

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.

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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. Quantitative 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 determining 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 mechanism. 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 Le Bret (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 data 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 Le Bret (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

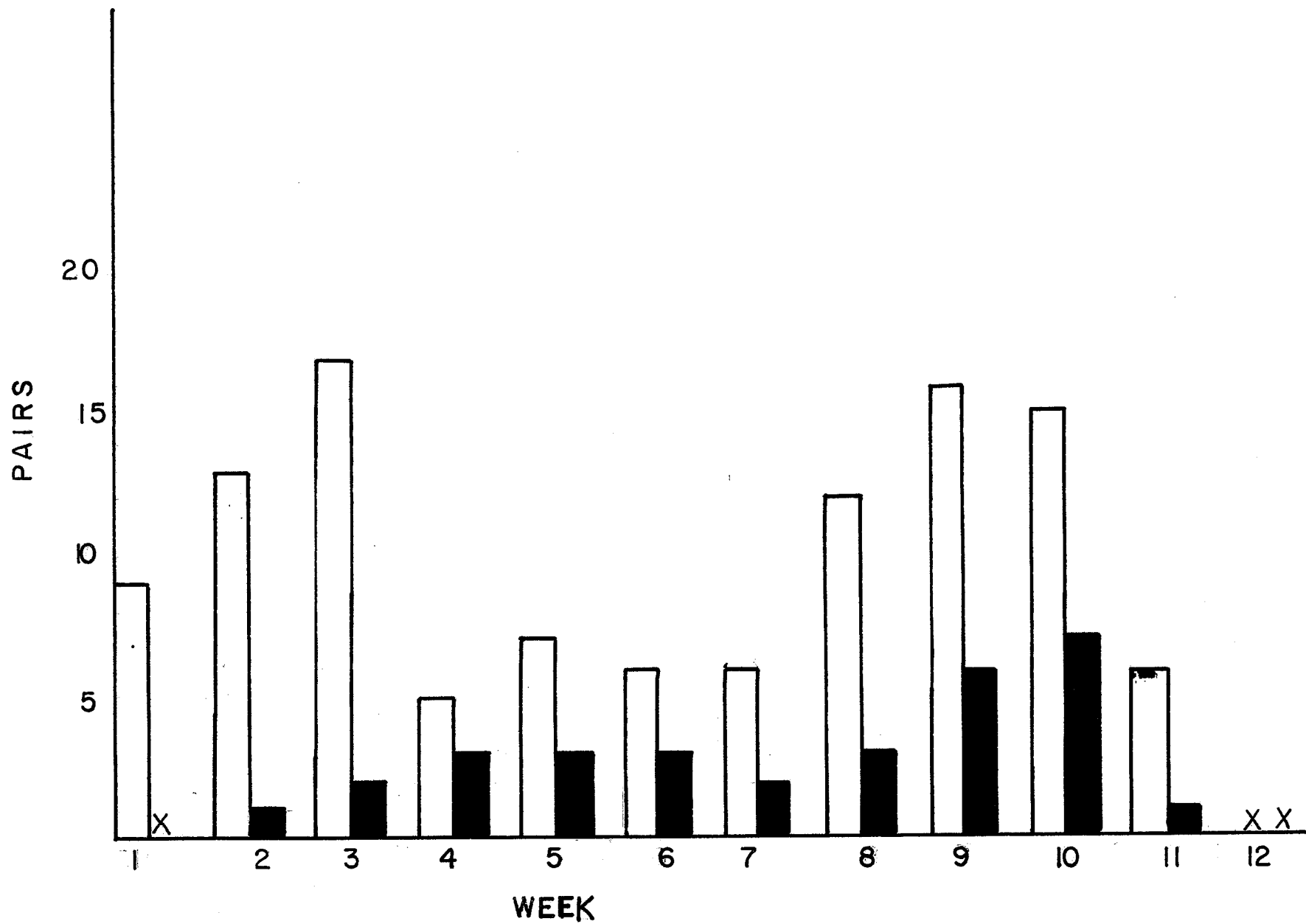
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Figure 1. Territorial and non-territorial pairs
on the study area, 20 Apr. - 5 July, 1970.

non-territorial pairs

territorial pairs

X no pairs



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, ($\chi^2 = 88$, $P < .001$) and for an additional single male ($\chi^2 = 212$, $P < .001$).

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,

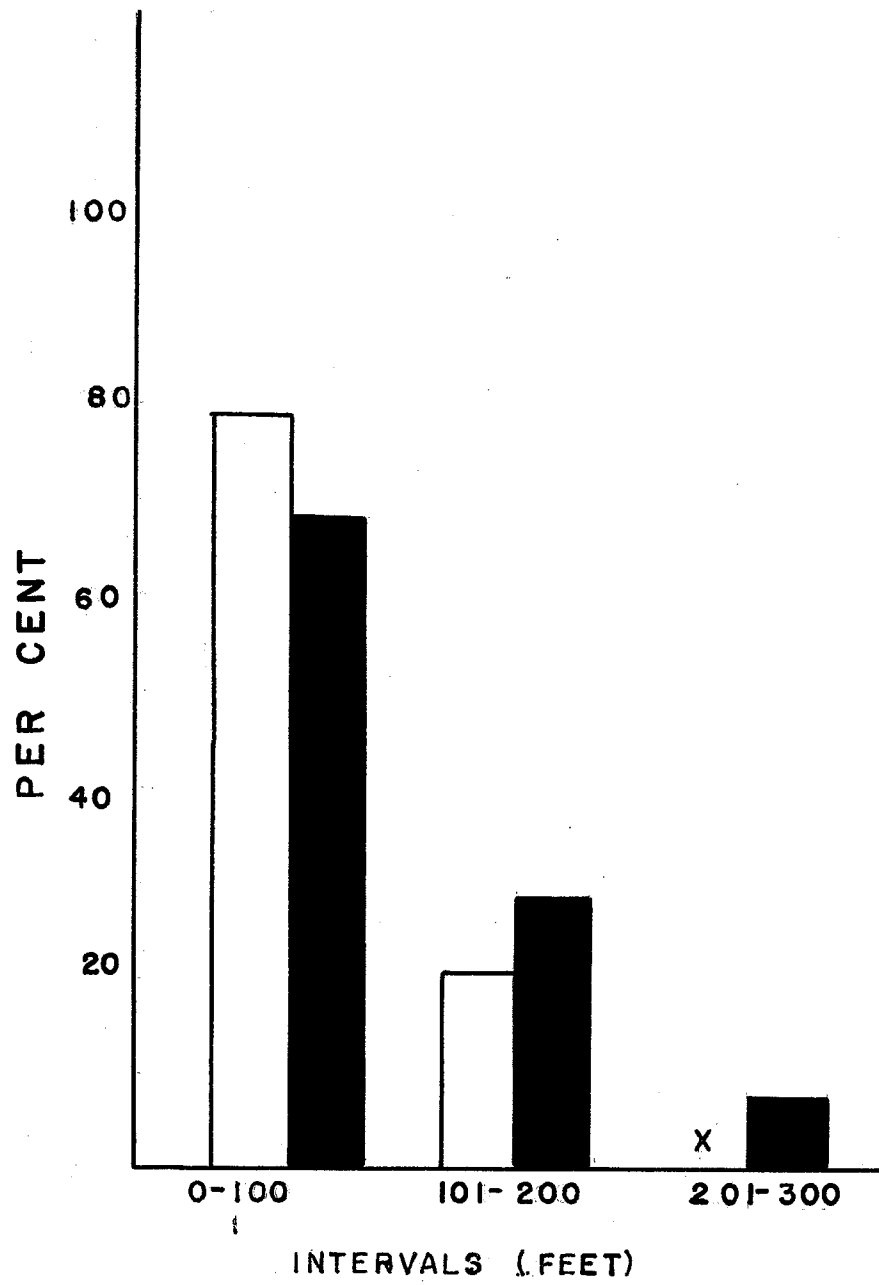
Figure 2. Distance of aggressive interactions from the loafing during laying and incubation, composite of 9 marked males, including 144 aggressive interaction observed over 12 weeks.

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

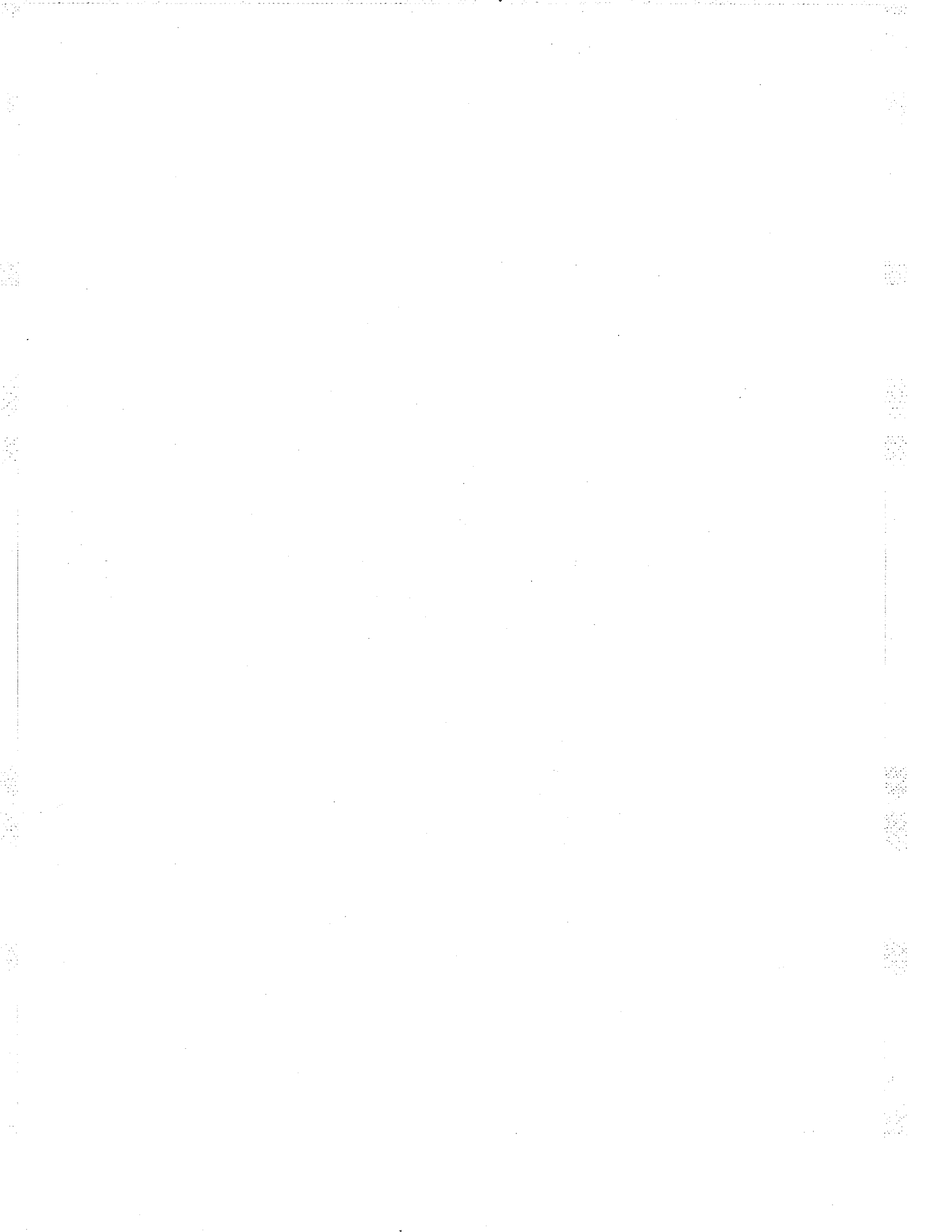


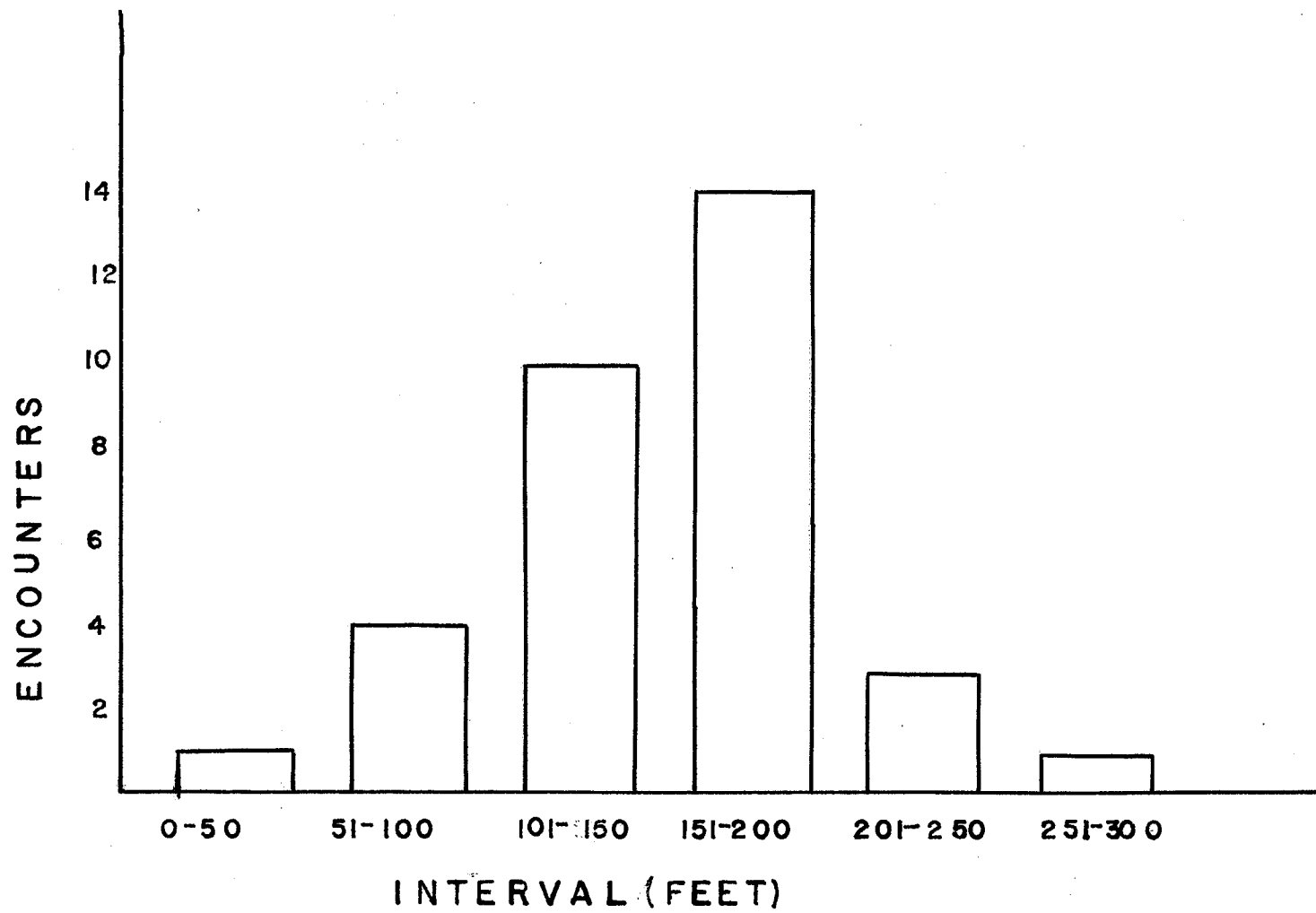
males returned to the territory on 188 (95.5%) occasions, suggesting that the behaviour of the male is related to the physical site also and not just the position of the female.

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 ($\chi^2_{25.7}$, $P < .001$).

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





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.

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

Scale:

○ loafing bar

x nest

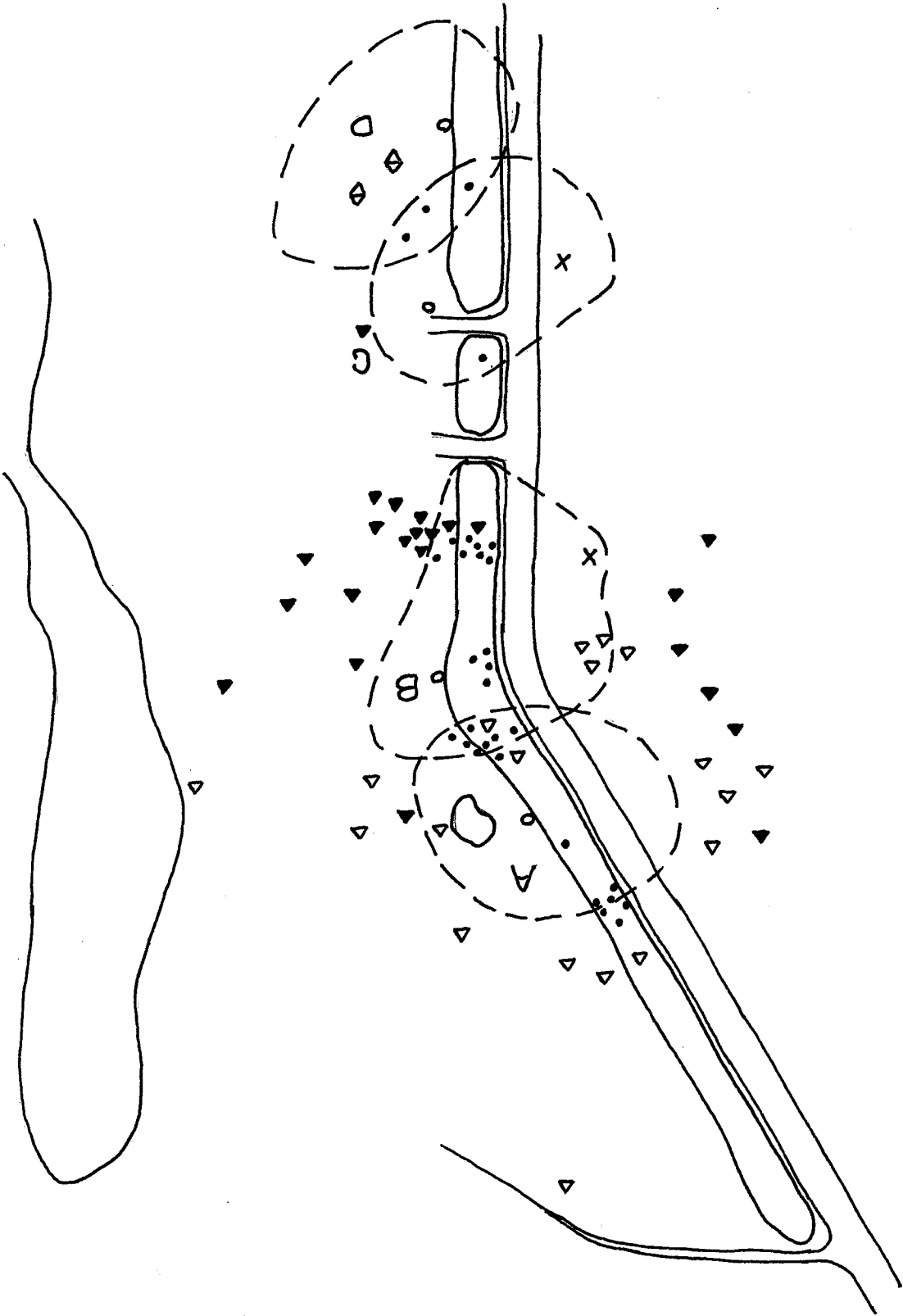
• boundary conflict

---maximum area used

△ End of pursuit, drake A

▲ End of pursuit flight, drake B

◊ End of pursuit flight, drake D



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