal rapid flights. Both the resident pursuing drake and the drake of the pursued pair were frequently heard vocalizing during flights, but I could rarely determine with accuracy which drake was definitely calling at a given time.

The pursuing drake often shifted his attention to the male of the pursued pair when pecked by this bird. This shift of attention usually coincided with the termination of the pursuit by the pursuing drake. In addition to overt harassment by the female's mate, the latter was also observed to threaten the pursuing drake, as noted by McKinney (1965). This behaviour, which consisted of rapid (1 - 2 second) thrusting movements with the bill, was typically seen when the drake was above or beside the pursuing drake. When flying between the female and the pursuing drake, the female's mate occasionally (10 - 15%) pulled his neck back and assumed a

posture similar to the posture associated with the repulsion call described by Dzubin (1957) for the female mallard. The drake momentarily hovered at this time, as if to block the pursuing drake's access to the female.

Inciting posture, which consisted of the female pointing her bill at the pursuing drake when he flew below or beside her, was occasionally (5-10%) seen during the chase. At this time, females were typically heard to vocalize, the call being similar to the inciting call of the mallard (Dzubin,1957). The female also displayed a "repulsion" posture and call similar to that described by Dzubin (1957) in the mallard. The female, at this time, briefly hovered in flight.

The "repulsion" call and associated posture was most often noted when a female appeared reluctant to leave an area, i.e., when she circled the defended area, but made no obvious attempt to land. This circular flight, which occurred in 89 (33%) of the flights, differed from the more frequent straight flights (67%), in which the female immediately flew from the defended area pursued by the defender. These two distinct flight patterns also differed in duration, circular flights being longer than straight flights as described below.

Flights were considered long (>15 sec.) or short (1 - 15 sec.) on the basis of the median of 266 flights, which fell in the 10 - 15 second interval. There were 145 (55%) short flights and 121 (45%) long flights based on this criterion. Of the 145 short flights, 119 (82%) were in the 0 - 10 second interval. No flight exceeded 120 seconds and only

18 (7%) fell in the 60 - 120 second interval.

All short flights were straight. In contrast, 89 (73%) of the long flights were circular, the remainder (27%) being straight. These long duration flights most often (77%) involved intruding pairs which flew over the defended area with no obvious intention of stopping, the pair being 200-300 yards away before the pursuing drake drew close. In flights of relatively long duration (i.e. greater than 15 seconds) it appeared that the members of the pursued pair attempted to stay close together, the male often staying in front of the defending drake. This behaviour was seen primarily when a female kept circling the defended area, as if reluctant to leave it.

Flights were considered vigorous or non-vigorous according to the behaviour of the pursuing drake. Vigorous flights were considered to be those in which the resident drake flew close enough to the pursued bird to peck and apparently cause evasive action on the part of the pursued bird. Such vigorous flights were typically short, and rapid in terms of distance moved over time. There were 209 (78%) vigorous flights based on the above criteria.

Each chasing drake was on his territory prior to all flights, and with his mate prior to 188 (71%) flights. Drakes showed no apparent reluctance to leave mates in order to pursue intruders. The pursuing drake returned to his territory after 264 (99.2%) flights and usually flew directly to the region of the major loafing site. Only 5 (1.9%) intruding pairs returned to the territory after the flight

ended, and in each case, the pursuing drake pursued the pair again, until they left the area.

A total of 106 (39%) flights involved males only. Approximately 90-95 per cent of these all-male flights involved only two birds, the remainder three, the maximum number noted on the study area. The third male was usually a drake that chased an existing flight involving two males as they proceeded over his territory. When flights involved an unmated drake as the pursued bird, the pursuit was usually short and straight. However when neighbouring territorial drakes were involved in pursuits as pursuer and pursued, flights were often long and circular. Of the circular flights which lasted over 60 seconds, 15 (83%) involved neighbouring drakes. Drakes appeared to pursue other drakes with as much vigour as they pursued females, particularly when flights involved neighbouring drakes in the process of establishing territories.

Daily and seasonal frequency of flight activity.

In the captive shovelers studies by McKinney (1967), a peak of activity occurred just after dawn and was followed by a period of sleeping during the middle and late morning. There were indications of a secondary peak in the afternoon. In the wild population I observed at Delta, I found, similarly, that morning flight frequency was high, almost twice that of each of the two subsequent periods (Fig. 1). Flight frequency during the period 05:00-10:00 was significantly

($x^2 = 50.0, p < .001$) greater than the remaining two periods. Flight frequency data (Fig.1) provided no evidence for a secondary peak in the afternoon. Some evidence for this was observed, however, when the data were analysed according to the period in which maximum activity occurred on each individual day (Fig.2). Most activity was still seen in the period 10:00 to 17:00 but maximum daily activity was observed on 5(11%) days during the period 17:00 to 22:00, whereas it never occurred during the midday.

Supplementary data on daily activity was obtained from two marked individuals that were observed for most of the duration from dawn until dark, on five occasions. For these individuals, flight activity invariably peaked in the 05:00 to 10:00 period, thereby corroberating the above described results. These individuals were observed during the period just after territories were established.

Flight frequency was also analysed, on a weekly basis, for the twelve week season encompassing the total time Shovelers were breeding on the study area (Fig.3). The first three weeks correspond approximately to the pre-laying period for the study area.

There were no territories established during the first week, and hence no flights by territorial males. Flight frequency increased in weeks two and three as territorial pairs became established. Flights declined in weeks four through seven apparently due to the fewer non-territorial pairs characteristic of the incubation period. During the

Figure I. Occurrence of maximum pursuit flight activity, based on 3 daily periods, over 12 weeks (45 days). $x^2 = 50.0, P < .001$

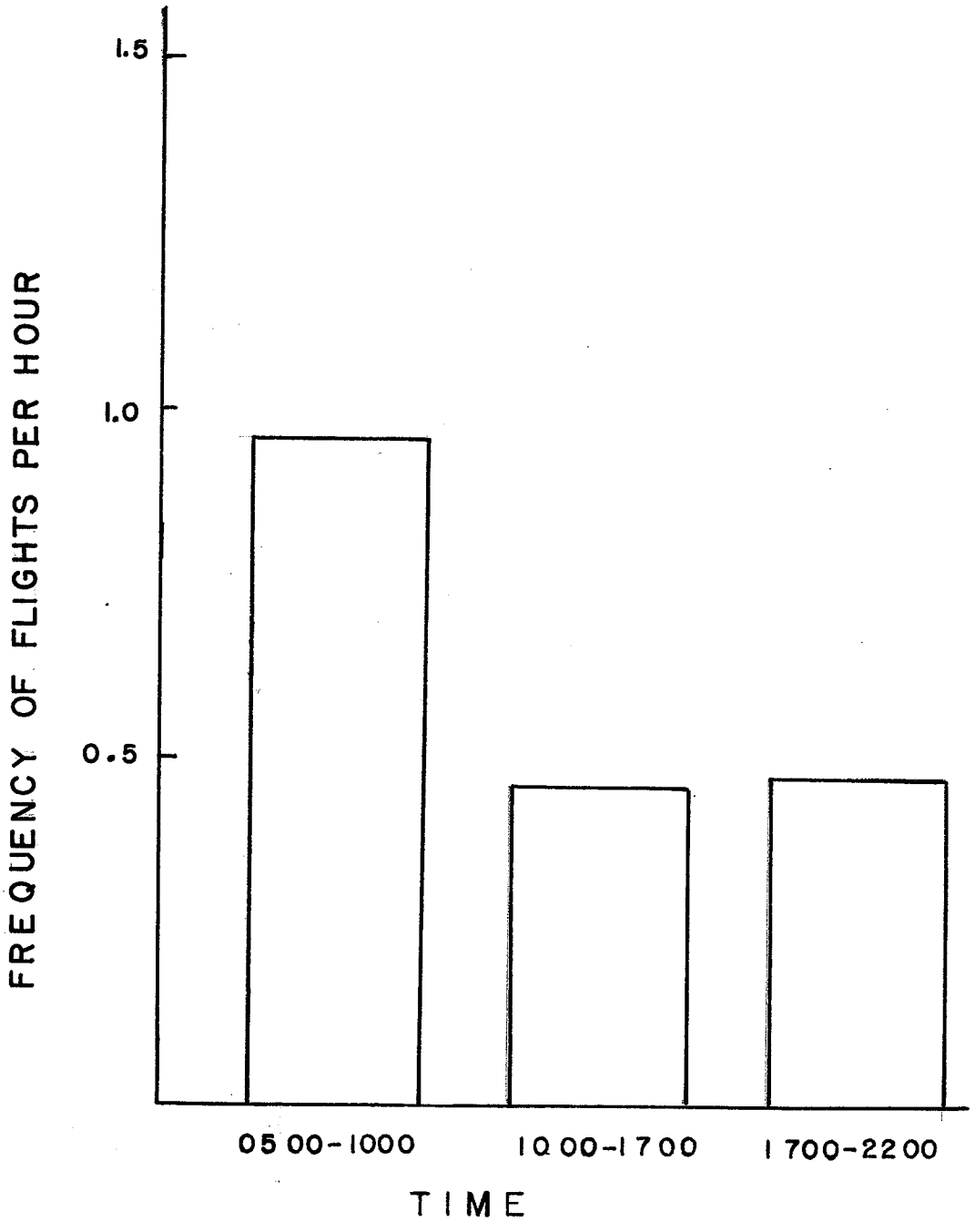

1.5
1.0
0.5
FREQUENCY OF FLIGHTS PER HOUR
0500-1000
1000-1700
1700-2200
TIME

Figure 2 Daily prusuit flight activity during pre-laying, laying and incubation. Observation periods: 05:00-10:00 (195 hr.), 10:00-17:00 (119 hr.), 17:00-22:00 (89 hr).

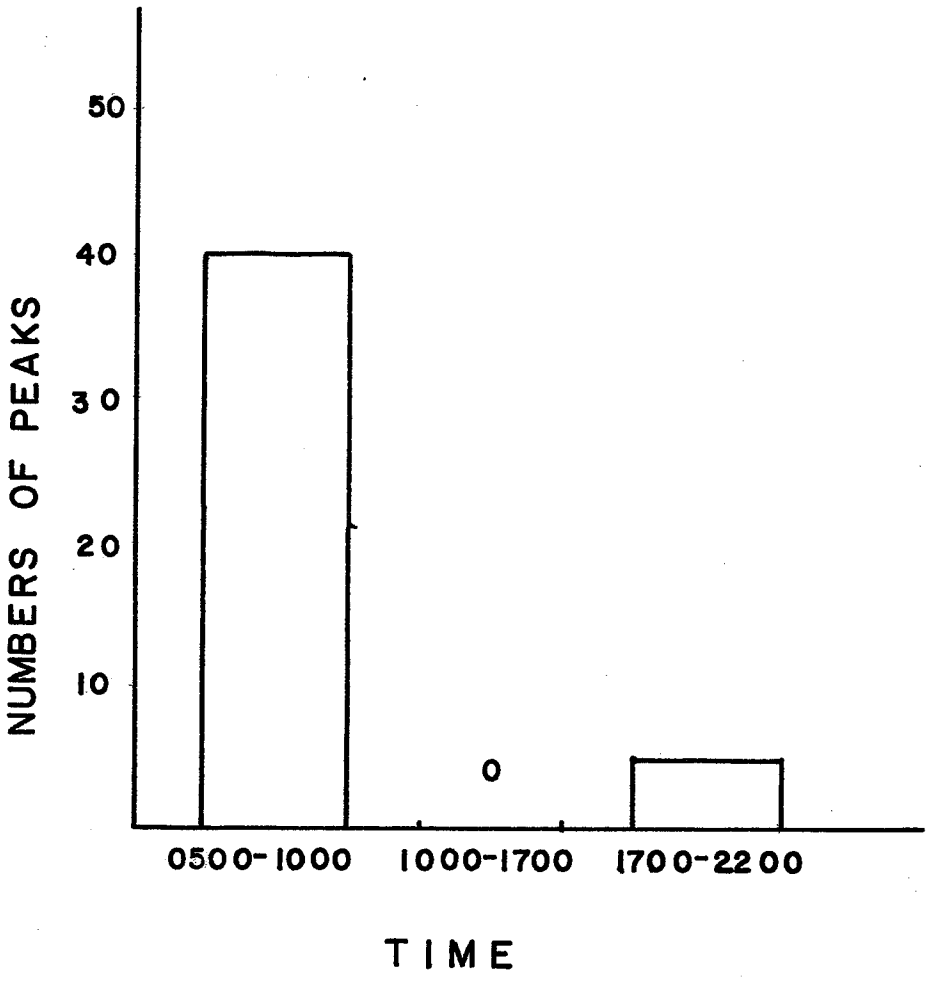
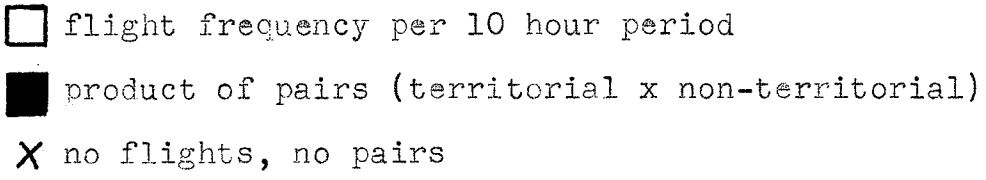
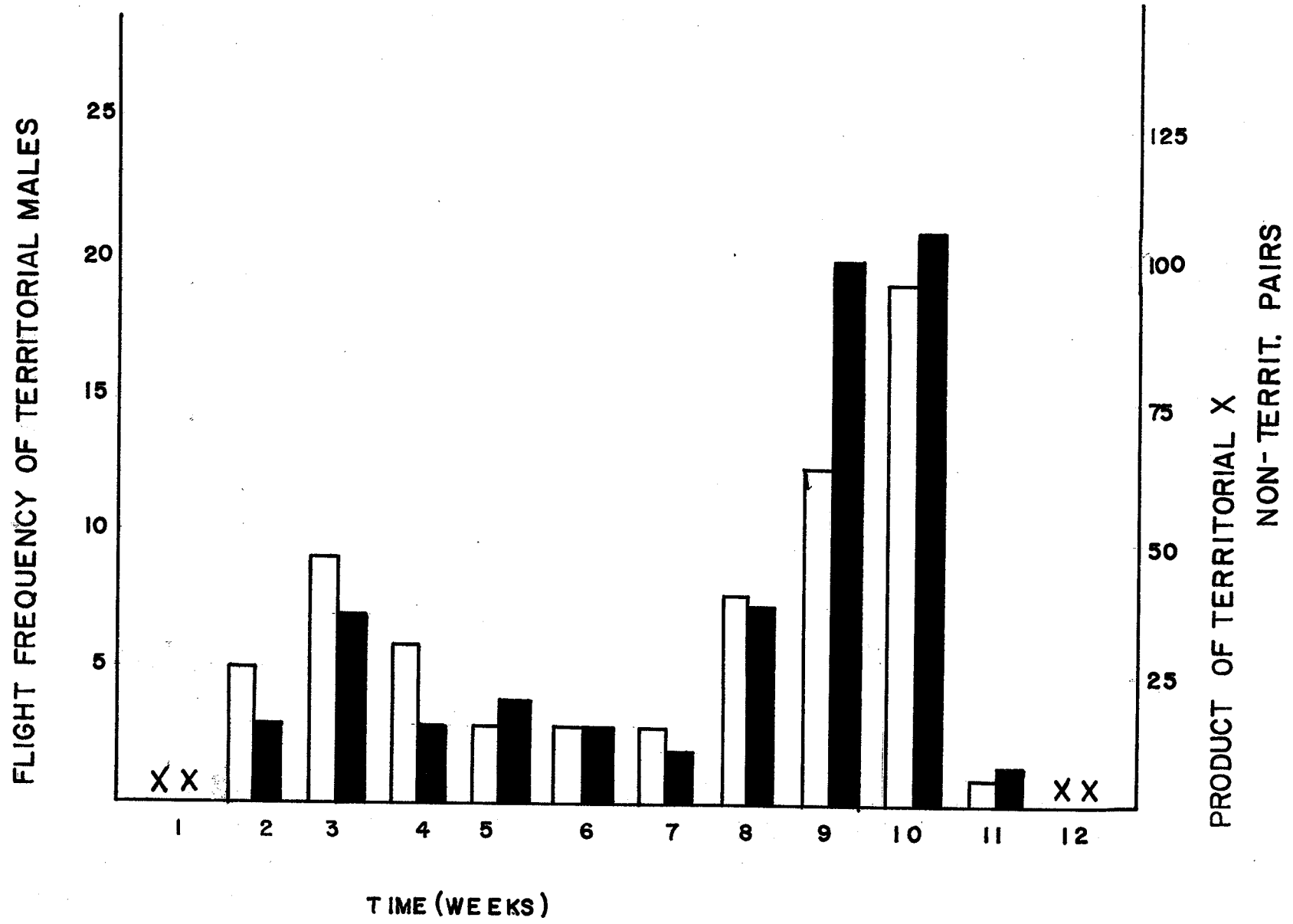

NUMBERS OF PEAKS
50
40
30
20
10
0
0500-1000
1000-1700
1700-2200
TIME

Figure 3. Frequency of flights made by territorial males and an estimate of potential interactions based the number of territorial and non-territorial pairs on the study area. Statistic rank correlation (r) = .868 $P < .01$




FLIGHT FREQUENCY OF TERRITORIAL MALES
25
20
15
10
5
X X
1
2
3
4
5
6
7
8
9
10
11
12
X X
TIME (WEEKS)
125
100
75
50
25
PRODUCT OF TERRITORIAL X
NON-TERRIT. PAIRS

incubation period all nests were predated and territories were subsequently deserted by pairs. Most pairs left the study area entirely. However, new pairs came into the study area during week eight and quickly established territories, resulting in an increase of flight frequency (Fig. 3). Pairs continued to enter the study area during weeks nine and 10 and these birds further contributed to the high levels of flight seen at this time. These birds were presumably re-nesting birds, although no direct proof of this could be obtained. The influx of pairs onto the study area occurred at a time when few suitable breeding areas existed elsewhere on the marsh (see part 1, discussion).

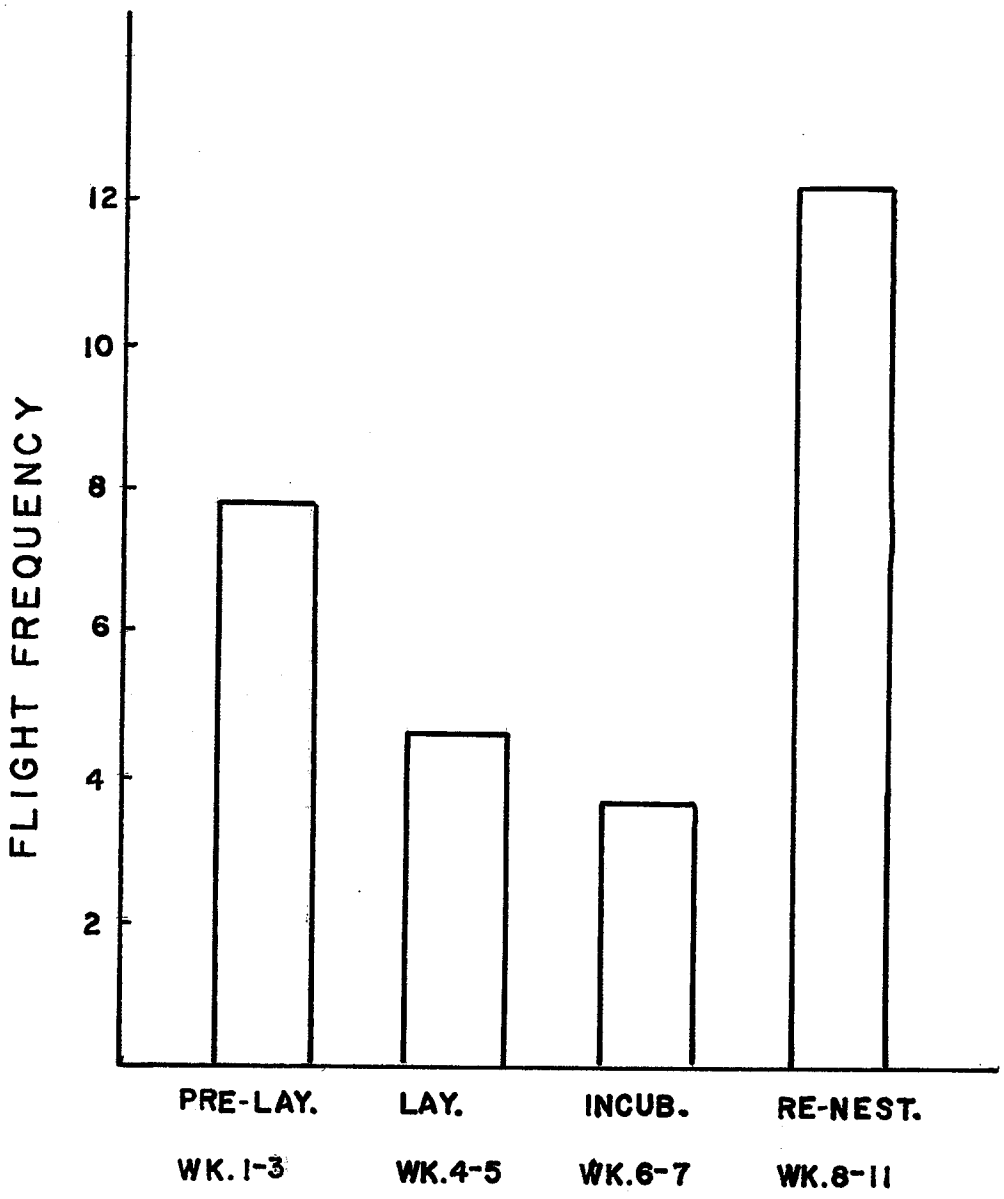
An abrupt drop in pursuit flights occurred in week 11, apparently due to another wave of predation that occurred during that week, which resulted in almost complete desertion of the area by shovelers. Five pairs remained. These were pairs that had not previously held territories on the study area, and they did not subsequently establish territories there. No shoveler pairs were seen during the twelfth week.

The apparent differences in flight frequencies over the breeding season illustrated in Fig. 3 were further analysed according to the four major breeding season periods described above. This grouping indicated that there is no significant difference ($x^2 = 6.45, P > .05$) between the four breeding periods (Fig. 4). However, flight frequency was significantly higher ($x^2 = 4.8, P < .05$) during re-nesting than during incubation, the re-nesting period being a

Figure 4. Flight frequency per 10 hour observation period, during the entire reproductive season.

Chi-square statistic, between the four periods : $x^2 = 6.45$, $P < .05$

Chi-square statistic, between incubation and re-nesting: $x^2 = 4.8$, $P < .05$


FLIGHT FREQUENCY
12
10
8
6
4
2
PRE-LAY.
WK. 1-3
LAY.
WK.4-5
INCUB.
WK.6-7
RE-NEST.
WK.8-11

period when most pairs were actively searching for territories and nest sites.

Observations, as described above, indicated that most flights were due to territorial drakes chasing non-territorial intruders. If so, then it might be expected that flight frequency would correlate with the number of possible interacting pairs, calculated as a simple product of the numbers of territorial and non-territorial pairs in the vicinity. To examine this possibility in more detail, weekly averages of the number of territorial pairs and the number of pairs attempting to establish on the study area, were determined. The numbers of territorial pairs and those attempting to establish in the area were then multiplied to determine an estimate of the number of potential interacting pairs (Fig. 3). Comparison of these values with the number of actual flights shown in figure 3 indicate that a strong positive correlation existed between weekly flight frequency and the number of possible interactions ($r=.868$, $P<.01$). This high correlation suggests the interesting possibility that flight frequency could be used to provide a valid, if indirect, measure of the number of interacting pairs in the area, provided variation in daily and seasonal frequencies are taken into account.

Behaviour during successive portions of the reproductive period.

Although pursuit flights tended to be similar throughout the breeding season, they did differ in some aspects,

eg. duration, vigour and trajectory, as detailed below relative to three major periods: pre-laying (39 flights), laying (33) and incubation (35), plus re-nesting (159 flights).

Pursuits involved both pairs and either one or two drakes as pursued birds throughout the entire season (Fig. 5a). However, significantly more flights involved pursued pairs than drakes during the pre-laying (93%) ($x^2 = 33$, $P < .001$) and laying (78%) ($x^2 = 8.7$, $P > .01$) periods. There was no significant difference in flights during the incubation (37%) ($x^2 = 2.2$, $P > .05$) and re-nesting (49%) ($x^2 = .03$, $P > .05$) periods. Comparing the periods, there were significantly fewer pursuits involving pairs during the incubation period than during pre-laying ($x^2 = 10.7$, $P < .01$) and laying ($x^2 = 3.85$, $P = .05$). These results were expected since many pairs were searching for breeding sites during the pre-laying and laying periods and frequently encountered territorial drakes. There was no significant increase in flights involving pursued pairs during the re-nesting period, ($x^2 = 2.9$, $P > .05$) apparently because few territories existed on the study area when other pairs were searching for breeding sites, thus reducing the frequency of encounters between territorial drakes and non-territorial pairs. With the possible exception of the re-nest period, flights involving pursued pairs decreased with advancing season and flights involving only drakes increased.

Prior to the initiation of pursuit flights, the pursuing drake was either with his mate or alone on territory

(Fig 5b). The male and female were together before most flights (91%) ($x^2 = 24.6$, $P < .001$) during the pre-laying period. This tendency changed during laying and incubation when pairs were together only 13 (42%) ($x^2 = 1.06$, $P > .05$) and 16 (56%) ($x^2 = 0.24$, $P > .05$) times. Pairs were again usually together during the re-nesting period (78%) ($x^2 = 49.8$, $P < .001$), presumably reflecting the fact that most re-nesting females were again in the pre-laying phases of the reproductive cycle. Comparing the periods, the pursuing drake was with his mate prior to flights significantly more often during pre-laying than during laying ($x^2 = 20.4$, $P < .001$) or incubation ($x^2 = 16.7$, $P < .001$), reflecting the fact that females were at the nest more often during the latter two periods. The pairs were together significantly more often during the re-nesting period than during the laying ($x^2 = 84.7$, $P < .001$) or incubation ($x^2 = 14.9$, $P < .001$) periods. There is no significant difference ($x^2 = 2.7$, $P > .05$) between the pre-laying and re-nesting periods.

Flights tended to be in essentially straight lines rather than circular, during the pre-laying (76%) ($x^2 = 9.2$, $P < .01$), incubation (80%) ($x^2 = 12.6$, $P < .001$) and re-nesting (64%) ($x^2 = 12.6$, $P < .001$) periods, but not during the laying (56%) ($x^2 = 0.26$, $P > .05$) period (Fig. 5c). Comparison between the periods shows no significant trends.

There was no significant difference between short (1 - 15 sec.) and long (>15 sec.) flights within or between periods (Fig. 5d). Although these results may in part reflect the method used to dichotomize flights into long or

short duration, they do provide evidence that there was no increase in flight duration during incubation as might have been expected if territorial drakes had shifted from territorial defense pursuits to "attempted rape flights".

Most flights were vigorous as opposed to non-vigorous during pre-laying (82%) (χ^2=25.2, P<.001) and laying 72% (χ^2=6.8, P<.01) but not during incubation (49%) (χ^2=0.03, P>.05). Vigorous flights were again common during the re-nesting period (84%) (χ^2=77.2, P<.001) , (Fig. 5e). Differences in vigour of flights between the periods did not reach statistical significance. Chasing thus appeared to maintain its vigour for individual territorial drakes until it ceased totally during incubation; it did not gradually decrease in vigour throughout this period.

Throughout the entire season, the pursuing drake usually returned to the origin of the flight. This was most marked during pre-laying (100%) (χ^2= 39.8, P<.001) and only slightly less so during laying (97%) (χ^2=29.2, P<.001), incubation (97%) (χ^2=31,0, P<.001) and re-nesting (93%) (χ^2= 118,P<.001) (Fig. 5f). There is no significant difference in results between periods. Although not illustrated in Fig. 5, it is important to note that intruders that were pursued by a drake usually left the area being defended. During pre-laying intruders left on 35 (90%) of occasions, during laying, 32 (96%), incubation 35 (100%) and re-nesting 149 (94%) of occasions. Birds that returned were invariably pursued again by the defender.

In general, flights during the pre-laying period were

Figure 5. Pursuit flight characteristics during the pre-laying (39 flights), laying (33), incubation (35) and re-nesting (159) periods. Figures within histograms indicate actual number of flights.

A- Pursuits involving pursued pairs, remainder involved pursued mate(s).

B- Pursuits in which pursuer with mate on the territory prior to flight, in remainder pursuer was alone.

C- Pursuits that were straight in trajectory, remainder were circular.

D- Pursuit duration: short, 1-15 sec., remainder were long 15 sec.

E- Pursuit vigour: vigorous, remainder were non-vigorous, see text for explanation of terms.

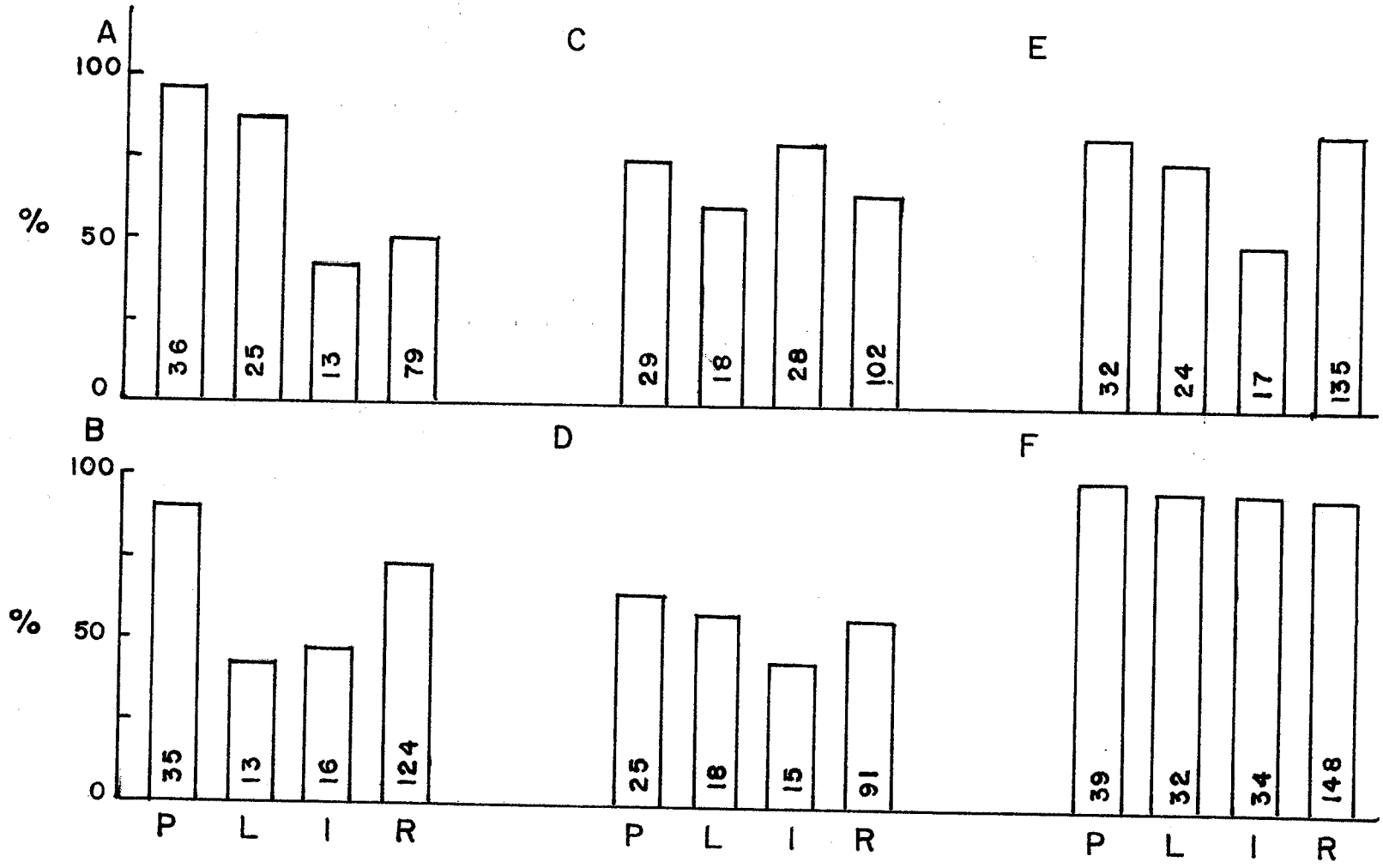
F- Pursuits in which the pursuer returned to the territory after the flight, in the remainder the pursuer flew elsewhere after flight.

Legend P pre-laying period

L laying period

I incubation period

R re-nesting period


A
C
E
100
%
50
0
36
25
13
79
29
18
28
102
32
24
17
135
B
D
F
100
%
50
0
35
13
16
124
25
18
15
91
39
32
34
148
P
L
I
R
P
L
I
R
P
L
I
R

usually short, straight and vigorous with the pursuing drake leaving his mate to pursue an intruding pair. Flights during the laying period were usually short, vigorous flights against intruding pairs. Flights during the incubation period were straight but they could not be characterized by any other characteristic used. During the re-nesting period, flights were primarily short, straight and vigorous with the pursuing drake leaving his mate to pursue intruders. The pursuing drake returned to his territory after flights in each period.

Thus, each flight characteristic; i.e. vigour, duration, trajectory etc., was often highly typical within the early and late periods, the incubation period being an obvious exception. Moreover, for most flight characteristics, differences were not significant between periods. Exceptions also occurred here, however, as shown by the flights involving pursued pairs, which decreased from pre-laying, through laying, to incubation periods. Also the pursuing drake was with his mate prior to flights during the pre-laying period more than during the incubation period. The same result exists between the re-nesting and incubation periods.

Frequency of "attempted-rape flights"

'Attempted rape flights' are prolonged, vigorous chases, involving pursuit of a female by a number of males, the flight ranging far from the origin and sometimes ending in promiscuous rape (McKinney 1965). McKinney (1967),

reporting on the behaviour of captive shovelers, says that "males frequently chased strange females, but clear attempts to rape were infrequent and successful rape was rare," To asssess the incidence of "attempted-rape flights" in the wild population on the study area at Delta, I analysed pursuit flights relative to each of the above criteria.

Flights involving defending drakes were classed as described above, as either short (1 - 15 sec.) or long ($\geq$15 sec.). Prolonged flights are here considered to include flights of 30 seconds or more. There were 56 (21%) such flights, ranging from 30 to 60 seconds duration. Twenty-nine of these 56 flights involved drakes only, thus casting doubt on the possibility that they could validly be considered as "attempted-rape flights". Of the 27 remaining flights, 18 were circular flights which involved pursued pairs whose female apparently tried to remain in or near the defended area while the defender continued his pursuit. In these instances, it seems likely that the pursuer continued pursuit merely because the female remained in the area, hence there is little basis for assuming sexual intent. There remain only nine prolonged flights, involving females, which ranged any appreciable distance from the origin. These flights were vigorous and the pursuing drakes pecked at the pursued female. However, except for flight duration, these flights did not appear to be at all different from the short pursuit flights described previously. In none of these were there

instances of actual sexual behaviour that would provide evidence indicating these flights could be interpreted as "attempted rape".

As reported above, I also noted behaviour on the pursuer's territory prior to pursuit flights on 54 occasions. The defender approached the female close enough to make contact with her on only 10 of these 54 occasions. When the defender approached close to the female, he typically pecked at her back and tail feathers, but made no attempt to grasp her by the neck or mount her.

The only evidence I obtained that pursuit flights may on occasion involve attempted rape came from observations of 23 flights in which the defender and pair landed together, away from the territory. The defender, on two occasions, attempted to mount the female. In the remaining 21 (91.3%) instances, however, the defender sat near the pair for 10 - 30 seconds, pumping his head, and then flew back to his territory. The presence of the female's mate, who typically stayed between the defender and the female while on the water, may have deterred the defender from attempting to mount the female.

Multiple bird pursuits involving more than one pursuing drake were not observed on the study area except among unmated drakes. These drakes appeared to be courting the female rather than attempting to catch her. No pecking at the female was observed. These flights generally lacked the vigour of pursuits involving territorial drakes. Two multiple bird flights, involving drakes of

unknown status, were seen in an area other than the study area, but again no attempted rapes were observed.

Taken together, the above data provide little evidence that flights were other than aggressively motivated. Although there may have been up to two flights that could be considered "attempted rape" flights, the rarity of such observations and the hostility characteristic of such flights when they do occur, clearly provides no evidence that rape is typical in this species.

Discussion

As described by McKinney (1965), pursuit flights may be of two quite different, although not mutually exclusive, types, viz., (1) as rape or attempted rape flights, or, (2) as aggressive flights directed against an intruder that approaches a pursuer's mate or territory. Data from my study of wild shovelers at Delta is in essential agreement with McKinney's (1967) data for captive birds in that rape or attempted rape flights were extremely rare, whereas aggression during territorial defense was common. The implications of these results for the motivational and functional interpretation of the pursuit flight in shoveler are treated in more detail below.

Motivation of Shoveler pursuit flights

Sexually motivated flights would presumably be prolonged; often ending in rape after the female was forced to the ground. However, this behaviour was rare, most (98.7%) flights involving a territorial drake as the pursuer falling into McKinney's (1965) "three-bird flight" category. Aggressive pecking of the pursued female by the pursuer during flights, further suggested that aggression, rather than sex, was the prime motivation involved.

Comparison with other species also suggests a reduced involvement of sexual motivation in shoveler pursuit flights. In the mallard, for example, Lebret (1961) states that "attempted rape flights" are especially common during the incubation period, while McKinney (1965) con-

cluded that rape flights in ducks characteristically correlate with a weakening pair-bond. Analysis of shoveler flights at Delta, however, revealed no apparent seasonal shift in the motivation of the pursuing territorial drake, from aggressively motivated flight, early in the season when the pair-bond was strong, to sexually motivated flight during incubation, when the pair-bond weakens. Rather than changing over the season, flights retained their hostile character throughout the reproductive period, even including the days immediately preceeding the dissolution of the pair-bond. At this time, chasing ceased entirely before the drake deserted his territory, but there was no evidence indicating a shift from aggressively motivated flight, i.e. the "three-bird flight", to sexually motivated flights. These results for territorial drake shovelers thus do not support the contention that the "attempted-rape flight" is a characteristic of a weakening pair-bond, at least for shovelers on my study area. They are broadly consistent, however, in the sense that the extended pair-bond characteristic of shovelers does apparently correlate with greatly reduced levels of "attempted-rape flights" compared to other Anas species.

Function of Aerial pursuit

Although some authors have found that chasing had little effect on the population densities studied (e.g. Gates, 1962 for Gadwall), McKinney (1965:pp 103,104) on

the basis of an extensive review of the problem, considered that, "chasing tends to produce some degree of dispersion and that it has a significant effect on breeding densities". He further states that, "in the Shoveler, Mallard and Gadwall, chasing appears to produce a spacing of pairs at a time when they are establishing home ranges".

Results of my study at Delta (Part 1 of this thesis), in agreement with earlier studies of Hochbaum (1944), Sowls (1955) and McKinney (1967), indicate that at Delta the Shoveler males are clearly territorial. Although there is overlap of home ranges, as described by Poston (1969), territories were maintained as exclusive areas. Despite lack of precise definition of territorial boundaries, it was evident that neighbouring pairs rarely transgressed on the area defended by another drake after the initial period of chasing which usually occurred between neighbours. As described below, several lines of evidence suggest that pursuit flights on the study area played an important role in the establishment and maintenance of these territories, and thus also functioned in dispersion of pairs.

After chases had terminated, behaviour of both the defending drake and the intruder provided one means of assessing the dispersal and territorial functions of flights. Defending drakes returned to the origin of the flight, usually at or near the major loafing site, in 96.2 per cent of encounters, thereby indicating a high degree of localization on the area. Subsequent intruders were similarly chased. This "localized aggression" suggests

territorial behaviour is involved. Typically, (94.1% of observed instances) pursued birds did not return to the territory of the defender, a result that is clearly consistent with the hypothesis that such flights serve a dispersal function. Moreover, in the 5.9 per cent of encounters in which the pursued bird did return to the defended area with the pursuer, they were chased again so that no pair succeeded in displacing an established pair which was actively defending an area.

A further indication that the pursuit flight was a factor in influencing density on the study area was provided by the observations of four marked males that were attempting to establish territories on the same portion of the ditch (see appendix for detailed description). These drakes began to compete for space on the ditch on approximately the same day. Two drakes were successful but only after a period in which they directed 24 pursuit flights at the unsuccessful birds who were relegated to spending most of their time either in the dry meadows adjacent to the ditch or in a vegetation-filled pond some distance from the ditch. The females of the territorial drakes then established nests, but those of the remaining two pairs, against which the 24 pursuit flights were directed by the territory holders, did not, even though both females spent approximately three weeks searching for nest sites in the immediate area. The two unsuccessful pairs eventually left the study area, and did not subsequently nest there. From my observations it seemed clear that pursuit flights as well

as other forms of hostile behaviour by the established territorial drakes, influenced the ability of these pairs to remain in the area.

From the above data, it seems likely that the Shoveler pursuit flights were a factor in establishing, and maintaining, the integrity of territories and thus influencing the density of nesting pairs. Regardless of the motivation involved in the pursuit flight of the Shoveler, my data strongly suggests that the flight functions, at least in part, as a breeding pair spacing mechanism, and is thus a manifestation of highly developed territorial behaviour of the Shoveler.

SUMMARY

The motivation and function of pursuit flights, especially as they relate to territorial behaviour, was studied in a breeding population of shovelers at Delta, Manitoba.

Behaviour during flights was observed for the entire breeding season. Flights were primarily of short duration and in a straight trajectory away from the territory, during the entire season. Pursuing drakes returned to their territories in 96.2 per cent of encounters indicating a high degree of localization. Flights were also vigorous throughout the season except during incubation when pair-bonds weakened to dissolution. Early in the season, most flights involved pursued pairs; more flights involved pursuit of intruding drakes during the incubation period. The pursuer was with his mate, prior to flights, primarily during the pre-laying period. During other periods, the pursuing drake was alone on the territory, usually at or near the leafing bar.

Flight frequency peaked in the morning (05:00-10:00) and was directly correlated with the number of potential interacting territorial and non-territorial pairs on the study area. Pursued birds left the defended area in 94.1

per cent of encounters, indicating that pursuit flights functioned in the establishment and maintenance of the territory and thereby influenced the spacing of breeding pairs in the area.

The behaviour of the pursuing drake, prior to, during and after flights, toward an intruding female suggested that hostility was the prime motivation for the pursuit flight. Only 1.3 per cent of flights, during the entire season, were considered sexually motivated. During incubation, when pair-bonds were weakening, sexually motivated flights were not seen. Thus it appears that aggression rather than sex was the prime motivation underlying pursuit flights.

LITERATURE CITED

Dzubin, A. 1957. Pairing display and spring and summer flights of the Mallard. Blue Jay 15: 10-13.

Gates, J. and J.R. Beer. 1956. A marsh bird study spring 1955. Flicker 28: 16-21.

Gates, J. 1962. Breeding biology of the Gadwall in northern Utah. Wilson Bull. 72: 102-108.

Geyr von Schweppenburg, H. 1924. Zur secualathologie der stockente. Jour. fur Ornith. 72: 102-108.

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

Hori, J. 1963. Three-bird flights in the Mallard, Wildfowl Trust 14th. Ann. Rep. : 124-132.

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. Rep. 92-106.

McKinney, F. 1967. Breeding behaviour of captive Shovelers. Wildfowl Trust 18th Ann. Rep. :108-121.

McKinney, F. 1970. Displays of four species Blue-winged ducks. Living Bird 9th Ann. Rep. :29-64.

Poston, H.J. 1969. Relationship between the Shoveler and its breeding habitat at Strathmore, Alberta, Saskatoon Wetlands Seminar. Can. Wildl. Serv. Rep. Series, 6: 132-137.

Siegfried, W.R. 1965. The Cape Shoveler. Anas Smithii (Hartert) in Southern Africa. Ostrich, 36: 155-198.

Smith, R.I. 1963. The social aspects of reproductive behaviour in the Pintail (Anas acuta acuta, L.) Unpubl. Ph. D. Thesis, Utah State Univ., Logan.

Sowls, L.K. 1955. Prairie Ducks. Wildlife Management Institute, Washington, D.C.

Appendix 1

Flight Behaviour and Territorial Defence in 4 marked males.

Detailed information on territorial interaction was gathered on four marked drakes that were attempting to establish territories at the same location. The flight behaviour of these birds was observed from 16 to 22 June, 1970. Observation time totalled 79 hours.

Two pairs, subsequently called pairs 1 and 2, succeeded in establishing adjacent territories in the area. The remaining two pairs, subsequently called pairs 3 and 4 were harrassed by drakes 1 and 2 and did not succeed in establishing territories in the area. The nests of 1 and 2 were destroyed, presumably by a predator, between 20 June and 24 June. The female of pair 1 had been incubating approximately 2 - 3 days and the female of pair 2 was still laying at the time. The four interacting pairs were believed to be renesting pairs because the breeding season was well advanced, and all four drakes had begun replacing nuptual body plummage with eclipse plummage; drake 1 was completely brown on the chest and flanks by 26 June. These pairs could, of course, have been late nesting pairs which had not previously nested.

Comparison of flights made by drakes, during the 3 periods of observation throughout the day verified the earlier finding (Fig. 3) that most flights occurred in the early morning period. Thus drake 1 was observed in 29 flights during the period 05:00-10:00 (30.5 hours of observation). During the period 10:00-17:00 (14 hours), 1 flight

Defending drake	total encounters	total flights	Pursued drake or pair								other	
			pr.1	dr.1	pr.2	dr.2	pr.3	dr.3	pr.4	dr.4	pr.	dr.
1	34	30			-	6	-	16	1	-	2	5
2	17	15	-	3			-	7	-	-	2	3
3	1	1	-	-	-	-			-	1	-	-
4	2	1	-	-	-	1	-	-			-	-

was observed. From 17:00-22:00 no flights were observed during 6.5 hours of observation.

Table 1 indicates aggressive encounters among the principal drakes and between them and other shovelers from 19 to 29 June. As indicated in table 1, drake 1 encountered intruders on or over his territory on 34 occasions. Thirty pursuit flights resulted from these encounters. Drake 2 had only half as many encounters, while drakes 3 and 4, which were attempting to defend the same water areas as drakes 1 and 2, chased other shovelers on only 2 occasions.

Flights between neighbouring drakes 1 and 2 occurred in 9 instances (table 1). Of the 9 flights between 1 and 2, drake 1 chased drake 2 six times, of which 4 were short flights occurring within one hour. These flights occurred during the period when both drakes were establishing territories. From my on-the-spot observations, it seemed clear that chasing behaviour as noted above, contributed to the establishment of a reasonably clearly defined common boundary between the territories of drake 1 and 2.

Drakes 1 and 2 chased drake 3 a combined total of 23 times (table 1). Drake 3 was a persistent drake, in that he tried repeatedly and unsuccessfully, to utilize the defended areas of drakes 1 and 2. Drake 3 usually encountered drakes 1 and 2 while his mate was searching for a nest-site at which time he was attempting to utilize the ditch area defended by drakes 1 and 2.

Drake 1 was never chased by drakes 3 or 4 and drake 2 was chased only once by drake 4.

Most of the chasing by drakes 1 - 4 was among themselves. Birds from other parts of the study area or from outside the study area comprised only 12 of 45 flights that drakes 1 and 2 were involved in, and none of the flights by 3 and 4. Both drakes 1 and 2 chased a pair that landed in the territory of drake 1. Drake 1 chased this pair and the flight crossed the loafing site of drake 2 who immediately pursued the 3 birds. Drake 2 flew past drake 1 and attempted to peck the female of the pair. Drakes 1 and 2 returned to their respective territories after the short flight.

Most pursuits involved drakes only. For drakes 1 and 2, 40 of 45 flights were against intruding drakes. Drakes 1 and 2 pursued each other on 9 of 40 flights.

Flight behaviour of male 1 reflects general flight behaviour as discussed under the headings; Behaviour during 3 major periods plus the re-nesting period, and General description of aerial pursuit flights. The following results describe the flight behaviour of these drakes within the same broad categories discussed under the indicated separate headings (data is included in analyses in Fig. 1).

Drake 1 was with his mate prior to flights on 19 (63%) occasions. The drake returned to his territory and mate, when there, after each (30) pursuit. There were 28 (93%) vigorous pursuits. Drake 1 was involved in 17 (57%) straight flights and 13 circular flights. The circular flights were predominantly with drake 3 who was reluctant to leave the ditch area. Intruders were intercepted flying over the territory on 10 (33%) occasions. The encounters which

occurred on the territory were all on the ditch. Boundary conflicts with drake 2 usually resulted in short (0-5 seconds) aerial pursuits. Flights in general, involving drake 1, were short with 14 (45%) in the 0-5 second interval, 11 (35%) in the 6-10 second interval, 2 (8%) in the 11-20 second interval and 3 (12%) in the 30-45 second interval. Short flights, as previously defined (0-15 sec.), occurred on 26 (86%) occasions. The 3 flights in the 30-45 seconds interval involved drake 3. These results reflect the general flight behaviour during the re-nest period.