Clutch predation in relation to nest density in Mallard and Tufted Duck

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Introduction

Many nesting studies on waterfowl report the proportion of nests destroyed by predators (Hilden 1964; Havlin 1966a, b, 1971; Bengtson 1972; Newton & Campbell 1975; Duebbert & Lokemoen 1976) but few studies have related the proportion of nests destroyed by predators to nest density. Hill (1984) showed that clutch predation was only weakly density dependent in the Mallard *Anas platyrhynchos* population breeding on the Sevenoaks reserve in Kent and that predator control removed this relationship.

This paper now aims to examine the evidence for between year density dependent clutch predation in the Mallard and Tufted Duck *Aythya fuligula* on other areas and to investigate daily changes in predation in relation to nest density. Nest success has been shown to be higher for nests in tall vegetation (Hill, in press), therefore this paper investigates whether nests are aggregated in patches of tall cover and whether this aggregation further leads to an increase in the proportion destroyed by predators.

Study areas

The work was conducted on two separate study areas, i) Linford, which is a 300 ha complex of 7 flooded gravel quarries situated alongside the upper reaches of the Great Ouse in Buckinghamshire, and ii) Willen, which is a man-made balancing lake (used to prevent flooding), the north section of which has a 3.5 ha island in its centre where Mallard and Tufted Duck breed.

Methods

The nest census

Each of the lake areas at Linford, particularly the associated islands, together with Willen island, were searched approximately every four days during the breeding seasons 1980 and 1981, so that nests could be found during the laying period. The method of nest searching was considered reliable, rarely allowing nests to be missed. During 1974–1979 two other observers censused the same area at Linford. Predation was determined by searching for egg remains and no nest markers were used. Observer-induced bias was considered negligible particularly in view of the results of Keith (1961), Willis (1973), and Livezey (1980), which failed to demonstrate any observer effect. Other likely biases in the census are discussed in Hill (1982). The majority of predation was caused by Carrion Crows *Corvus corone* and Magpies *Pica pica* at Linford and rats *Rattus norvegicus* at Willen (Hill, in press).

Inter-nest distance measurements

A computer program (written in Algol 68) was used to calculate daily changes in nest density and nearest neighbour distances. The four variables calculated by the program are: NNA – the mean distance of the four nearest nests to nest i for the period nest i was in existence; NNB – the mean distance of the nearest nest for the period nest i was in existence; NNIA – the mean distance of the nearest four nests at the time nest i was initiated; and NNIB – the distance to the nearest nest at the time nest i was initiated.

Vegetation mapping on Willen Island

In order to calculate the areas of vegetation of different height categories, the island was transected at 10 m intervals and vegetation heights (0 cm, 0–25 cm, 25–50 cm, >50 cm) measured at 10 m intervals along each transect. The islands at Linford were too small and nest density was too low to detect differences in the choice of nest sites based on vegetation height.

Statistical tests were taken from Sokal & Rohlf (1969).

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Results

Between year density dependent clutch predation

During the years 1974–1981, excluding 1976, the percentage of nests destroyed by predators increased with an increase in the number of Mallard nests at Linford (r^2 = 0.79 $P < 0.02$, slope ± s.e. = 1.5 ± 0.26, df = 5, $P < 0.01$) (Fig. 1). For two years only, 1980 and 1981, data were obtained for Tufted Duck nests but these have been excluded from the analysis. However, they tended to fit the line through the Mallard data points. In 1976 clutch predation in Mallard was lower than would have been predicted from the above relationship.

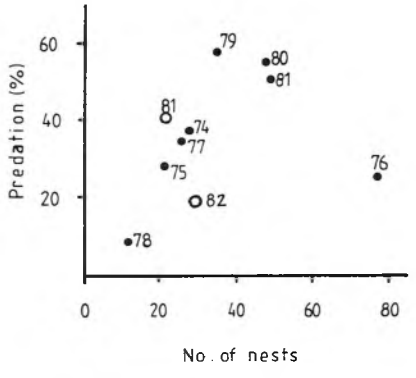

Figure 1. Density dependent clutch predation in the Mallard at Linford between 1974–1981 (closed circles). Open circles represent two years data for Tufted Duck.

Daily changes in the number of nests

Nest density is continually changing as nests are destroyed by predators, deserted or hatched off, and this makes the relationship outlined above more difficult to interpret because the relationship is based solely on the number of nests started throughout the whole season. The number of nests in existence at any one time is shown in Figure 2 for Linford and Willen during the period of this study. At Linford in 1980 nest density peaked at 24 in the beginning of May with the onset of the Tufted Duck breeding season. The earlier peak in 1980 was attributable to Mallard nests and peaked at 19 nests. In 1981 at the same site breeding started earlier due to warmer February weather and a peak of 16 nests was reached by the end of March and beginning of April. However, a freak snowfall thawed in late April and all except one nest were lost to resulting floods. Nest density began to rise again and peaked at 14 nests approximately 15 days after the flood. There then followed a decline as further nests were preyed upon. Tufted Duck then began breeding which raised the extant nest density to its pre-flood peak of 16 nests. Nest density on Willen island in 1981 markedly increased with the onset of breeding in the Tufted Duck and peak nest density reached 28 nests. This declined rapidly to 10 nests because of rat predation. After the peak, nest density remained constant at 10 nests until hatching commenced. In each case the distribution of predated nests through the season tended to follow the distribution of extant nests such that predation was highest at high nest density and lowest at low density. At Willen rat predation lagged behind the increase in nest density caused by the increase in the number of Tufted Ducks starting nests (Fig. 2).

Aggregation of nests in tall vegetation

Do ducks of both species nest closer together in tall vegetation at the expense of increasing the predation rate in a density dependent manner? High nest density on Willen island allowed the calculation of nest densities in patches of vegetation of different height categories. Significantly more nests of Mallard and Tufted Duck were found in patches of tall vegetation than would be expected by chance alone (X^2 = 18.76, n = 62, $P < 0.005$). Nests therefore tended to be aggregated in patches of tall vegetation and tended to avoid short vegetation (Table 1).

Differences in nearest neighbour distances between Mallard and Tufted Duck nests

At Linford in 1980 and Willen in 1981 Mallard nests tended to be further from another nest than did those of Tufted Ducks (Table 2). In part this is due to the fact that Tufted Duck breed later than Mallard and over a shorter period of time. At Linford in 1981 when many Mallard nests were destroyed by floods there was no significant difference between Mallard and Tufted Duck nests for three of the four nearest

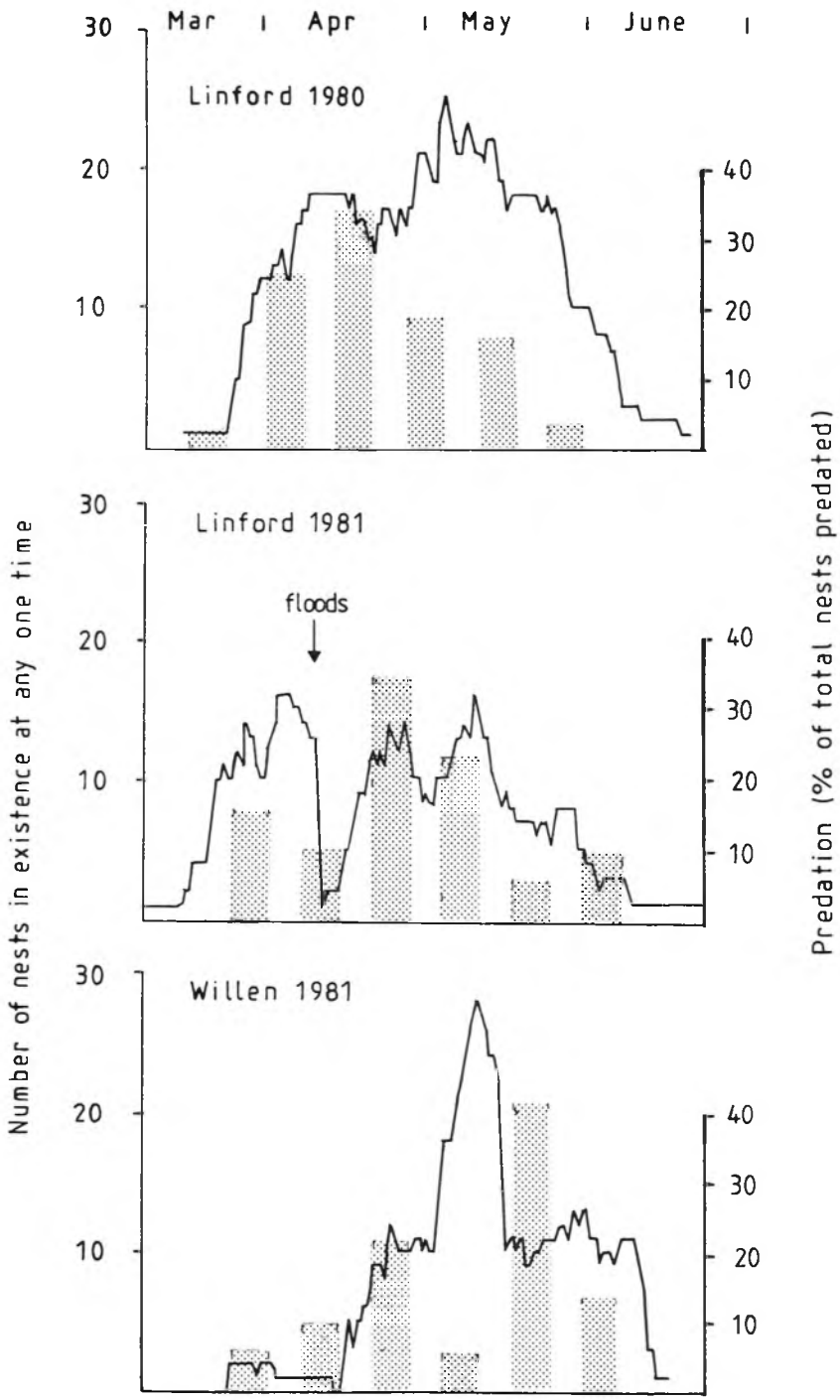

Figure 2. Daily changes in the number of Mallard and Tufted Duck nests in existence at Linford in 1980 and 1981, and Willen island in 1981. The shaded histograms represent the distribution of predated nests through the season.

Table 1. The number of Mallard and Tufted Duck nests in patches of vegetation of different heights.

Vegetation height (cm)	Area (ha)	Observed no. nests	Nest density no./ha.	Expected no. nests
>50	0.83	26	31.3	15.3
25–50	1.33	23	17.3	24.5
<25	0.52	12	23.1	9.6
0	0.68	1	1.5	12.5

Table 2. Differences in nearest neighbour distances (m) between Mallard and Tufted Duck nests.

	No. nests		Nest density*		Variable	Mean		P
	Mallard	Tufted	Mallard	Tufted		Mallard	Tufted	
Linford 1980	47	32	1.31	0.89	NNA	258	156	<0.02
					NNB	123	65	<0.03
predation (%)			55	19	NNIA	285	133	<0.003
					NNIB	146	61	<0.027
Linford 1981	49	22	1.36	0.61	NNA	309	351	NS
					NNB	182	147	NS
predation (%)			51	41	NNIA	336	312	NS
					NNIB	255	100	<0.1
Willen 1981	20	42	6.3	13.2	NNA	74	35	<0.001
					NNB	57	20	<0.002
predation (%)			85	57	NNIA	73	36	<0.0001
					NNIB	49	19	<0.0004

* Number of nests per hectare.

neighbour measurements. In both species predation was highest on Willen island where nest density was also highest and where, consequently, inter-nest distance was reduced (Table 2).

Discussion

Mallard and Tufted Duck nests in tall vegetation are more successful than those in short vegetation and those on islands are more successful than those on the mainland (Hill, in press). Nest density can also affect predation; the proportion of Mallard nests destroyed by predators, mainly Carrion Crows and Magpies, increased as the density of nests increased. At high nest density there was some evidence from one year that predation declined perhaps as a result of predator "saturation". A daily plot of extant nests revealed that there are important daily changes in the number of nests in existence at any one time and this can affect the interpretation of density dependent predation when considered purely as absolute nest density for one season. On Willen island there was evidence that nest-sites could be limiting because nests tended to be aggregated in patches of tall vegetation, avoiding patches of shorter vegetation. On some breeding sites where tall vegetation is scarce, it is possible that a higher proportion might therefore nest in poorer cover open to higher predation. This would explain the between year effect of density dependent clutch predation in the Mallard. Tufted Duck on the other hand nest closer together, particularly in tall vegetation, even though close nesting is conducive to higher predation (Hill, in press). Within areas of uniform vegetation, Tufted Duck nest closer together than would be expected by chance, whereas Mallard nests in such areas are effectively distributed at random (Bengtson 1970). Mallard females also tend to nest closer to other species, avoiding other Mallard (Newton & Campbell 1975).

Under circumstances where nest-sites are limiting, density dependent clutch predation would cause a certain amount of compensation in the number of broods successfully hatched. However, this relation-

ship is far from "perfect" as another study on a Mallard population in Kent has shown (Hill 1984). On that water body clutch predation was only weakly density dependent and consequently there was little variation in the production of broods caused by variation in nest success.

Density dependent clutch predation caused by a species such as the Carrion Crow could be a result of an increase in the reproductive or immigration rate of the predator population in response to an increase in prey (nest) density, corresponding to the numerical response. At Linford it is unlikely that corvids could respond so dramatically to an increase in nest density via increased reproduction or immigration. It is more likely that corvids spent more time searching in an area where they have been previously successful, corresponding to the functional response of Holling (1959). In an area with a high nest density nests are easier to find.

Duebbert (1969) and Duebbert & Lokemoen (1976) failed to find density dependent clutch predation in the Mallard. Bjarvall (1970), however, increased predation by increasing nest density using artificial nest sites. Havlin (1971) found that Tufted Duck nest success was related to nest density – ducks nesting at high density suffered higher relative nest losses through increased interactions between individuals which increased desertion and the subsequent amount of predation. Potts (1980) found that clutch predation in the Grey Partridge *Perdix perdix* was the only natural density dependent mortality factor operating and foxes *Vulpes vulpes* were found to prey upon incubating females to a greater extent when nests occurred at high density.

Some species of birds nest at very high density in association with other species, gaining a certain amount of protection from predators in doing so. Tufted Ducks on St. Serfs island, Loch Leven, Scotland, nested at higher density within a cology of Black-headed Gulls *Larus ridibundus* than outside the colony (Newton & Campbell 1975). Predation on those nests within the colony was less than on those outside because the gulls excluded Jackdaws *Corvus monedula* which were the major egg predators. Goransson *et al.* (1975) undertook an experimental approach to clutch predation in relation to nest density and showed that predation was higher at high nest density than at low nest density, but that within a colony of Lapwings *Vanellus vanellus*, which exhibit anti-predator mobbing attacks, predation was reduced.

Where weak density dependence is operating on clutch predation the provision of habitat suitable for establishing nest-sites should significantly increase the number of broods which hatch on a water-body. However, where there is more density dependence operating the provision of nesting habitat will have much less of an effect on the number of broods produced. In the Grey Partridge, habitat management devoted to increasing the number of nest-sites is only effective at increasing the brood production rate when predator control is undertaken. This suggests that predator control, in association with habitat management devoted to increasing the abundance of suitable nesting vegetation, could significantly increase duck breeding density, particularly on those inland water bodies which, at present, are used by very few breeding birds.

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Summary

Clutch predation in relation to Mallard *Anas platyrhynchos* and Tufted Duck *Aythya fuligula* nest density was studied at two inland lakes. A between year analysis for one site showed that the proportion of Mallard nests destroyed by predators, mainly Carrion Crows *Corvus corone*, Magpies *Pica pica* and rats *Rattus norvegicus*, increased with an increase in nest density. The number of nests in existence at any one time changed continually because of predation, desertion, hatching or new nests being started. Nests of both species were aggregated in patches of tall vegetation on the one site where the analysis was possible. There was evidence that nests closer together (i.e. where nests were at high density) were less successful than those further apart. Tufted Duck nests were closer to another nest than those of Mallard.

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