

## Predation on birds' nests in relation to antipredator aggression and nest density: an experimental study

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Artificial birds' nests containing 2 eggs were placed in 5 study plots (area 4 ha) at densities of 1 to 4 nests ha<sup>-1</sup> and exposed for short periods (1–3 days) to predation, mainly by *Corvus corone cornix* L. and *Larus argentatus* Pont. Predation rates were high (75 to 96 % on average in 6 experiments) and positively correlated with nest density in 4 plots. In the fifth plot, individuals of *Vanellus vanellus* L. and, to a lesser extent, *Numenius arquata* L. were present and defended their ranges against predators. A significantly lower frequency of predators over this study plot than the others was recorded, and the rate of predation (26%) on the artificial nests in this plot was also significantly lower. The importance of this result for some current hypotheses about the role of predation in bird communities is pointed out.

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Искусственные птичьи гнезда с 2 яйцами помещались на 5 опытных участках (площадью 4 га) по 1–4 гнезда/га, и в течение 1–3 дней их оставляли открытыми для хищников, преимущественно *Corvus corone cornix* L. и *Larus argentatus* Pont. Активность хищников была высокой (75–96 % в среднем из 6 опытов) и прямо зависела от плотности гнезд на 4 участках. На пятом участке обитали *Vanellus vanellus* L. и в меньшем количестве *Numenius arquata* L. которые защищали свои территории от хищников. На этом участке наблюдалась значительно более низкая численность хищников, чем на других, и количество разрушенных искусственных гнезд составило 26 %. Подчеркивается значение этих опытов для некоторых рабочих гипотез о роли хищников в комплексах птиц.

## 1. Introduction

It has long been known that some birds benefit from the protection against nest predators afforded by colonies of, for example, gulls *Larus* and terns *Sterna* (Bergman 1946, 1957, Ahlén and Andersson 1970, Bengtson 1972). However, it has also been suggested that some noncolonial species, owing to their aggressiveness, may confer the same advantage on other species (Hagen 1947, Kvaerne 1973). Such effects may disturb the positive relationship between population density and predation rate recently demonstrated by Krebs (1971) for a great tit *Parus major* L. population and thought to be valid for entire bird communities by Fretwell (1972).

On the basis of a field experiment we evaluate the effects of density and antipredator aggression on the survival of populations of artificial nests. The anti-predator defense was provided mainly by a few pairs of lapwing *Vanellus vanellus* L. breeding within our study area.

## 2. Study area and methods

The experiment was carried out on a heath known as Skanörs Ljung in the southwestern corner of Sweden (55°24'N, 12°54'E). It has a uniform vegetation dominated by *Calluna vulgaris* L., *Erica tetralix* L., *Myrica gale* L. and *Molinia caerulea* L. Across the heath runs a trench carrying a little water and surrounded by somewhat wetter ground than the rest. The distance from the study plots to the nearest woodland edge was about 150 m. Human disturbance during our study period in April and May 1974 was negligible.

Five plots, each 200 × 200 m (area 4 ha), were provided with clutches of 2 eggs at densities of 1, 1.5, 2, 3 and 4 nests ha<sup>-1</sup> (see Fig. 1). Densities were allocated to plots at random. Within plots the nests were evenly dispersed. A plastic tab was hidden under one of the eggs, so that the site could still be recognized even if the eggs had been removed by a predator.

Nest site coordinates were located and retrieved with the aid of a measuring rope carried across the plot. At the borders of the plots thin metal rods served as

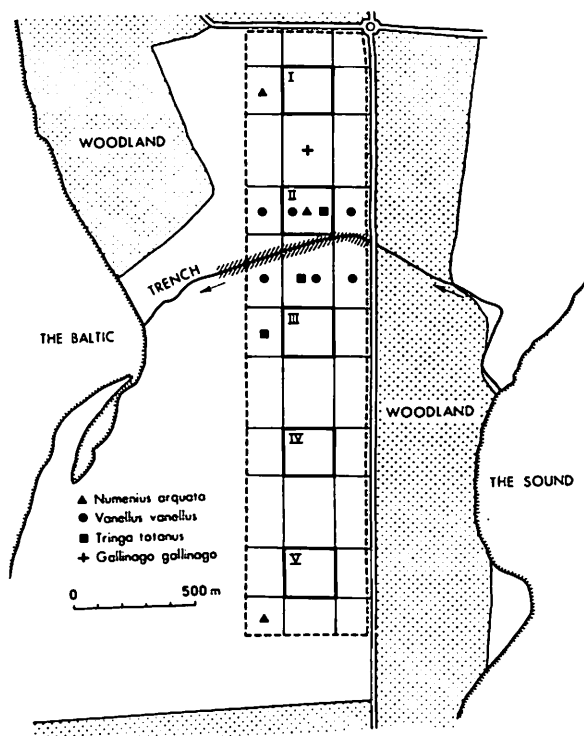


Fig. 1. Experimental area (dotted line) with the study plots I to V and the approximate location of wader territories.

markers. This procedure made it unnecessary to mark the nests, which is important, since such marks may become incorporated into a predator's searching image and hence affect predation rates (Hammond and Forward 1956). At the start and end of each experiment we frequented the experimental area for about 90 min. No searching predators were seen during these periods.

We used dwarf hens' eggs (41 g, 48 × 36 mm) painted so as to resemble lapwings' eggs. Nests were placed in the open without any shelter. Each experiment was terminated after 3 or 1 days (see Tab. 1). Remaining eggs were removed, and only after a lapse of several days was a new experiment initiated.

Tab. 1. A = number of exposed nests, B = percentage of nests robbed by the end of the experiments. Plot size 4 ha. See Fig. 1.

Experiment No.	Experimental period	I		II		Plots III		IV		V		Total	
		A	B	A	B	A	B	A	B	A	B	A	B
1	16-19 April..	4	0	12	0	6	50	8	87	16	94	46	54
2	22-25 April..	16	100	6	33	8	100	12	100	4	100	46	91
3	29-30 May..	12	67	16	0	6	83	8	100	4	100	46	54
4	8- 9 May..	12	92	16	37	8	100	4	75	6	67	46	65
5	14-15 May..	6	100	12	42	4	75	16	100	8	100	46	83
6	21-22 May..	16	100	4	100	12	100	8	100	6	100	46	100
Average .....		11.0	86	11.0	26	7.3	89	9.3	96	7.3	93	11.7	75

3. Results

Fig. 1 shows within which squares wader territories were situated. Note that plot II was the only one with breeding waders, presumably owing to the slightly wetter ground there. Total wader density in the experimental area amounted to 0.10 pairs ha<sup>-1</sup>. Other large breeding birds included one pair of pheasant *Phasianus colchicus* L. and partridge *Perdix perdix* L. and three of mallard *Anas platyrhynchos* L. and eider *Somateria mollissima* L., respectively. These birds were censused only within the study plots and the directly intervening rectangles and attained a combined density of approx. 0.25 pairs ha<sup>-1</sup>. Passerines (chiefly meadow pipit *Anthus pratensis* L.) censused only within the study plots occurred in a total density of about 3 pairs ha<sup>-1</sup>.

The results of the experiments are presented in Tab. 1. Clearly plot II deviated from the rest; the rate of nest predation was significantly lower in this plot than in all the others ( $\chi^2$ , two-tailed,  $p < 0.001$ ). The other four plots did not differ significantly from each other. A special comparison between plots I and II (in which we collected data about predator activities – see below) revealed that nests in plot I were significantly more preyed upon than those in plot II in 4 out of 6 experiments (Fisher exact probability tests, two-tailed,  $p < 0.05$ ), with no differences in the first and last experiments.

In Tab. 2 we examine the relationship between nest density and predation after exclusion of plot II. Obviously predation rates were higher at higher nest densities. Cross-wise testing demonstrated that densities of 2 and 4 nests ha<sup>-1</sup> were significantly more preyed upon than 1 and 1.5 nests ha<sup>-1</sup> ( $\chi^2$ , one-tailed,  $p < 0.005$ ). A density of 3 nests ha<sup>-1</sup> was not significantly different from the two lowest densities ( $p < 0.03$ ).

As indicated in Tab. 1, exposure duration was 3 days in the two first experiments but in a later period this was shortened to 1 day because of the rapid removal of eggs. Therefore we have separately analyzed the two first experiments and the rest, respectively. If plot II is excluded, cross-wise testing within each of the two periods revealed that densities of 1 and 1.5 nests ha<sup>-1</sup> were significantly less preyed upon than the higher densities (Fisher exact probability tests,  $p < 0.05$  and, in one case,  $p < 0.07$ ), except for a density of 3 nests ha<sup>-1</sup> during the later sequence of four experiments. It

Tab. 2. Relationship between density of artificial nests and predation rates.

Density nests ha <sup>-1</sup>	% predation	
	Total	Excluding plot II
1	75	70
1.5	67	73
2	98	98
3	67	90
4	72	98

Tab. 3. Predator activities and rates of antipredator attacks (chiefly by lapwings) in plots I and II. See Fig. 1.

Predator	Plot I		Plot II	
	<i>Corvus</i>	<i>Larus</i>	<i>Corvus</i>	<i>Larus</i>
Attacked (min).....	0	1	8	13
Not attacked (min)....	180	132	4	66
Predator present (min) .	180	133	12	79

is notable that the predicted differences in predation rates between the three highest nest densities were not observed.

Predation rates on the artificial nests increased throughout the study period except between the second and third experiments, when the exposure time was altered from 3 days to 1. Between experiments 1 and 2 and between 5 and 6 the differences were significant ( $\chi^2$ , two-tailed,  $p < 0.01$ ).

As shown in Fig. 1, the low nest predation rate in plot II was associated with the presence of several wader territories. Lapwings (94% of the time) and curlews *Numenius arquata* L. (6%) spent 34 min attacking potential predators, according to a special study covering 90 min each morning and evening, respectively, during the last 8 days of the study period. The only potential predators recorded were hooded crow *Corvus corone cornix* L. and herring gull *Larus argentatus* Pont., and lapwing and curlew were the only species seen attacking them. Tab. 3 demonstrates that the frequency of attacks was much higher inside plot II than in plot I, the difference being highly significant ( $\chi^2$ , two-tailed,  $p < 0.001$ ). In fact many predators were seen off by the lapwings before reaching study plot II. This early defence probably explains why predators spent much less time inside plot II in comparison with plot I (Tab. 3).

4. Discussion

Predation rate increased during the study period (Tab. 1). Predator learning is one likely explanation. Within the range of nest densities provided, predation rate was found to be density dependent. Note that the densities of the artificial nests were low (cf. Tinbergen et al. 1967), in the order of what might be expected in open habitats; they were certainly far from those of colonial birds.

Is it possible that the lower frequency of predators over plot II was caused by some factor other than the lapwings' defence? One might imagine that predators would visit an area less often if nests were comparatively hard to find, for example, because of dense cover. However, to the human eye, nests were at least as conspicuous in plot II as elsewhere. Thus, the lower frequency of predators over this plot was probably not due to the nests being better hidden there.

Many eggs were found bearing marks of avian predators, and crows were seen carrying away eggs. We have

no evidence for predation by mammals, but a fox *Vulpes vulpes* L. was sighted within the study area on two occasions.

Our field procedures were designed to prevent the provision of marks in the terrain that might guide predators to the nests, and our movements in the study area did not create any visible tracks in the vegetation.

The pattern of density dependent predation was markedly disturbed by the effects of the lapwings whose aggressiveness against predators greatly reduced the predation rate of the artificial nests located within or near lapwing territories. This shows that the addition of a population to a community may reduce (and not increase) the predation rates for other community members. This is in contrast to Fretwell's (1972) hypothesis that "the nest mortality of each open nest would be dependent on the density of all open nests, irrespective of species". It may be an important adaptation for these other species to incorporate the presence of aggressive species into their own mechanism of habitat selection.

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