

# Spacing and chasing in breeding ducks

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## Summary

The behaviour of breeding ducks is described in terms of the relationship of the pair to its home range and the responses of pairs to one another. There are specific, sex, and seasonal variations in the characteristics of the home range. Interactions between pairs involve five types of response: displays, attack, escape and avoidance, sexual pursuit, sociability. Chasing activities of paired males can be hostile or sexual in nature, the latter involving attempts to rape strange females. The characteristics of aerial pursuits ('three-bird flights' and 'attempted rape flights') of *Anas* species are believed to be determined by variations in the pursuing male's tendencies to (a) stay with or near his mate, (b) attack other males, (c) rape strange females. Male hostility is associated with the existence of a strong pair-bond; raping is associated with a weak bond. A typical 'three-bird flight' results from conflict between the pursuing male's tendency to chase the female of a strange pair (with intent to rape and/or possibly attack her) and his tendency to remain near his mate.

Parts of the home range of each pair are shared with other pairs. Where a shared resource is localised in distribution, such as an island suitable for nesting, pairs tend to aggregate. Colonial nesting develops as a result of strong homing tendency in adult and young females, and high productivity in an area with light predation. The behaviour of a number of species appears to be adapted to the various types of resource-sharing required in different habitats.

Chasing activities – both hostile and sexual in nature – are believed to bring about dispersion of various types. In a species with a small home range, a high level of hostility, and a strong pair-bond (e.g. Shoveler), a pattern close to classical 'territorialism' is apparent. In more mobile species, there is much overlapping of ranges and the degree of dispersion of pairs (and resulting dispersion of nests) can vary considerably with local conditions.

The primary function of chasing and the spacing resulting from it is thought to be the dispersion of nests as an anti-predator mechanism.

## Introduction

Ducks are primarily social birds but during at least part of the breeding season pairs of many species show a tendency to spread out over the nesting habitat. Chasing behaviour often coincides with the break-up of flocks and the period during which pairs are dispersed. The occurrence of both spacing and chasing is well established for many species, but the survival value of these phenomena and the behavioural mechanisms involved are still uncertain.

In 1924, Geyr von Schweppenburg suggested that certain aerial chases of the Mallard *Anas platyrhynchos*, described originally by Heinroth (1911), represent attempts by a paired male to drive off other pairs from the nesting area. He believed that such behaviour helps to preserve an exclusive breeding area for each pair, ensuring an adequate food supply for the young. Although Geyr's interpretation of Mallard pursuit flights has been questioned by several authors, and his paper provided the stimulus for a long controversy on all types of aerial behaviour, the idea that ducks are territorial has come to be widely accepted. This is particularly true in North America where the territory concept provides the basis for 'the breeding pair count' method of censusing populations. The major credit for development of the theory of duck territory must go to Hochbaum (1944), who stressed the importance of the phenomenon in the species breeding on the Delta Marsh in southern Manitoba.

Hochbaum applied to ducks the theory of territory propounded in detail by Howard (1907–14, 1920) and subsequently developed by other ornithologists, especially Lack (1939), Nice (1943) and Tinbergen (1939). 'Territory' was defined, in the same way as it is today, as 'a defended area'. Hochbaum contended that each paired male defends a certain stretch of water against intrusion by other sexually active birds of the same species, the main function of this behaviour being to prevent interruption to the pair 'during the copulation link of the reproductive cycle'. Hochbaum believed that 'the nesting population of any breeding marsh is determined by the territorial distribution of pairs'.

Subsequent research by Sowls (1955) and Dzubin (1955), on individually marked birds, showed that Hochbaum's original conception of territory was too rigid. There are not always 'definite boundaries to defended areas' and the home ranges of neighbouring pairs often overlap. Recent studies by Lebet (1961) and Hori (1963) on the Mallard have indicated that aerial pursuits, of the type called 'territorial defense flights' by Hochbaum, sometimes occur away from the nesting grounds. As a result of this discovery, Lebet has suggested that the term 'territory' should not be applied to the Mallard, while Hori believes that neither the Mallard nor the Shoveler *Anas clypeata* holds territory. Bezzel (1959) has also criticised Hoch-

baum's theory, concluding that 'the territory plays a small part in the structure of a breeding population'. Gates (1962) believes that in the Gadwall *Anas strepera* territorial behaviour was ineffective in limiting the number of pairs nesting on his study area in Utah.

These findings appear to cast considerable doubt on the validity of the concept of duck territoriality. In fact, however, the main criticisms have been directed at (a) the use of the word 'territory' where evidence for a *defended area* is not obvious, and (b) the idea that behaviour involved in the defence of an area has an important effect on the density of breeding populations. Thus much attention has been given to inquiring whether and how ducks 'defend areas' and how chasing behaviour (especially aerial pursuit) is related to such areas. The broader biological problems of pair-spacing – the pattern of pair distribution on the breeding grounds, the mechanisms by which this is achieved, and the survival value of the different patterns found in different species – have received less emphasis.

As Tinbergen (1957) has stressed, it is important to distinguish between the components of what we call 'territorial behaviour'. In most birds these appear to be (a) attachment to a site and (b) hostility, two distinct forms of behaviour which, when they occur simultaneously, give the impression of 'defence of an area'. It seems best to avoid 'a purely speculative assumption that the area carries special significance to the bird as an object to be defended' (Emlen, 1957).

In this paper, I will discuss the factors which appear to be involved in pair-spacing in those species of duck which have been studied in some detail. I have avoided the words 'territory' and 'defence' except in referring to the ideas of other workers. In this way, I hope to concentrate attention on 'doings and happenings rather than objects and entities' (Emlen, 1957).

#### **The pair and its home range**

During the main part of the breeding season – egg-laying, incubation, and rearing of the brood – female ducks must restrict their movements to an area quite close to the nest-site. For at least part of this period, the male occupies approximately the same region. Sowls (1955) called this area the 'home range', a term previously applied to mammals, defining it as 'the area within which a bird spends its period of isolation between the break-up of spring gregariousness following spring arrival and the reformation of fall gregariousness'. During this 'period of isola-

tion', however, there are seasonal changes in the relationship of each duck to the area it occupies, and there are also important differences between the ranges of males and females. In some species, the places visited by each bird probably change to some extent from day to day, and many factors influence the location, size, and permanence of the various 'ranges' occupied successively by each individual. An understanding of these changing relationships between the members of the pair and the areas they occupy is fundamental to the study of pair-spacing. Unfortunately, only a few studies of marked birds have been made, and surprisingly little is known about the daily movements of individual ducks during the breeding season.

#### **Homing**

Tendencies for adult females to return to breed in the same area in successive years and for young females to breed close to the area in which they grew up have been demonstrated for a number of species and are probably general in ducks. In hole-nesting species such as the Goldeneye *Bucephala clangula* (Siren, 1957), Bufflehead *Bucephala albeola* (Erskine, 1961), Wood Duck *Aix sponsa* (Bellrose, Johnson and Meyers, 1964), and Shelduck *Tadorna tadorna* (Hori, 1964) some females have been shown to use the same site in successive years. Mendall (1958) believes that Ring-necked Ducks *Aythya collaris* will also do this but, as Bellrose *et al.* (*loc. cit.*) have shown for the Wood Duck, an unsuccessful nesting attempt may cause a bird to choose a different site the following year. The Eider *Somateria mollissima* also shows faithfulness to the nest-site (Gudmundsson, 1932; Cooch, 1957) but other ground-nesters select new sites each year (Koskimies and Routamo, 1953; Sowls, 1955).

In most migrant ducks, precise homing by males is thought to be a rare event, but there is little direct evidence since few males are banded on the breeding grounds. Most pairs are formed on the wintering grounds or during spring migration, the bonds being broken again when the male leaves his mate in the middle of the breeding season. (It is possible that some pair-bonds remain intact through the summer when a female loses her clutch and does not attempt to re-nest, but this has not been proved with marked individuals). Thus unless the members of the pair meet again on the wintering grounds or at some stopping place on migration they must form a new pair-bond each year. Many birds from a particular section of the breeding range tend to follow similar

migration routes and winter in approximately the same areas, but nothing is known of the frequency with which mates reunite. No doubt there is much variation between species and between populations. Some re-pairing of the same individuals occurred in a resident population of Mallards (Weidmann, 1956). In a captive flock of Shovelers, some birds re-paired while others deliberately chose new mates (McKinney, in prep.). Erskine (1961) has shown that male Buffleheads tend to return to the same wintering areas in successive winters, and if their mates are faithful also to these places, pair-bonds could be renewed. On present evidence, however, it is likely that most ducks change mates annually, females returning to a familiar home range, males following their mates to an unfamiliar breeding area each year.

Sea Ducks (*Mergini*) do not breed in their first year, but sub-adults are seen on the breeding grounds and presumably youngbirds gain valuable experience during their period of maturation. In Anatini, young birds do breed in their first spring, but they have several disadvantages. In plumage development and time of pairing, young Shovelers lag some weeks behind adults, and they tend to be less successful in competitive pairing situations (McKinney, in prep.). In the Pintail *Anas acuta* (Sowls, 1955) and Gadwall (Gates, 1962), adult females return early to their breeding home ranges, young birds arriving later. Under crowded conditions, late arrivals may have to move some distance from the area with which they are most familiar. Thus experienced, adult ducks probably have 'first choice' of mates and of home ranges, and in general adult females will have the greatest familiarity with the breeding home range.

When breeding habitat deteriorates or disappears, homing traditions are broken and pairs must establish new home ranges. This is a rare event in Eiders, colonies remaining on the same islands for centuries, but it is a common phenomenon in species dependent on water areas in regions which fluctuate between conditions of drouth and flood. The drying-up of a pothole may cause a pair to move only a few hundred yards, but widespread drouth on the North American prairies or over wide areas in Australia can cause massive movements of breeding populations (Frith, 1959).

#### **The pre-nesting period and nest-site selection**

The interval between arrival in the general vicinity of the breeding area and the beginning of nesting varies between species

and also in accordance with variations in weather and habitat conditions. The Mallard and Pintail are early spring migrants and early nesters, and in southern Manitoba laying normally begins soon after the break-up of migrant flocks (Hochbaum, 1944; Sowls, 1955). In the Gadwall, however, Gates (1962) found that an interval of a month may elapse between the arrival of residents and the laying of the first eggs.

There is little information on the movements of pairs during this pre-nesting period. In many species, it is difficult to distinguish returning residents from migrants on passage. Limited observations on marked Canvasbacks *Aythya vallisneria* by Dzubin (1955) and on Gadwall by Gates (1962) suggest that pairs are more mobile during the period before nesting than after breeding begins.

Pairs assumed to be involved in selecting a home range or a nest-site are seen making flights over the nesting terrain. Hochbaum, (1944) saw 'nuptial flights' performed by pairs of all species of *Anas* and *Aythya* that he studied, and it seems likely that these are, at least in part, reconnaissance flights. Sowls (1955) noted Mallard and Pintail pairs making evening flights over nesting cover a few days before egg-laying began. Mendall (1958) suggests that aerial reconnaissance by Ring-necked Duck pairs occurs mainly during the period between arrival and the beginning of nest-site selection, which may be as long as two weeks. Smith (1963) describes 'exploratory flights' in Pintail pairs, and similar manoeuvres occur in the Velvet Scoter *Melanitta fusca* (Koskimies and Routamo, 1953) and Common Eider (Cooch, 1957; McKinney, 1961).

In species which nest some distance from water, parts of the habitat suitable for the nest-site are presumably selected during these reconnaissance flights. The final selection of the site is made on foot in the case of ground-nesters, by swimming in species using emergent vegetation, and by flying from tree to tree in the case of hole-nesters (see descriptions in Hochbaum, 1944; Mendall, 1958; Leopold, 1951). In all species studied to date, the male accompanies the female during her exploration of potential nest-sites. I have found no precise information on the area covered by a pair of any duck species during this period of pre-nesting flights.

#### **Nest-construction and laying**

In the Canvasback (Hochbaum, 1944), Redhead *Aythya americana* (Low, 1945), Blue-winged Teal *Anas discors* (Glover, 1956), and other *Anas* species (Sowls, 1955) nest-construction may begin several

days to a week before laying starts. Information is scanty, however, and it is quite possible that some individuals select the site, scrape the nest-bowl, and lay the first egg, all on the same day. Eggs are usually laid in the morning hours, the male remaining in the vicinity while the female is at the nest. At this stage, the pair-bond is still very strong and Hochbaum (1944) noted that males may have special waiting places close to the nest.

Dzubin (1955) found considerable specific differences in the ranges occupied by Canvasback, Mallard, and Blue-winged Teal pairs during the pre-nesting and laying phases, the Canvasback being most mobile, the Teal least.

#### Range during incubation

Once the female begins to incubate, the male sees her only for short periods when she leaves the nest. Most species have one or two such periods each day, when the female feeds, bathes and preens. (Incubating Eiders do not feed; the female leaves the nest only briefly at 2 or 3-day intervals, to drink). Especially during morning and evening hours, males spend much of their time on certain water areas - 'waiting areas' (Dzubin, 1955), where dry-land 'loafing spots' (Hochbaum, 1944) are used by many species. It is to one of these places that the female flies when she comes off the nest. If the male is there, the two birds remain together until the female returns to the nest. The pair-bond remains intact only as long as the male frequents these areas.

Females seem to travel no farther than is necessary when they leave the nest. Ground-nesters often fly to the nearest water, and this is where many male 'waiting areas' are situated. There are variations in the distances involved, some species such as the Pintail nesting much farther from water than others. The distance between nesting cover and feeding grounds also varies with local conditions (Bezzel, 1959; Gates, 1962).

There are specific differences in the mobility of paired males during the incubation period. In Manitoba pothole country, Dzubin (1955) found that drakes of Canvasback, Mallard, Pintail, and Red-head ranged widely during the incubation period but Blue-winged Teal did not. At Ogden Bay, Utah, Smith (1955) and Gates (1962) noted that Mallard ranged most widely, Cinnamon Teal *Anas cyanoptera* and Shoveler least, while Gadwalls were intermediate in range. In Maine, Mendall (1958) found that Ring-necked Ducks have a much smaller range than Black Ducks *Anas rubripes*.

#### Break-up of the pair

Dzubin (1955) found that the drake Mallard's range increases once his mate has begun to incubate and he gradually spends less and less time at the waiting areas. So the members of the pair meet less often, and the pair-bond appears to become progressively weaker until it is finally broken when the male moves away. The break-up may be more abrupt in other species, but there is little precise information on this point.

The stage of the breeding cycle at which the male breaks off contact with his mate varies between species (Table I), and there are also considerable individual variations (e.g. Stotts and Davis, 1960). In most species, the male leaves at some stage during incubation. During late nestings or re-nesting attempts, the male leaves earlier than in the case of early nests.

Striking effects of the chronology of the breeding season have been noted by Alex Dzubin (*in litt.*). He reports that in the early mild spring of 1958 in southern Saskatchewan, when Mallard broods began to appear by 15th May, he recorded 15-20 cases of males accompanying broods; in most years, when hatching peaked after 25th May, only 1-3 records were obtained.

Since most ducks will re-nest if the first clutch is lost, the stage at which the male deserts his mate may have an important effect on the female's behaviour between nesting attempts. If the male has left, as must often be the case in species where the bond breaks early, the female must either find a new mate or be fertilized by a male other than her mate. Re-pairing with a new mate has been recorded for Gadwall (Gates, 1962) and Pintail (Smith, 1963). In species such as the Shoveler, in which the male remains until late in incubation, the original pair-bond is probably maintained through all nesting attempts.

#### Range of the female and brood

After the ducklings leave the nest, the factors controlling the female's mobility change. She is no longer tied to the nest-site and its immediate surroundings, but as she leads her brood her movements are now restricted to ground and water surfaces. In some cases, the areas frequented by the female and brood are close by the nest site. Mendall (1958) noted that some Ring-necked Duck families spent the entire rearing period within an area a few hundred yards long, provided adequate food and cover were available and there was no disturbance. Other Ring-necks, which nested on small marshes, had to lead their ducklings a mile or more to suitable habitat.

**Table I. The stage of the breeding cycle at which the pair-bond breaks.**

<i>Species</i>	<i>First week of incubation</i>	<i>Mid-incubation</i>	<i>Last week of incubation</i>	<i>After hatching</i>
<i>Anas acuta</i>	X <sup>3,6,13</sup>			
<i>Anas platyrhynchos</i>	X <sup>3,6,8,13</sup>	X <sup>2</sup>	Rare <sup>2</sup>	Rare <sup>15</sup>
<i>Anas rubripes</i>				
early nests:	X <sup>6,13</sup>	X <sup>4</sup>	X <sup>4</sup>	
late nests:	X <sup>14</sup>	X <sup>14</sup>		
<i>Anas strepera</i>				
early nests:		X <sup>4</sup>	Rare <sup>4</sup>	
late nests:	X <sup>4</sup>			
<i>Anas discors</i>		X <sup>2</sup>	Rare <sup>2,3,6,13</sup>	
<i>Anas cyanoptera</i>			X <sup>12</sup>	
<i>Anas clypeata</i>			X <sup>5,6,10,12,13</sup>	Once <sup>12</sup>
<i>Aythya vallisneria</i>	X <sup>6</sup>	X <sup>2</sup>		
<i>Aythya americana</i>	X <sup>6</sup>			Once <sup>6</sup>
<i>Aythya collaris</i>				
early nests:			X <sup>11</sup>	
late nests:	X <sup>11</sup>			
<i>Aythya affinis</i>		X <sup>6</sup>		
<i>Aix sponsa</i>				
early nests:			X <sup>1</sup> X <sup>9</sup>	
late nests:	X <sup>9</sup>			
<i>Melanitta fusca</i>	X <sup>7</sup>			
<i>Oxyura jamaicensis</i>				X <sup>6</sup>

<sup>1</sup> Dixon, 1924; <sup>2</sup> Dzubin, 1955; <sup>3</sup> Evans and Black, 1956; <sup>4</sup> Gates, 1962; <sup>5</sup> Girard, 1939; <sup>6</sup> Hochbaum, 1944; <sup>7</sup> Koskimies and Routamo, 1953; <sup>8</sup> Lebreton, 1961; <sup>9</sup> Leopold, 1951; <sup>10</sup> McKinney, unpublished; <sup>11</sup> Mendall, 1958; <sup>12</sup> Smith, 1955; <sup>13</sup> Sowls, 1955; <sup>14</sup> Stotts and Davis, 1960; <sup>15</sup> Dzubin (*in litt.*).

On pothole nesting terrain, where many water areas of different types are located close together, families regularly make overland crossings of several hundred yards. Evans, Hawkins and Marshall (1952) reported specific differences in the mobility of broods on the Minnedosa pothole country of Manitoba: Pintails moved most, Ruddy Ducks *Oxyura jamaicensis* did not move, while other species of *Anas* and *Aythya* moved varying distances during the course of the brood period.

In some species, spectacular travels are undertaken by very young ducklings. Leopold (1951) observed newly-hatched Wood Ducks being led across the Mississippi River to secluded feeding areas. Allowing for the current, the families had to swim a distance of about three-quarters of a mile, and they accomplished the trip in about 20 minutes. The Eiders of the Inner Farne lead their young ducklings across 1½ miles of open sea to the mainland coast of Northumberland, where they spend the rearing period. Black Duck broods hatched on Ile aux Pommés, Quebec make a crossing of 3½ miles to the mainland shore of the St. Lawrence immediately after leaving the nest (Reed, 1964). Dzubin (*in litt.*) has records of

newly-hatched Mallard broods moving 3 miles and 3½ miles in two days.

#### Exclusiveness of the home range

Except in the case of very isolated pairs, home ranges are shared to varying degrees with other members of the same species. The greatest overlap is probably found in the colonial-nesting Eiders, in which areas used for feeding, resting, nesting, and brood-rearing are occupied by many birds at the same time. Most species of ducks freely share brood-rearing areas. In some species, such as the Gadwall (Hammond and Mann, 1956) and Black Duck (Stotts and Davis, 1960) nesting concentrations are found on islands, and in these situations there is much overlap. In *Aythya* species, such as the Canvasback (Dzubin, 1955) and Ring-necked Duck (Mendall, 1958), several paired males may share the same waiting areas while their mates are incubating. Among the *Anas* species which have been studied, the home ranges of Shoveler pairs probably overlap the least, as a result of the energetic chasing activities of paired males (see pp. 93-4). Even favoured loafing spots may be shared by pairs of Gadwall, Mallard and Blue-winged Teal, being occupied by different pairs at different times (Sowls, 1955; Dzubin, 1955; Gates, 1962).

### The behaviour of the pair in relation to other birds

Social responses appear to play an important role in determining patterns of pair-spacing. In attempting to understand the pattern found in each species, it is particularly important to know how pairs behave when they encounter other birds, how the behaviour varies with the stage of the breeding cycle, and how the encounters are related to the components of the home range occupied by the pair.

### Types of response

Five types of response can be distinguished when pairs come in contact with other ducks: (a) visible and/or audible displays, (b) attack, (c) escape and avoidance, (d) sexual pursuit and/or rape, (e) sociability.

There is strong circumstantial evidence that certain displays of paired males are expressions of hostile tendencies and that they have threat function. Hochbaum (1944) noted the association of the male Canvasback's 'Sneak' with hostility. Similar postures, with the neck stretched forward over the water, are seen in male Goldeneyes and Buffleheads immediately before an underwater attack. Hostile Pumping in the Blue-winged Teal and Shoveler is closely linked with aggression. The threat function of these displays is indicated by the observed avoidance responses in other birds. No doubt other species have similar displays, but although there may be evidence that the performing bird has a tendency to attack, threat function is often more difficult to prove e.g. 'Rab-rab' palaver of the Mallard (Weidmann, 1956), Cooing-movements of the Eider (McKinney, 1961).

Overt attack and escape are commonly observed in paired ducks. Attack behaviour patterns vary greatly in intensity and duration, from momentary intention movements to prolonged pursuits. Chasing can occur on land, over the surface of the water, underwater, and in the air, but there are variations from species to species. In certain highly aquatic species (e.g. *Aythya* species, Ruddy Duck) showing a relatively low level of aggressiveness, encounters generally involve at most a rush across the surface of the water. At higher intensities, a short attack flight can occur, and in the Shoveler vigorous aerial pursuits are seen. Underwater attacks are performed by aggressive male Goldeneyes and Red-breasted Mergansers *Mergus serrator*. The response to an attack is usually retreat by the other bird, but occasionally this does not occur and fighting ensues.

Inter-specific hostility is rare. It occurs in Barrow's Goldeneye *Bucephala islandica*,

males threatening and chasing a variety of other species (Myres, 1957; personal observation). Generalised aggressiveness toward other birds is also shown by some incubating ducks and by females with broods, but only when they are approached closely.

The role of 'avoidance', in the sense of an active search for isolation from other birds, is very difficult to assess. Mendall (1958) has observed pair-spacing in the Ring-necked Duck without obvious hostility, but the possibility should not be ruled out that this results merely from 'retreat without being involved in a hostile encounter'. Avoidance of this type may well be a common phenomenon in many species. It is possible to find an 'isolated pair' of a certain species, and breeding populations may be so thinly distributed that pairs seldom encounter other members of the same species. But the factors responsible for such situations are unknown. In some years, only a few Green-winged Teal *Anas crecca carolinensis* breed on an area of the Delta Marsh occupied by hundreds of Blue-winged Teal pairs. This pattern of distribution could result from precise homing by a few females during a period of low population numbers, rather than a deliberate attempt by these pairs to isolate themselves.

Aggressive behaviour is identified on the basis of the movements involved and the result of the encounter. Rushes across the water or aerial pursuits involving two males, or intention movements of advancing performed by a female toward a strange male clearly fall into this category. Similar activities performed by a paired male and directed toward a strange female present a different problem. Some of these chases end in rape of the strange female. I have records of rape in the Mallard, Pintail, Gadwall, Shoveler, Blue-winged Teal, Cinnamon Teal and Baldpate *Anas americana*. Very often, however, these chases end inconclusively; the male chases for some distance and then gives up. In other species, in which rape has not been recorded (e.g. Lesser Scaup *Aythya affinis*), paired males make rushes toward strange pairs on the water, directing their attention to the female. In these cases, it is very difficult to determine whether the male's intention is rape, attack, or a combination of the two. Some authors (e.g. Weidmann, 1956; Bezzel, 1959) believe that all such chases in the Mallard are sexually motivated; Lebret (1961) believes that some chases 'have no other source than intolerance' while others are the result of an attempt to rape (see pp. 93-4).

In most species, pairs are sociable during

spring migration and immediately after arrival on the breeding grounds. Flocks break up when pairs begin to establish their home ranges. At the same time, aggressive or sexual chasing appears in many species, and these activities clearly conflict with sociability. The balance between these opposing tendencies – to associate with other birds and to chase them – is different in various species. At one extreme, Eiders remain sociable even during the selection of nest-sites, pairs walking about close together with only mild indications of hostility. Male Shovelers, on the other hand, remain intolerant of the approach of other Shovelers until late in the incubation period. Dzubin (1955) noted one form of 'compromise' in Blue-winged Teal pairs which he believed were distributed in 'communities'; although hostile encounters were frequent, the strife did not seem to discourage community gatherings. In most species of *Anas* and *Aythya*, paired males begin to associate in groups, for parts of the day at least, soon after incubation begins.

#### **Responses on the wintering grounds and during spring migration**

In many species, it is known that aggressive behaviour accompanies the process of pair-formation which takes place several weeks or even months before the breeding season begins. Males are aggressive toward other males, and females threaten males which they are rejecting. These responses continue after the pair-bond is formed, both male and female making threat movements or chasing unpaired males which show an interest in the female. The details vary from species to species, but the pattern is basically the same in all ducks that I have watched. Such behaviour is usually referred to as 'defense of the mate' or 'mated female distance' (Koskimies and Routamo, 1953).

Hostility between pairs can also occur both on the wintering grounds and during spring migration. This was a common reaction between pairs of Blue-winged Teal and Shoveler that I watched in Louisiana in March, before the birds started on their northward migration. I have seen similar behaviour among newly-arrived pairs of Shovelers and Canvasbacks at Delta in late April. I have also seen intense hostility among Common Goldeneyes as early as mid-April in Manitoba, males driving other birds away from stretches of ice-free water to which they were temporarily confining their activities. (I do not know if these birds stayed to breed nearby, but I suspect that they did not). In contrast, Hochbaum (1944: p. 43)

was impressed by the absence of friction in migrant flocks of Mallard, Pintail, and Lesser Scaup pairs at Delta. This could reflect true specific differences, but temporarily reduced hostility might also be expected in tired migrants and in response to cold weather. A cold snap in early spring brings aerial chasing to a halt in Mallards, when pairs are forced to congregate on small open-water areas (Dzubin, *in litt.*).

Lebret (1961) has observed chases by a paired male directed at the female of another pair in European Teal *Anas crecca crecca* and Pintail during spring migration, before the birds had reached their breeding grounds. These chases had the same appearance as Hochbaum's 'territorial defense flights' (see p. 93).

#### **Responses of the pair on the breeding grounds**

(a) Behaviour toward unpaired males. Paired males continue to show hostility toward unpaired males after arrival on the breeding grounds, and in general this response seems to persist as long as the pair-bond remains intact. Again there are specific and individual variations which have not been studied in detail. Sometimes a lone male is tolerated close to a pair. Hochbaum (1944: p. 70) distinguished two types of unmated males, those which are 'sexually active' and those which are not ('novice drakes'), and he believed that the latter are tolerated while the former are driven off by paired males. There have been no studies of marked birds and this point needs further investigation.

(b) Behaviour toward other pairs. Most studies of interactions between breeding pairs have been made on *Anas* species, and almost all attention has been concentrated on the aerial pursuits which are so striking in this group. These are discussed below, but I will first refer to the characteristics of encounters on the water which are important in many species.

In spite of their strongly social habits, Eider pairs engage in frequent mildly hostile encounters: both sexes give displays, make threatening movements, and males in particular peck at males of other pairs when groups of pairs come close together on land or on the water. In the Canvasback and Lesser Scaup, similar encounters occur between swimming pairs, but in most cases males seem to direct their attention to the female of another pair. These chases seldom involve more than short rushes across the surface of the water and chasing males rarely take to the air. Aerial pursuits appear to be absent also in the European Pochard *Aythya ferina* and Tufted Duck *Aythya fuligula* (Bezzel,

1959). In the Ring-necked Duck, Mendall (1958) noted very little aggression between pairs; it was apparent only in crowded habitats and was confined to the period of nest-site selection. Hostile encounters between pairs are frequent and often energetic in Barrow's Goldeneye (Munro, 1939), Bufflehead (Munro, 1942), and American Goldeneye (personal observation). In these species, males direct their threat postures and underwater attacks toward other males; at times they will take wing, flying short distances to attack.

In the Shoveler and Blue-winged Teal, paired males on their home ranges usually react to the appearance of swimming birds of the same species (pairs, solitary males or females) by giving Hostile Pumping, swimming toward the intruder(s), and if necessary by chasing with a rush across the water or an aerial pursuit. When two well-matched males meet on the water and neither retreats, spectacular fights occur, the birds thrashing around one another with circular manoeuvres.

The most obvious feature of encounters between pairs in many *Anas* species are the aerial pursuits. Most observers have distinguished two types:

(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. This descriptive term was first used as an adaptation of 'three-bird chase' (Dzubin, 1957) at the 1958 Delta Seminar, and it has since been adopted by Hori (1963). These flights have been called 'Vertreiben' by Geyr (1924), 'territorial defense flights' by Hochbaum (1944), and 'expulsion flights' by Lebret (1961).

(ii) *attempted rape flights* (1957 Delta Seminar; Lebret, 1961) 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 was forced to the ground.

The distinction between these flights, their relationship to other aerial behaviour patterns, and the motivation of the pursuing male(s), have been subjects of argument for many years and there are still conflicting opinions (for references see Geyr, 1961; Lebret, 1961). Recent studies on the Pintail (Smith, 1963) and Shoveler (McKinney, in preparation) suggest that a comparative approach may be helpful in elucidating these problems.

During the period when aerial chases occur (pre-laying, laying, and incubation

phases), paired males are observed in four basic types of 'social' activities: (a) accompanying the mate (or remaining nearby while she is at the nest), (b) behaving aggressively toward other birds (males in particular), (c) pursuing females other than the mate, and (d) associating peacefully with other males. The amount of time spent in each of these activities varies between species and also with different stages of the mate's breeding cycle. In wild populations, of course, the situation is enormously complex as a result of individual variation in the timing of the reproductive cycle and the procedure of re-nesting after the loss of a clutch (in some cases with a new mate). The need for a complete knowledge of the 'history' of the individual birds under observation is obvious.

A comparison of paired-male behaviour in the Pintail, Mallard, and Shoveler (Table II) suggests that specific variations in tendencies to stay with or near the mate, to attack other males, to associate with other males, and to rape strange females can account for many of the different characteristics of pursuit flights in the three species.

In the Pintail, Smith (1963) found that paired males are not aggressive to one another, and many can use the same water areas without friction. They frequently leave the mate to pursue and attempt to rape strange females. Many of these pursuits are energetic and prolonged, the birds covering great distances. The sight of such a flight stimulates other males to join in. Thus three-bird flights frequently develop into attempted rape flights and Smith could not draw a sharp distinction between the two. Many flights proceed to a great height and come to an end when the female makes a spectacular dive toward the ground. Males are most active in chasing strange females at the same stage of the breeding cycle when their mates are being chased, i.e. the period just before and during egg-laying.

In the Mallard, paired males do show overt aggression toward other males (Dzubin, 1955; Gates and Beer, 1956; Lebret, 1961), although such behaviour is considered rare by Dzubin, and it was not recorded by Hori (1963). The distinction between three-bird flights and attempted rape flights is clearer in this species: immediately before and during laying most pursuits are brief, they cover a small area, and the pursuing male generally returns to his starting point after flying a distance of up to half a mile (Dzubin, 1957). Males begin to associate in groups during parts of the day early in the incubation period, although the pair-bond may still be intact.



Attempted rape flights are common, once incubation has begun, and Lebreton (1961) believes that they are associated especially with the time when the pair-bond is breaking. They have not been recorded reaching the great heights that they do in the Pintail. In general, Mallard pursuits are less prolonged and cover less ground than those of the Pintail.

In the Shoveler, paired males are hostile toward other males and vigorous pursuits occur as long as the pair-bond remains intact, which is usually late in incubation. Females of strange pairs are also pursued but, at least while the pair-bond is strong, rape is rare. Three-bird flights are common, the pursuing male centring attention on the strange female, but her mate often threatens and pecks toward him in flight. These pursuits are typically short, the chasing male returning quickly to his starting point.

The behaviour of some other Anatini seems to fit fairly closely to each of these three types, although the evidence is even less complete and each species will have to be studied very carefully. The Green-winged Teal is similar to the Pintail in that paired males frequently leave their mates to join in energetic attempted rape flights. The Blue-winged Teal and Cinnamon Teal, on the other hand, show their close phylogenetic relationship to the Shoveler by their strong development of aggression between males, long-lasting pair-bonds, and typically short pursuit flights. The distinction between three-bird flights and attempted rape flights is apparently as clear in the Gadwall (Gates, 1962) as in the Mallard, but in the former overt hostility between males is frequent in flight.

#### **The motivation of chasing behaviour**

In general, aggressive behaviour in paired males is associated with the presence of a strong pair-bond. This is illustrated well by the relationship of male aggressiveness to the presence and location of the mate. In the Velvet Scoter, Koskimies and Routamo (1953) described an area around the pair which is defended by the male and moves with the pair. Dzubin (1955) described a 'moving territory' in the Canvasback - an area around the female, about six feet in diameter, in which the male is aggressive toward other birds: paired males rest peacefully together while their females are at the nest, but as soon as one male is joined by his mate he becomes aggressive. Similar behaviour was recorded by Mendall (1958) in the Ring-necked Duck. As a result of studies on Mallard, Gadwall, Shoveler, and Cinnamon Teal, Smith (1955) concluded that there is 'an area of

intolerance around the breeding pair which moves as the pair moves'.

In the Blue-winged Teal, Dzubin (*loc. cit.*) noted that males are aggressive toward other birds in the absence of the mate, but 'the presence of the female increases the male's aggressiveness'. I have noted the same phenomenon in a male Shoveler; after his mate's clutch was removed and she began to spend all her time with him during the 're-nest interval', the male showed increased hostility, apparently as a response to the female's presence. Gates (1962) observed that 'territorial chasing' (= three-bird flights) in the Gadwall 'normally occurred only when the pair was together', and he concluded that this type of chasing 'appeared to represent the defense of the mated hen rather than defense of the nesting area'.

Many paired males also behave aggressively while the mate is on the nest, but there need be no fundamental difference in the cause of the hostility. These males know where the nest is situated and intense hostility in the vicinity of the nest, as recorded in male Canvasback and Blue-winged Teal by Dzubin (1955), is probably related primarily to the female's presence there. Thus the aggressive responses of paired males on the breeding grounds are basically similar to those shown by males during pair-formation, and by paired males on the wintering grounds and during spring migration. There may be threshold differences, but I suggest that the restriction of the male's responses to a certain area is primarily a result of the female's attachment to the area she selects for breeding and subsequently her attachment to the nest.

A male Shoveler can be found day after day on the same small pothole, spending much time resting on a certain log. But when this bird pursues a passing male or pair there is no need to suppose that he is 'defending' either the water area or the log. The approximate location of 'waiting areas' is determined by the position of the mate's nest; their precise location, by the habitat preferences of the species and the individual's relationship with other birds. If conditions are favourable, the waiting areas are on the nearest piece of water (Dzubin, 1955; Stotts and Davis, 1960), but in other cases they must be further away to satisfy the requirements of the waiting male. Thus the use of 'loafing spots', 'waiting areas', or 'territories' (in Hochbaum's sense) is dependent on the existence of the pair-bond, and I believe that hostility of males using them regularly is primarily an expression of the male's attachment to his mate.

Participation in attempted rape flights is characteristic of males with a weakening pair-bond. In the Mallard and Gadwall, attempted rape flights are seen once incubation has begun when paired males are showing less attachment to the mate and to the waiting area near the nest. In the Pintail, this behaviour appears even earlier (before and during laying), but in this species the pair-bond is weak and hostile reactions are absent.

The 'three-bird flight' appears to have evolved as a form of 'compromise behaviour' resulting from conflicting tendencies. This is indicated by the various 'levels of intensity' in these flights detected by Hori (1963) and Smith (1963). The diagnostic feature of Hochbaum's 'territorial defense flights' was the return of the pursuing male to his starting point. This is the pattern so typical of the Blue-winged Teal and Shoveler, in which pursuits are short. Again the importance of the pair-bond is shown, the quick return reflecting the male's attachment to his mate.

In theory, the pursuit of the female of a strange pair by a paired male could be motivated by either attack tendency, rape tendency, or a combination of the two. As I have suggested (Table II), these two

tendencies conflict with the sociability of males and with the male's attachment to his mate, respectively. Thus while I agree with the general belief that many pursuits are motivated primarily by 'sexual tendency', it should be stressed that this is specifically a 'rape tendency' which is in conflict with the pursuer's 'tendency to remain with or near the mate'. I cannot agree with the proposal of Hori (1963) that predominant sexual tendency is coupled with a 'social tendency' in the case of three-bird flights (though the latter may be a factor inducing some males to join in attempted rape flights). In the Shoveler particularly, three-bird flights occur at a time when the pursuing male is intolerant of other males and a tendency to be sociable is virtually absent.

Since overt hostility toward the male of a pair can be associated with the pursuit of his mate, the possibility that chasing males are responding (at least in part) aggressively to the female should not be overlooked. The phenomenon of 're-directed aggression' (Bastock *et al.*, 1953) may be involved: when a male's tendency to attack another male is inhibited, he re-orientates his hostility toward the female.

**Table II. A comparison of the broad features of social behaviour and some characteristics of pursuit flights in three species of *Anas*.**

<i>Amount of time paired male spends</i>	<i>stage of mate's breeding cycle</i>	<i>Pintail</i>	<i>Mallard</i>	<i>Shoveler</i>
	Early	X	XX	XXX
Alone on waiting area	Late	o	o	XXX
	Early	XXX	X	o
Associating with other males	Late	XXX	XXX	X
	Early	o	X	XXX
Attacking other males	Late	o	o	XXX
	Early	XXX	X	X
Attempting to rape strange females	Late	XXX	XXX	X
	<i>Characteristics of pursuit flights</i>			
Average height		XXX	XX	X
Average duration		XXX	XX	X
Average distance covered		XXX	XX	X
Frequency of flights involving only 3 birds		XXX	XXX	XXX
Frequency of flights involving many males		XXX	XXX	X
Aggression between males in flight		o	X	XXX

The ratings X, XX, XXX represent relative degrees of development of each behaviour pattern (or characteristic) in the three species (o = absent). These approximate ratings are based on the studies of Dzubin (1955), Hochbaum (1944), Lebret (1961), Smith (1963), Sowls (1955), and on my own observations. 'Early' = pre-laying, laying and early incubation; 'Late' = late incubation.

### Dispersion and aggregation of pairs

All ducks lead semi-aquatic lives: they need both water areas and adjacent land areas to satisfy all their needs. The detailed nature of these requirements vary between species, in accordance with different ways of life. Extreme cases are represented by the Ruddy Duck and the Laysan Duck *Anas laysanensis*. The former is almost exclusively aquatic, but it is dependent on marsh edges for nesting and brood-rearing cover. The Laysan Duck is predominantly terrestrial: it makes only limited use of salt water and apparently is capable of surviving without fresh water (Warner, 1963). Most species fall between these extremes, making daily use of water areas and shorelines, but each has slightly different habitat-preferences. Above all, the ecology and behaviour of each species are influenced by the pattern of land-water interspersions in the habitat.

These relationships between land and water areas can be extremely complex. Even for one species they may differ from one region to another; frequently they change in the course of one season, and from one year to the next. The need for most species to be adaptable to varying conditions is obvious, and it is not surprising to find that some parts of the breeding range of each pair are 'shared' with other pairs. To understand the pattern of pair-spacing, it is necessary to know the degree to which this sharing occurs and the way in which it is achieved. Particularly important is 'the distribution of the breeding requirement which is most limited' (Smith, 1955). This sharing is obvious where the requirement takes the form of 'an island' - whether it is a true island in the sense of an isolated land mass, or whether it is an isolated water area, food source, waiting area, or tract of nesting-cover.

The sharing of one or more breeding requirements by a number of pairs may be advantageous or disadvantageous to the species, and complex 'mechanisms' have evolved which tend to preserve the optimum condition of adaptedness. In ducks, as in many other animals, social behaviour patterns appear to be of prime importance in the operation of these 'mechanisms' (see Wynne-Edwards, 1962).

Homing by both adult and young females must produce a tendency for breeding pairs to become concentrated. If the homing is precisely to the nest-site, a dense colony would tend to form; if the birds return merely to the 'home range', a less concentrated aggregation of nests would result. In many environments, however, concentrations of nests are

especially vulnerable to predation and in practice such sharing of a localised nesting area occurs only on islands or in other situations where nesting losses are low.

Precise homing to the nest-site and the establishment of dense nesting colonies do occur as a typical pattern in the Common Eider. A major factor producing such colonies seems to be the lack of mammalian egg-predators. On mainland areas, Eider nests are farther apart (Lack, 1954). The social behaviour of this species is adapted to colonial nesting, pairs showing only mild hostility toward one another. In contrast, male King Eiders *Somateria spectabilis* are more aggressive in the nest area (Pettingill, 1959), and this species does not form colonies on islands.

Nesting concentrations occur on islands in lakes, the most famous being at Myvatn in Iceland (Scott, 1952). A hatching success of 90% has been recorded in 160 nests on Gadwall Island, North Dakota, in contrast to an average of 50% for the same species (mostly Gadwall) on the mainland nearby (Hammond and Mann, 1956). Comparatively dense breeding populations of Goldeneye and Wood Duck have been built up gradually over a number of years in various places in Europe and North America by saturating an area with predator-proof nesting-boxes. In addition to homing and high productivity, an additional factor in producing these nesting concentrations may be a tendency for females to be faithful to a site where a nesting attempt has been successful (Mendall, 1958).

Hammond and Mann (*loc. cit.*) found that the Gadwall was especially prone to form island nesting concentrations. Mallard, Pintail, Lesser Scaup, and Redhead also used these same islands but the numbers of Shoveler and Blue-winged Teal were no greater than on nearby mainland habitat. At Myvatn, Greater Scaup *Aythya marila* and Oldsquaw *Clangula hyemalis* were the most abundant nesters, but here also many other species used the islands (Scott, *loc. cit.*). In southern Alberta, Keith (1961) found that Lesser Scaup and Mallard favoured islands, while Black Ducks are known to concentrate on islands off the coast of Maine (Gross, 1945) and in Chesapeake Bay (Stotts and Davis, 1960). In other regions, all these species may be found nesting in a dispersed pattern; their use of islands apparently results from local traditions built up gradually as a result of especially favourable conditions for high production.

For the *Aythya* species, the increased proximity of pairs caused by nesting on islands probably presents little difficulty

since these birds show a low level of aggressiveness and they do not engage in aerial pursuits. Gadwall, Mallard, and Black Duck do show these responses, however, and in some ways their behaviour must be modified to enable nesting concentrations to occur. The mobility of pairs is probably important, so that not all activities need be accomplished on the island. Hammond and Mann believe that many Gadwalls use the islands only as a place for a nest-site; they fly to and from feeding and resting places on the mainland. On the other hand, the Black Ducks of Chesapeake Bay have waiting areas on the island shore at the spot nearest to the nest; although aggressive encounters and aerial chases were observed, these were considered to be 'surprisingly infrequent' (Stotts and Davis, *loc. cit.*).

In the grassland area of Kindersley, Saskatchewan, Alex Dzubin (*in litt.*) has studied the behaviour of a high Mallard population in which many pairs are forced to share small water areas (e.g. 25-30 pairs to a 5-acre pothole). In contrast to the behaviour of this species in parkland habitat where there are many potholes close together, the Kindersley Mallard drakes are unable to exclude other pairs from specific waiting sites. There is frequent shifting of areas from which males begin chases and, because of the constant presence of other pairs nearby, chasing is directed mainly at birds flying overhead, especially females going to and from their nests. Dzubin concludes that some pairs are forced to delay nest-initiation when they are constantly chased away from such a water area. When the chasing activities of early breeding males wane in intensity, there is a chance for other pairs to become established and begin breeding. I have observed the same phenomenon when Shoveler pairs are crowded in pens.

In contrast to the Mallard, which may be found breeding in a wide variety of habitats, the Pintail appears to be specially adapted to nesting in the vicinity of a 'water island'. Pintails prefer open prairie and tundra where nesting cover is sparse and water areas few and often isolated. The studies of Smith (1963) in southern Alberta show that the lack of aggressiveness between males allows many pairs to make use of one lake for feeding and nesting, but the extreme development of raping activity tends to cause dispersion of females at the time of nest-site selection, thus producing dispersion of nests. Smith believes that this nest dispersion has survival value in reducing the level of egg-predation. The mobility of Pintail broods and the grey cryptic coloration of the

ducklings are presumably adaptations for the long overland trips necessary to reach water. At Kindersley, Dzubin finds similar wide dispersion of nests in the Mallard (up to 1 mile from water), probably as a result of intense chasing activity. Although egg-predation may be reduced by this dispersion, duckling mortality is high in dry seasons, up to 40% of broods never reaching water.

In contrast to the Mallard and Pintail, the Shoveler behaves in a way much more like that of a territorial passerine. The home range is small, and males are aggressive toward any intruder. The pair-bond is strong and promiscuous tendencies are weak. This type of behaviour produces a clear pattern of pair-spacing, the nest being situated close to the mate's waiting area. Thus, largely through hostility between pairs there is a tendency for nests to be spaced out. The behaviour of this species appears to be adapted to marsh habitats which provide all requirements of the pair within a relatively small, discrete area. For this reason, the Shoveler is a good example of a species with highly developed 'territorial behaviour' of the type envisaged by Hochbaum.

#### The functions of chasing

In ducks, as in other birds (Hinde, 1956), there is little direct evidence on the effects of chasing. The frequency and intensity of chasing by males have been observed to increase as the number of pairs in an area increases (e.g. Hammond and Man, 1956; Mendall, 1958; McKinney, *in prep.*), or when habitat changes enhance the visibility of adjacent pairs (Hochbaum, 1944). It is generally assumed that, under such conditions, the density of breeding pairs is being limited by chasing, and that the same process is effective to a lesser degree at lower densities. In some instances, however, it appears that breeding populations can increase in density almost indefinitely in spite of chasing (Hammond and Mann, *loc. cit.*; Gates, 1962) and some authors (e.g. Bezzel, 1959) have suggested that chasing has little effect on duck populations.

In this paper, I have tried to show how such contradictory views can be reconciled. Although the evidence is circumstantial, I believe that chasing tends to produce some degree of dispersion and that it has a significant effect on breeding densities. The absence of a neat pattern of exclusive territories with defended boundaries does not necessarily conflict with this generalisation. The ability of pairs to share certain parts of their home ranges and to adapt their behaviour to local habitat conditions

can be essential, adaptive attributes. The behaviour of each species must be the result of a compromise between the advantages of spacing-out and those derived from sharing the available resources.

Hochbaum (1944) suggested that the primary function of territorial behaviour in ducks is that it permits uninterrupted copulation between the members of the pair, but there is little evidence to support this theory. Eiders successfully accomplish copulation under the crowded conditions prevailing at colonies, and I found the same to be true in artificially crowded pairs of Blue-winged Teal and Shoveler. It is true that interruptions occur but, viewing the problem from an evolutionary point of view, it is difficult to believe that it had to be 'solved' through the enormous expenditure of energy involved in chasing.

Hochbaum's argument depended mainly on the timing of chasing behaviour; it peaks in frequency and intensity just before and during egg-laying, at the time when fertilisation must be occurring. This generalisation has since been confirmed in a number of species (e.g. Sowls, 1955; Dzubin, 1955; Mendall, 1958; Gates, 1962; Smith, 1963). As well as being the period of fertilisation, however, this is the time when nest-sites are selected. In the Pintail, Smith (1963) believes that dispersion of nests over the available habitat is a direct consequence of sexual chasing activity, but in other species the effect is probably indirect. In the Shoveler, Mallard, and Gadwall, chasing appears to produce a spacing of pairs at the time when they are establishing home ranges. On mainland habitats, where preferred nesting-cover is dispersed, this will lead to a dispersion of nests. Evidence from nesting concentrations (p. 96) strongly suggests that such nest dispersion has survival value as an anti-predator device. This suggestion was made with respect to gulls by Tinbergen (1952) and the same idea was proposed by Hammond and Mann (1956) for ground-nesting ducks. The survival value of nest dispersion in Black-headed Gulls *Larus ridibundus* has since been demonstrated experimentally by Tinbergen *et al.* (1962).

In areas where many species of duck nest side by side in the same nesting cover, it is perhaps surprising to find that interspecific territorialism (Simmons, 1951, 1956) is not widespread. Presumably the advantages of such responses in producing dispersion of all duck nests are outweighed by the disadvantages of the time and effort which would be required. Furthermore,

the species-composition varies so much from one area to another that the response would have to be very generalised. In many cases, such behaviour would entail 'wasted' energy, chases being directed at birds which are not using the same type of nesting cover. The same principle seems to apply in other groups of birds, interspecific territorialism having evolved only where its advantages are great. The occurrence of interspecific hostility in Barrow's Goldeneye is of great interest and it deserves further study.

Geyr (1924) suggested that territorial behaviour in the Mallard ensures an adequate food supply for the brood. In theory this could be an important ultimate function of pair-spacing, but the evidence suggests that it is of secondary importance in ducks. Broods have considerable powers of mobility and, in most duck breeding habitats, food supply is abundant. The argument that pair-spacing produces nest dispersion may apply in some cases also to broods, high densities being more vulnerable to predation, but again direct evidence is lacking. On the whole, dispersion of pairs is more likely to be primarily an anti-predator device; if young are not produced, there is no need for a food supply.

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## References

- BASTOCK, M., D. MORRIS and M. MOYNIHAN. 1953. Some comments on conflict and thwarting in animals. *Behaviour* 6: 66-84.
- BELLROSE, F. C., K. L. JOHNSON and T. U. MEYERS. 1964. Relative value of natural cavities and nesting houses for Wood Ducks. *J. Wildl. Mgmt.*, 28: 661-676.
- BEZZEL, E. 1959. Beiträge zur Biologie der Geschlechter bei Entenvögeln. *Anz. Orn. Ges. Bayern*, 5: 269-355.
- COOCH, G. 1957. A report on the biology and management of the Northern Eider (*Somateria mollissima borealis*), Cape Dorset Area, N.W.T. Can. Wildl. Serv., unpubl. report.
- DIXON, J. 1924. Nesting study of the wood duck in California. *Condor* 26: 41-66.
- DZUBIN, A. 1955. Some evidences of home range in waterfowl. *Trans. 20th N. Amer. Wildl. Conf.*: 278-298.
- DZUBIN, A. 1957. Pairing display and spring and summer flights of the Mallard. *Blue Jay* 15: 10-13.
- EMLEN, J. T. Jr. 1957. Defended area? - A critique of the territory concept and of conventional thinking. *Ibis* 99: 352.
- ERSKINE, A. J. 1961. Nest-site tenacity and homing in the Bufflehead. *Auk* 78: 389-396.
- EVANS, C. D. and K. E. BLACK. 1956. Duck production studies on the prairie potholes of South Dakota. *U.S. Fish and Wildlife Service, Spec. Sci. Rpt. Wildlife*: No. 32.
- EVANS, C. D., A. S. HAWKINS and W. H. MARSHALL. 1952. Movements of waterfowl broods in Manitoba. *U.S. Fish and Wildlife Service, Spec. Sci. Rept. Wildlife*: No. 16.
- FRITH, H. J. 1959. The ecology of wild ducks in inland New South Wales. II. Movements. *C.S.I.R.O. Wildlife Research* 4: 108-130.
- GATES, J. M. 1962. Breeding biology of the Gadwall in Northern Utah. *Wilson Bull.* 74: 43-67.
- GATES, J. M. and J. R. BEER. 1956. A marsh bird study spring 1955. *Flicker* 28: 16-21.
- GEYR VON SCHWEPENBURG, H. 1924. Zur Sexualethologie der Stockente. *J. f. Orn.* 72: 102-108.
- GEYR VON SCHWEPENBURG, H. 1961. Zum Verhalten der Stock- und Schnatterente. *J. f. Orn.* 102: 140-148.
- GIRARD, G. L. 1939. Notes on life history of the Shoveler. *Trans. 4th N. Amer. Wildl. Conf.*: 364-371.
- GLOVER, F. A. 1956. Nesting and production of the Blue-winged Teal (*Anas discors* Linnaeus) in Northwest Iowa. *J. Wildl. Mgmt.* 20: 28-46.
- GROSS, A. O. 1945. The black duck nesting on the outer coastal islands of Maine. *Auk* 62: 620-622.
- GUDMUNDSSON, F. 1932. Beobachtungen an isländischen Eiderenten (*Somateria m. mollissima*). *Beitr. Fortpfl. Vögel* 8: 85-97.
- HAMMOND, M. C. and G. E. MANN. 1956. Waterfowl nesting islands. *J. Wildl. Mgmt.* 20: 345-352.
- HEINROTH, O. 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verh. V. Int. Orn. Kongr., Berlin*: 589-702.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis* 98: 340-369.
- 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.
- HORI, J. 1964. The breeding biology of the Shelduck *Tadorna tadorna*. *Ibis* 106: 333-360.
- HOWARD, H. E. 1907-14. *The British Warblers*. London.
- HOWARD, H. E. 1920. *Territory in Bird Life*. Murray, London.
- KEITH, L. 1961. A study of waterfowl ecology on small impoundments in south-eastern Alberta. *Wildl. Monogr.* No. 6, 88 pp.
- KOSKIMIES, J. and E. ROUTAMO. 1953. Zur Fortpflanzungsbiologie der Samtente *Melanitta f. fusca* (L.). I. Allgemeine Nistökologie. *Papers on Game Research*, 10.
- LACK, D. 1939. The behaviour of the Robin. Pt. 1. The life history with special reference to aggressive behaviour, sexual behaviour and territory. *Proc. Zool. Soc. Lond.* 109: 169-178.
- LACK, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford.
- LEBRET, T. 1961. The pair formation in the annual cycle of the Mallard, *Anas platyrhynchos* L. *Ardea* 49: 97-158.
- LEOPOLD, F. 1951. A study of nesting wood ducks in Iowa. *Condor* 53: 209-220.
- LOW, J. B. 1945. Ecology and management of the redhead, *Nyroca americana* in Iowa. *Ecol. Mon.* 15: 35-69.
- MCKINNEY, F. 1961. An analysis of the displays of the European Eider *Somateria mollissima mollissima* (Linnaeus) and the Pacific Eider *Somateria mollissima v. nigra* Bonaparte. *Behaviour*, Supplement 7. 124 pp.
- MCKINNEY, F. 1957-62. Reports of six annual seminars held at Delta Waterfowl Research Station (mimeo).
- MENDALL, H. L. 1958. The ring-necked Duck in the Northeast. *Univ. of Maine Studies*, Second Series, No. 73, 317 pp.
- MUNRO, J. A. 1939. Studies of waterfowl in British Columbia: Barrow's golden-eye and American golden-eye. *Trans. Royal Can. Institute* 22: 259-318.
- MUNRO, J. A. 1942. Studies of waterfowl in British Columbia: buffle-head. *Can. Jour. Res.*, Sec. D. 20: 133-160.
- MYRES, M. T. 1957. An introduction to the behavior of the goldeneyes: *Bucephala islandica* and *B. clangula* (Class Aves, Family Anatidae). Unpublished M.A. Thesis, University of British Columbia.
- NICE, M. M. 1943. Studies in the life history of the Song Sparrow. II. *Trans. Linn. Soc. N.Y.* 6: 1-328.

## References—continued

- PETTINGILL, O. S., JR. 1959. King Eiders mated with Common Eiders in Iceland. *Wilson Bull.* 71: 205-207.
- REED, A. 1964. The nesting of the Black Duck (*Anas rubripes*) at Ile aux Pommes, Quebec. Paper presented at Northeast Wildlife Conference, Hartford, Conn., January 1964. (Mimeo.)
- SCOTT, P. 1952. Myvatn 1951. *Severn Wildfowl Trust 5th Ann. Rep.*: 125-132.
- SIMMONS, K. E. L. 1951. Interspecific territorialism. *Ibis* 93: 407-413.
- SIMMONS, K. E. L. 1956. Territory in the Little Ringed Plover *Charadrius dubius*. *Ibis* 98: 390-397.
- SIREN, M. 1957. Telkän pesimisseutuja Pesäpaikka uskollisuudesta. *Suomen Riista* 11: 130-133.
- SMITH, R. I. 1955. The breeding territory and its relationship to waterfowl productivity at Ogden Bay Bird Refuge. Unpublished M.S. Thesis, Utah State Agric. College, Logan.
- SMITH, R. I. 1963. The social aspects of reproductive behavior in the Pintail (*Anas acuta acuta*, L.) Unpublished Ph.D. Thesis, Utah State University, Logan.
- SOWLS, L. K. 1955. *Prairie Ducks*. Wildlife Management Institute, Washington, D.C.
- STOTTS, V. D. and D. E. DAVIS. 1960. The Black Duck in the Chesapeake Bay of Maryland: breeding behavior and biology. *Chesapeake Science* 1: 127-154.
- 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. 1952. On the significance of territory in the Herring Gull. *Ibis* 94: 158-159.
- TINBERGEN, N. 1957. The functions of territory. *Bird Study* 4: 14-27.
- TINBERGEN, N., G. J. BROEKHUYSEN, F. FEEKES, J. C. W. HOUGHTON, H. KRUIK and E. SZULC. 1962. Egg shell removal by the Black-headed Gull, *Larus ridibundus* L.; a behaviour component of camouflage. *Behaviour* 19: 74-117.
- WARNER, R. E. 1963. Recent history and ecology of the Laysan Duck. *Condor* 65: 3-23.
- WEIDMANN, U. 1956. Verhaltensstudien an der Stockente (*Anas platyrhynchos* L.). I. Das Aktions-system. *Zeitschr. für Tierpsychol.* 13: 208-271.
- WYNNE-EDWARDS, V. C. 1962. *Animal Dispersion in relation to Social Behaviour*. Edinburgh and London.

## Breeding success of geese in west Spitsbergen, 1964

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### Summary

Details are given of the distribution of breeding Pink-footed, Barnacle and Brent Geese in Spitsbergen and of their past status. Counts were made in the south-west of Spitsbergen in the summer of 1964. Few young Barnacle Geese were reared but Pink-foot were more successful. Many nests were found and the factors affecting the choice of nest site are discussed: freedom from snow cover is the most important.

### Introduction

In the summer of 1964 two expeditions, one from Norway and one from Britain, visited adjacent parts of West-Spitsbergen with the object of investigating the status, distribution and breeding success of the Barnacle Goose *Branta leucopsis* Pink-footed Goose *Anser brachyrhynchus* and Brent Goose *Branta bernicla hrota*.

The Ornithological Group of the Norsk Polarinstittutt, consisting of L. Ljøterud, B. Mathiasson (assistants) and M. Norderhaug worked from 7th July to 31st August in the coastal region from Stormbukta north to Ohlshomen/Kapp Berg (areas 1-4 on map). They also continued their Little Auk *Plautus alle* studies, begun in 1962. The Wildfowl Trust Expedition of R. J. F. Taylor and M. A. Ogilvie covered the coastal area between Isfjord and Bellsund (partially) and from Bellsund south to Kapp Borthen, from 18th June to 26th July. The two expeditions worked independently, but study methods had been co-ordinated beforehand.

### Topography

The topography of the south-west coast of West-Spitsbergen is characterised by a flat plain varying in width from one to six miles and never rising above 300 feet. Steeply sided mountains reaching 3,000 feet form a boundary on the eastern edge of the plain. Two wide and extensive fjords, Bellsund and Hornsund, and one large glacier, Torellbreen, break the area into three distinct parts, geographically but not ecologically. There are numerous off-shore islets and rocks, of which the largest such as the Dunöyane and Isöyane groups and Ohlsholmen are barely one square kilometre in area. They are low, grass-covered and with a few small, shallow ponds. Large parts of the coastal plain are nearly barren or with scant vegetation. It is only round ponds and streams and close to the foot of the mountain cliffs with their very large colonies of sea-birds, mostly Little Auks, that the richest vegetation is found. An association between these lush areas and the distribution of the geese is