

Territorial behaviour of wild Shovelers at Delta, Manitoba

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Territory typically refers to 'any defended area' (Hinde, 1956) and this usage is adhered to in this paper. The status of territory in breeding ducks is less clear than in most other birds. Hochbaum (1944) considered it to be present in all dabbling ducks, but Sowls (1955), Dzubin (1955) and Lebreton (1961) did not agree.

In the Shoveler *Anas clypeata*, published accounts are conflicting. Hori (1963) concluded from his studies of wild Shovelers in Kent, England, that they were non-territorial. Poston (1968) also found little evidence for territorial behaviour near Strathmore, Alberta. 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. Detailed data relating to this behaviour in wild populations appears to be lacking. The present study was designed to obtain such quantitative data on the manner in which areas are defended, and the extent to which such defended areas, as opposed to the undefended portions of the home range, are used by pairs of Shovelers. Data were also collected on the types and frequencies of hostile male behaviour involved in territorial defence.

Study area

The study area lay 2.4 km south of Delta, Manitoba, and was a roadside ditch, 1.9 km long and 10–20 m wide, together with portions of adjacent meadows. The general features of the area in 1970 were essentially unchanged from a description given by Sowls (1955). A 12-week period of observation, 20 April to 10 July 1970, encompassed all known Shoveler breeding activity on the area (Figure 1).

The ditch and water on the adjacent east meadow were connected during the first 8 weeks of observation. The meadow water decreased progressively, however, from 26.8 ha (67 acres) during week 1, to 0.4 ha (1 acre) during week 8. The ditch proper, which became distinct from the drying meadow during week 9, contained water throughout the summer, and was crossed by four small dykes.

Vegetation of the flooded meadow began to emerge during week 5 and covered much

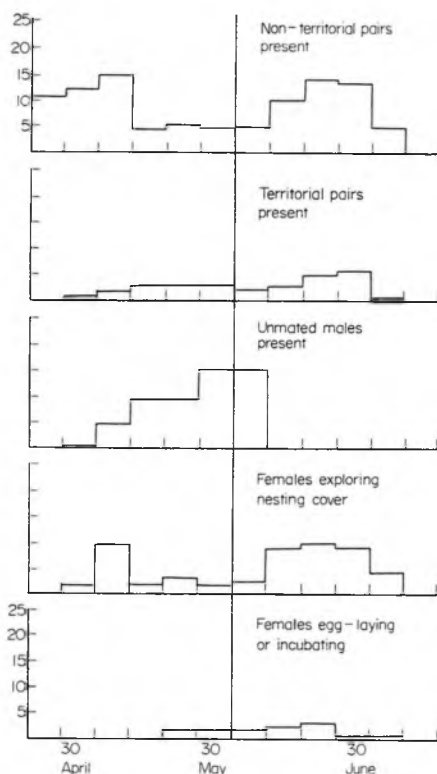


Figure 1. Number of Shovelers present and engaged in different activities during successive weeks during breeding period (20 April–10 July).

of it by week 7. Except for 0.2 km at the north end, the ditch was never clogged with vegetation, although *Typha* sp., *Scirpus* spp. and *Phragmites* sp. did appear in discontinuous patches along the sides of the ditch throughout the summer.

Methods

Seventeen males were trapped by placing a hand-reared captive female in a clover trap of the design described by Lincoln & Baldwin (1929). They were marked with nasal saddles (Bartonek & Dane, 1964) and released at the trap site. Mated males were caught by placing the trap at the male's major loafing spot on the ditch; unmated males were captured in the meadow. In addition, three females were caught on their nests, similarly marked and released.

A car was used to observe the area at the northern and southern limits of the study area, a 6-m observation tower near its centre. Wooden strips were placed at 30-m intervals out from the major loafing spots of males, and at 90-m intervals on the meadow, to enable the location of males to be estimated.

The first count was normally made as soon as the birds could be seen (approximately 05.00 hours) and lasted for 30 minutes. Subsequent counts of the same duration were done at 2-hour intervals, the last being just prior to dark (approximately 22.00 hours). This schedule was followed for 4 or 5 days each week, except the first and last, when it was reduced to 3 days.

In addition, 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 2 weeks from 1 May to 1 July to determine where Shoveler territories occurred.

Breeding chronology

Paired Shovelers began to use the flooded meadow during week 1. These pairs were non-aggressive upon arrival and often sat within 1.5 m of other pairs. Poston (1968) also found that newly arrived Shoveler males showed little hostility. Male threat display increased during week 2, being based on a 'moving territory' (Dzubin, 1955), in which the male defended the mobile female. During week 3, aggression increased further and pairs became isolated from each other.

Unmated males arrived during week 2 (Figure 1). They courted and chased mated females and made jump flights as described by Lebreton (1961) and McKinney (1970). From one to seven unmated males would harass a pair, whose male threatened and chased the intruders. During week 3, of seventeen pairs under observation, twelve began searching for nest-sites on the ditch. Unmated males remained on the flooded meadow at that time, rarely harassing pairs which were using the ditch.

Figure 1 also indicates the number of pairs on the study area that were considered 'territorial' and 'non-territorial' on the basis of evidence presented below. Twelve different pairs resided on the study area over the 12 weeks, the last pair having established themselves during week 10. Non-territorial pairs, apparently searching for suitable breeding sites, were present for periods ranging from 2 days to 3 weeks. There was an influx of non-territorial pairs in weeks 8, 9 and 10 (Figure 1). During week 10 and 11, all but

one nest on the study area was destroyed by predators and most pairs left the area. No new territories were subsequently established.

Aggressive behaviour and territorial defence

Direct observations of localized aggressive behaviour concerned, primarily, ten marked, paired males. Additional supporting evidence for territoriality was provided by observations of 'ritualized fighting' (McKinney, 1967), mainly at the apparent boundaries of defended areas.

Aggression in Shoveler males includes 'hostile pumping' (threat display), 'ritualized fighting', 'chasing', and 'three-bird flights' (see McKinney, 1967, 1970 for descriptions of these behaviours). The last named are referred to throughout this paper as pursuit flights.

'Hostile pumping' and associated calls were elicited in a resident male when an intruder approached the defended area. If the intruder continued into the territory, 'hostile pumping' was followed by 'chasing', then pursuit flights if the intruder did not immediately leave the area. 'Hostile pumping' and calling were also noted, in the apparent absence of other Shovelers, when the male returned to the defended area after pursuing intruders. At these times, he typically sat in the ditch near his loafing spot for 5–10 minutes or longer, often vocalized, and then went to the loafing spot. 'Hostile pumping' was also seen when a male approached a neighbouring territory whether or not the resident male was there.

'Chasing' was done primarily by territorial holders, who typically rushed over the water with the neck outstretched and bill slightly upward, often open, and pointed at the other male. The latter, usually unmated, showed little hostility toward the chaser and generally left the area quickly. 'Chasing' usually gave way to 'ritualized fighting' between holders of contiguous territories (see below).

In the Shoveler pursuit flights appear in part to function in driving away intruders, and hence do seem relevant to territorial defence.

Aggressive interactions were highly localized, occurring mainly in the vicinity of the loafing spot. Table 1 indicates the frequency of male sightings and of aggressive behaviour of resident males in relation to the loafing spot during the entire laying and incubation periods. There were significantly more sightings and hostile encounters close to the loafing spot (0–30 m) both for the com-

Table 1. Location of marked territorial males on their territories and of aggressive interactions between these males and intruders relative to the major loafing spot used

	Distance from major loafing spot		
	30 m	31–60 m	61–90 m
Location of spot sightings of 10 males (481 sightings)	399 (83%)	34 (7%)	48 (10%)
Location of males during bouts of observation (126 hours)	117 (93%)	6 (5%)	3 (2%)
Location of aggression (threat, chasing, ritualized fighting) of 10 males	257 (73%)	89 (25%)	8 (2%)
Location of boundary conflicts	5 (16%)	24 (71%)	4 (13%)

bined data on nine males ($\chi^2 = 88$, $P < 0.001$) and for an additional single male ($\chi^2 = 212$, $P < 0.001$).

The male was most visible to, and best seen by, intruders from either the prominent loafing spot or from the unbroken expanse of ditch. Most intruders approached along the ditch and rarely from the meadow behind. Almost all (95%) hostile displays occurred either at the loafing spot or in the ditch, suggesting that the water area rather than the meadow area was being defended. Prior to pursuit flights, the pursuer was usually on or near the loafing spot. After 264 (99.2%) such flights, the pursuer returned to the territory, usually within 30 m of the loafing point, which further indicates that aggression was territorial in function. Pursuing males whose mates were at the nest returned to the territory on 188 (95.5%) occasions, suggesting that the behaviour is related to the physical site and not just the position of the female. Vocalizing by the female at the nest was not detected during or after pursuits but this may have occurred and influenced the male's return.

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. As indicated in Table 1, most 'ritualized fighting' in the present study occurred in the area of 45–60 m from the loafing bar ($\chi^2 = 25.7$, $P < 0.001$).

Males on contiguous areas appeared to recognize common boundaries. They were to be seen sitting, relatively inactive, for as long as an hour within 3–6 m of each other,

each bird on its own territory. 'Hostile pumping', 'chasing' and occasionally 'ritualized fighting' occurred primarily when one male approached more closely to the other or crossed the common boundary. Such interactions by males with laying or incubating females typically occurred immediately after he had accompanied his mate to the nest-site and returned to the ditch. However, most boundary interactions occurred during the pre-laying period, the time of territory establishment. After the initial boundary interactions, the neighbour's territory was rarely entered whether or not the owner was present. Where boundary conflict had initially been intense, territorial males did not enter contiguous territories even after the neighbouring male had deserted.

Extensive 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) during the pre-laying period are illustrated in Figure 2. Although it is difficult to define exactly the location of boundaries where actual conflicts were not seen, the dashed lines delineate them approximately, on the basis of disputes that were seen (dots in Figure 2) combined with the almost exclusive use by the resident male of the remaining area. More than 70% of 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. Over 90% of encounters occurred on the ditch itself, apparently because most intruders landed there.

Pursuit flight endings are also included in Figure 2. They indicate that pursuits typically ended near, but outside the territory as defined by boundary conflicts *per se*. Pursuit

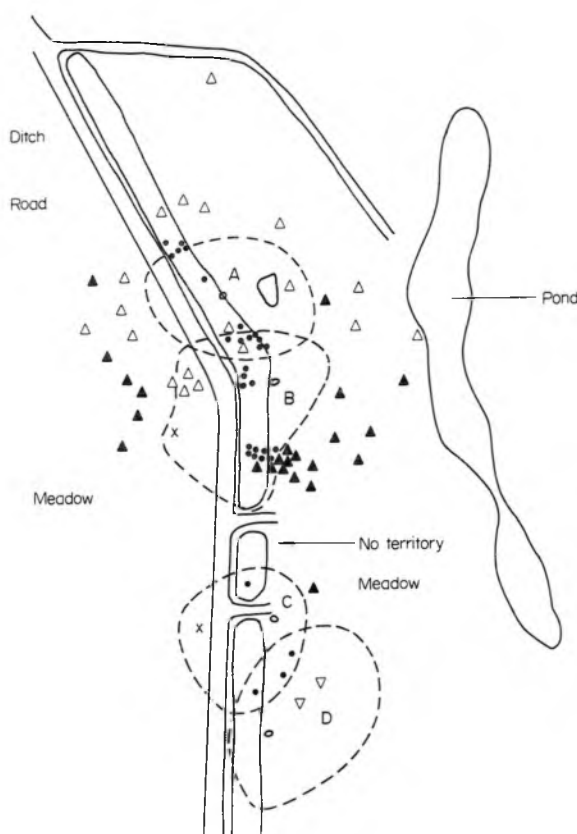


Figure 2. Coincident territories of four Shoveler males (A-D) along a roadside ditch. ---, Limit of area intensively used and defended; ●, disputes between Shoveler males; x, nest of resident female; O, loafing spot of resident male; △, ▲, ▽, end of pursuit flights made by males A, B, C, respectively.

flight behaviour between males A and B provided further evidence that neighbouring males recognize and observe a common boundary between their contiguous territories. These flights typically involved reversal of roles, the pursuer becoming the pursued, when crossing above the boundary line in the ditch.

Territory size

Estimates were obtained of the maximum space defended, actually only a very restricted portion of the total home range used by the pair (Dzubin, 1955). This was illustrated by territorial males which at times range far on pursuit flights.

As shown in Table 1 all defence during the laying and incubation periods occurred within 90 m of the loafing spot, thus making the maximum effective size of the territory approximately 0.9 ha (Table 2). There was

also a vertical component to territory size. Defending males would threaten intruders at more than 90 m (height estimated by comparison to power line poles) but rarely gave chase unless the intruder indicated the intention to land.

Dzubin (1955) observed that territories in the Mallard *Anas platyrhynchos* and Blue-winged Teal *Anas discors* may be larger during the early periods of nesting. A significant difference ($\chi^2 = 13.0$, $P < 0.001$) was also found in the mean area used by Shovelers before and after the onset of egg-laying (Table 2). Observations of three Shoveler males whose mates retained eggs for a considerable time revealed that defence was strong until it ceased abruptly during late incubation.

Territorial males ranged farther from the loafing spot during the early-morning (05.00–10.00 hours) period, apparently because, aggressive interactions, particularly pursuit flights, were triggered at this time by the

Table 2. Comparison of maximum size (hectares) of territories between the pre-laying and laying/incubation periods of ten Shoveler pairs

	Pre-laying	Laying/incubation
Mean area	2.9	0.9
Median area	3.2	0.6
Range in area	1.3–5.0	0.1–1.5

increased movement of non-territorial pairs. When non-territorial pairs were active later in the day, the same phenomenon was observed. Despite the temporal variations in aggression, territories did not change significantly in size as a function of time of day. Dzubin (1955) again reports a similar result for the Mallard and Blue-winged Teal.

There was no significant size difference between four territories established before 8 June and five later territories, despite the fact that the concentration of both territorial and non-territorial pairs on the study area was then greater. This suggests that territorial males do not occupy the largest possible area when pressure from other pairs is low. However, the concentration of pairs on the study area was not sufficiently great to determine this point conclusively.

Stability of territories

Major changes in boundaries did not occur when adjacent territories were abandoned due to nest failure. Stability was also maintained despite frequent hostile encounters between the territorial Shovelers (19% of all encounters observed), and between non-territorial Shovelers and the incumbents. Poston (1968) similarly noted that once established, Shoveler pairs were not displaced by other pairs.

Certain areas were used by successive pairs, rather than being occupied continuously by a given pair throughout the entire breeding season. One striking example of successive use of a portion of the study ditch by three males is indicated (Table 3) in relation to egg laying and nest losses. Duration

on the territory was based on first and last sightings of the male or female of the pair; duration of a male's dominance was based on his success in excluding others.

The importance of the nest was suggested by the almost immediate reversal in dominance between males 2 and 1 following nest loss by pair 1. Dominance may also alter prior to nest loss, however, for male 3 assumed dominance over male 2 about 10 days prior to the loss of the latter's nest, when the pair-bond was weakening and male 2 was spending much less time on the territory.

The use of the territory by the female may be severely restricted by the hostile behaviour of encroaching males. Female 2 did not forsake the territory for at least 6 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 using only a few square metres of water opposite the nest for feeding. Female 3 also used the territory after her mate deserted her, but loafed and fed within a smaller area, approximately 15 m in radius, than she used before her mate's departure. A similar restricted radius of activity was also noted for the only other two females whose nests were still viable when they were deserted by their mates. These observations suggest that the male is essential in maintaining the territory for the female.

Use of territory

In agreement with Poston's (1968) work on wild Shovelers, I found that pairs spent much of their daylight hours on the territory. During the pre-laying period, when the territory was being established, ten pairs spent from 2 to 4 hours on the territory (usually in the period 05.00–09.00 hours) when other pairs searched for nesting sites. They were not on the study area at other times. During late laying and incubation, males of ten 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.

Table 3. Use of the same portion of the ditch by three Shoveler pairs at different times

	Duration of pairs on territory	First egg to nest destruction	Period of dominance
Pair 1	27 Apr.–27 May	15 May–22 May	27 Apr.–23 May
Pair 2	15 May–17 June	1 June–16 June	24 May–6 June
Pair 3	6 June–9 July	12 June–9 July	8 June–9 July

Females spent all of the daylight period on the territory, even in the absence of their mates. Hochbaum (1944) suggested that females may not have observed territorial boundaries at such times, but their activities were none the less localized, usually around the loafing spot. Such females were rarely harassed by territorial or non-territorial males presumably because these males still associated the area with a hostile territorial male.

Discussion

Since Hochbaum (1944) reported territorial behaviour in ducks, several authors have criticized aspects of Hochbaum's conclusions while others state that territorial behaviour does not occur in the Mallard and Shoveler (Lebrecht, 1961; Hori, 1963). These differences of opinion are considered by McKinney (1965) to be due primarily to the dearth of evidence for defended areas. However, for the Shoveler and some other species, McKinney (1965) and Siegfried (1968) state that the concept of territoriality is valid and widely accepted. In agreement with McKinney's (1965, 1967, 1970) work on captive Shovelers, my observations of localized activity (Figure 2) including intraspecific hostility (Table 1) and exclusiveness of the localized area, all show that Shoveler males in a wild population may defend an area which is often contained within reasonably well-defined limits.

Poston (1969), working in a prairie pothole habitat where the concentration of breeding pairs was low, found home range size of Shovelers to be 73 acres (29.2 ha) while Gates (1962), who worked in habitat similar to that found at Delta, measured home ranges of not greater than 20 acres (8 ha). Mean territory size during the laying and incubation periods in the present study, 2.3 acres (0.9 ha), closely resembles Poston's (1969) estimate, based on two pairs, of 1.5 acres (0.6 ha) for the corresponding 'core area'. It seems likely that this confined area, which is not readily reduced by aggressive behaviour of intruders, must be considered the portion of the home range most crucial to reproductive success.

Functional significance of territory

Gates (1962), working with the Gadwall *Anas strepera*, and Poston (1968), working with the Shoveler, discounted hostility, a component of territorial behaviour (Tinbergen, 1957), as a mechanism limiting density of breeding pairs on their study areas. McKin-

ney (1965), however, believed that hostility in the form of aerial chasing, as is seen in the Shoveler, served to produce some degree of dispersion of pairs. 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 (Table 3), and in space as a result of territorial behaviour.

Several hypotheses to explain the function of spacing in ducks have arisen. Hochbaum (1944) theorized that it ensured successful copulation, while McKinney (1967) suggested that it was probably an anti-predator device (see also Errington, 1946; Tinbergen, 1939). Hochbaum, McKinney and Ward (Delta Seminar, 1969) also stressed the importance of food to breeding ducks, as did Geyr (1924) for the Mallard and Siegfried (1968) for the Southern Black Duck *Anas sparsa*.

In the Shoveler, although territorial behaviour does appear to ensure protection for the female from aggressive males, this may be little more than a secondary consequence of territory, as discussed by Hine (1956). Spacing to reduce predation (McKinney, 1965) seems reasonable and cannot be ruled out by the present data. Some resource essential to reproductive success may be defended, thereby justifying the considerable expenditure of energy by the resident male in maintaining the territory. Broods of dabbling ducks are very mobile (Evans & Black, 1955), and presumably feed little or not at all on the territory. However, the adult female may feed there exclusively during the later stages of laying, and for the entire incubation period because they spend little time off the nest (Ward, 1969). Certainly the laying and incubating female Shovelers in the present study fed for much of their time off the nest. The territory then appears to provide a measure of protection for the contained food resource and allow the female to utilize it undisturbed. If so, this would seem to be a reasonable functional explanation for the extended and well-developed territorial behaviour and pair bond of this species.

A further possibility is that an extended pair-bond and associated territorial behaviour might be especially important to Shovelers during re-nesting. Competition for territory sites was keen at this time because of drying of habitat and influx of new pairs. Those which were able to establish territories nested quickly, whereas the females of two non-territorial pairs did not nest at all.

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Summary

The territorial behaviour of wild Shovelers *Anas clypeata* was studied on a 1.9-km long roadside ditch at Delta, Manitoba, Canada. Most of the data used was derived from observations of seventeen marked males and three marked females. Breeding activity on the study area spanned 12 weeks and twelve different territorial pairs were observed. Breeding activity ceased late in the

season partly as a consequence of widespread nest predation.

Aggressive behaviour of territorial males took several forms and contributed to the establishment and maintenance of territories. Such behaviour occurred primarily within 30 m of the focal loafing spot and was not noted further away than 90 m.

Boundaries were well defined only where there were frequent interactions. Defence was primarily of the water area and not the adjacent meadows. There was a vertical component to the territory. The area used by pairs became significantly smaller (0.9 ha) after the onset of egg-laying. Territory size did not significantly change later in the season despite an increased concentration of pairs.

Territories were remarkably stable and no pairs lost territories as a result of hostility. However, stability may break down when the pair-bond weakens with advance of incubation or when the nest is destroyed. Certain areas were occupied by as many as three successive pairs.

Pairs spent virtually all their time on the territory after egg-laying was well advanced. Females still used the territory after dissolution of the pair-bond although their activities were restricted to the area around the loafing spot.

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