THE EFFECTIVENESS OF NEST DEFENCE BY BLACK-TAILED GODWITS *Limosa limosa*

R.E. GREEN[1], G.J.M. HIRONS[1] & J.S. KIRBY[2]

ABSTRACT This paper describes measurements of the frequency of aerial attacks on avian predators by nesting Black-tailed Godwits. The effects of these attacks on the ranging behaviour of Carrion Crows and the removal of eggs from artificial nests are assessed and compared with the effects of similar attack behaviour by Lapwings. A high proportion of the Carrion Crows and Grey Herons that approached Godwit colonies were attacked. Kestrels were attacked when Godwits had chicks but tended to be tolerated when they were incubating. This difference may be related to the risk of predation from this species at the two stages of breeding. Attacks by Godwits were more effective than those by Lapwings in excluding Carrion Crows and protecting artificial nests even though Lapwings attacked Crows in larger groups. It is speculated that body size has an important influence on the effectiveness of attacks on predators and the advantages of communal nest defence.

[1]Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, England SG19 2DL. [2]British Trust for Ornithology, Beech Grove, Tring, Herts, England HP23 5NR

INTRODUCTION

Waders (Charadriiformes: Charadrii) nest mainly on the ground in open, sparsely vegetated habitats where their nests and young are particularly vulnerable to predation. They exhibit a variety of adaptations which appear to reduce this risk, including cryptic colouration of the eggs or adult plumage, selection of nesting substrates which aid concealment (Pienkowski 1984), distraction displays and solitary or communal attack behaviour against predators. The conspicuous active nest defence behaviour of nesting Lapwings *Vanellus vanellus* and Black-tailed Godwits *Limosa limosa* has been described in detail and its effectiveness investigated by observation and experiment (Lind 1962, Goransson *et al.* 1975, Dyrcz *et al.* 1981, Byrkjedal 1985, Elliott 1985). In this paper, we assess the responsiveness of Black-tailed Godwits to different avian predators according to the stage of breeding and compare the effectiveness of attacks by Godwits and Lapwings in excluding Carrion Crows *Corvus corone* from the airspace above their nests and in protecting nests from predators.

METHODS

Study area

The work was carried out in April-June 1984 at the Ouse Washes, Cambridgeshire, England, a strip of pastureland 0.8-0.9 km wide and 31 km long that is used as a flood relief area. Black-tailed Godwits breed in loose colonies of a few pairs with nests 50-100 metres apart. Searches of the whole area were made to determine the distribution of all breeding pairs and most nests were located. Other waders were counted on the two Godwit study areas (see below) on two dates in May by walking the fields to approach every point to a maximum of 100 m. The positions of waders seen were mapped but no systematic attempt was made to locate nest sites.

Observations

We studied two Godwit colonies, called SW and FL, 3 km apart. In each colony the modal number of pairs with nests in early May was four, but there were one or two additional pairs associated

Received November 1989, accepted March 1990.

with each colony which did not nest or whose nests were destroyed by predators soon after laying. We watched from hides or vehicles on banks at the edge of the pastureland area and obtained information on interactions between Godwits and potential predators of eggs or young in two ways.

(1) Whilst collecting time budget data on pairs with eggs or young we recorded the closest approach to Godwit nests or broods within the breeding colony by any Carrion Crow, Grey Heron *Ardea cinerea*, Kestrel *Falco tinnunculus* or gull *Larus* spp. which came nearer than 300 m to nests or chicks. Aerial attacks on the intruding birds were described.

(2) During the period 20 April to 26 May, when 1-4 Godwit pairs were incubating in each colony, we observed areas of 45 ha (SW) and 65 ha (FL) centred on the colonies continuously for periods of 1-6 hours and recorded the activity of Crows. Movements of Crows were plotted on 1:3200 scale maps and foraging activities and interactions with Godwits, Lapwings and other crows were noted. All observations of crows were of solitary individuals or pairs. These birds were taken to be those that were nesting in trees near the edges of the study areas. Crows were seen to make forays out from the vicinity of their nests to quarter the fields or perch on fence posts. The continuous observations of Crows showed that study area SW fell almost entirely within the territory of one pair of Crows although an area at one edge was used by another pair. Area FL was divided almost equally between two pairs which occasionally met and disputed a well defined boundary. Area FL was too large to be observed from one place so half of the area was watched at a time. Total times watched were 25 hours for SW and 19 hours for FL.

Experiment

In area FL artificial nest scrapes about 10 cm in diameter were made in places with short vegetation. Three hens' eggs were placed in each nest. The eggs were clearly visible from above the nest. Nests were set out in three groups of ten, each covering an area of about 6 ha. The nests were not distributed on a regular grid, but none was placed closer than 30 m to another. One group was within the Godwit colony and the others were about 400 m from its centre. It was found subsequently (see Results) that the use of an area by Crows was influenced by its distance from the Crows' nest. The distance of artificial nests from the Crows' nest of the Crow territory within which they had been placed was not standardised. Means and ranges of these distances for the three nest groups were; A, mean 479 m, (range 407-559 m); B, 538 m (283-869 m); C, 696 m (562-838 m).

During the experimental period three pairs of Godwits were incubating and one pair had small chicks within the colony area. The artificial nests were checked daily and their contents recorded. Unfortunately one of the nest groups was monitored for a different period than the others because the setting out of one group was delayed for three days. Shallow flooding terminated the experiment after two nest groups had been monitored for seven days and the third for four days. Two eggshell dumps (i.e. areas to which Carrion Crows take eggs before removing the contents) were checked at 2-3 day intervals during the experiment and any remains of hens' eggs retrieved.

RESULTS

Responses of Godwits and Lapwings to avian predators

Carrion Crows, Grey Herons and Kestrels were the potential predators seen most frequently. They were recorded to approach to within 300 m of the nearest Godwit nest or brood on 232, 56 and 31 occasions respectively. Fewer than ten approaches were recorded for large gulls (*L. argentatus* and *L. fuscus*) and Marsh Harrier *Circus aeruginosus*. Small gulls (mostly *L. ridibundus*) were usually seen overflying the area at a considerable height and were ignored by the Godwits. Godwits and Lapwings pursued and swooped at avian predators singly or in concert with others. Of 268 attacks on Carrion Crows 65 (24%) were by both Godwits and Lapwings. Numbers of Lapwings involved in

attacks on Crows tended to be larger (mean 4.2, range 1-22, N = 221 attacks) than for Godwits (mean 1.9, range 1-6, N = 112). Carrion Crows were sometimes forced to the ground by these attacks.

The proportion of approaches that were attacked by Godwits was calculated for the categories of distance of closest approach 0-50 m, 50-100 m, 100-150 m, 150-200 m and 200-300 m. The results are shown in Fig. 1 divided according to the species of intruder and whether the majority of Godwit pairs in the colony were incubating or had chicks. Some distance categories have been combined to increase sample sizes. Results for the two colonies were similar and have been pooled. There was a significant tendency for Crows and Grey Herons to be more likely to be attacked by Godwits the closer they approached the colony (Fig. 1; test for linear trend in proportions carried out on disaggregated data, $P < 0.001$, $P = 0.007$ respectively). Differences between the incubation and chick rearing stages in the proportions of approaches that were challenged were tested by Mantel-Haenszel tests (Snedecor & Cochran 1980) to avoid pooling data for different colonies and approach distance categories into one 2 x 2 table. The proportion of Kestrel approaches that were challenged was significantly higher in the chick rearing than incubation period ($Z = 2.84$, $P = 0.005$) but there was no significant difference for Crows or Grey Herons ($Z = 0.68$, $P = 0.50$; $Z = 1.52$, $P = 0.13$).

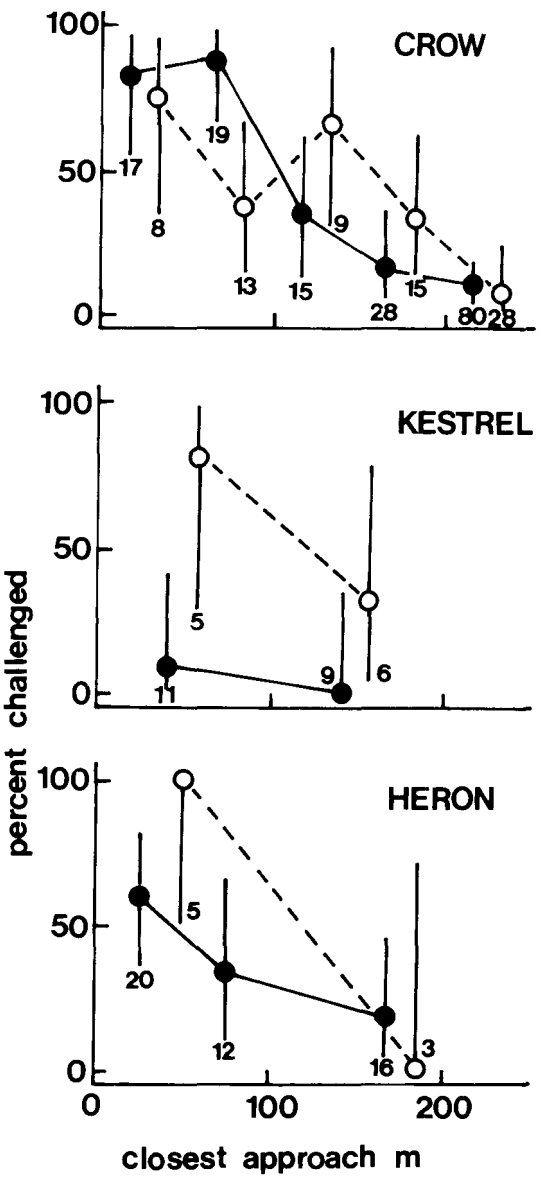

Fig. 1. The proportion of approaches by Carrion Crows, Kestrels and Grey Herons that were challenged by nesting Black-tailed Godwits in relation to distance of closest approach to the colony and stage of breeding (closed circles- incubation, open circles- chick stage). Vertical lines represent 95% exact confidence limits. The numbers of approaches observed are given below each point.

Effect of Godwit and Lapwing attacks on the ranging behaviour of Carrion Crows

Maps of crow movements during continuous watches were analysed by superimposing a grid of 100 x 100 m squares and recording the number of times a crow entered each square and whether or not it was attacked by Godwits or Lapwings while present. The rate of visiting by crows per hour and the proportions of visits that were challenged by Godwits and Lapwings are shown as contour maps in Fig. 2. The area defended by Godwits was well defined and included all the nests in both colonies. Insufficient information was available on the location of Lapwing nests to delimit their nesting colo-

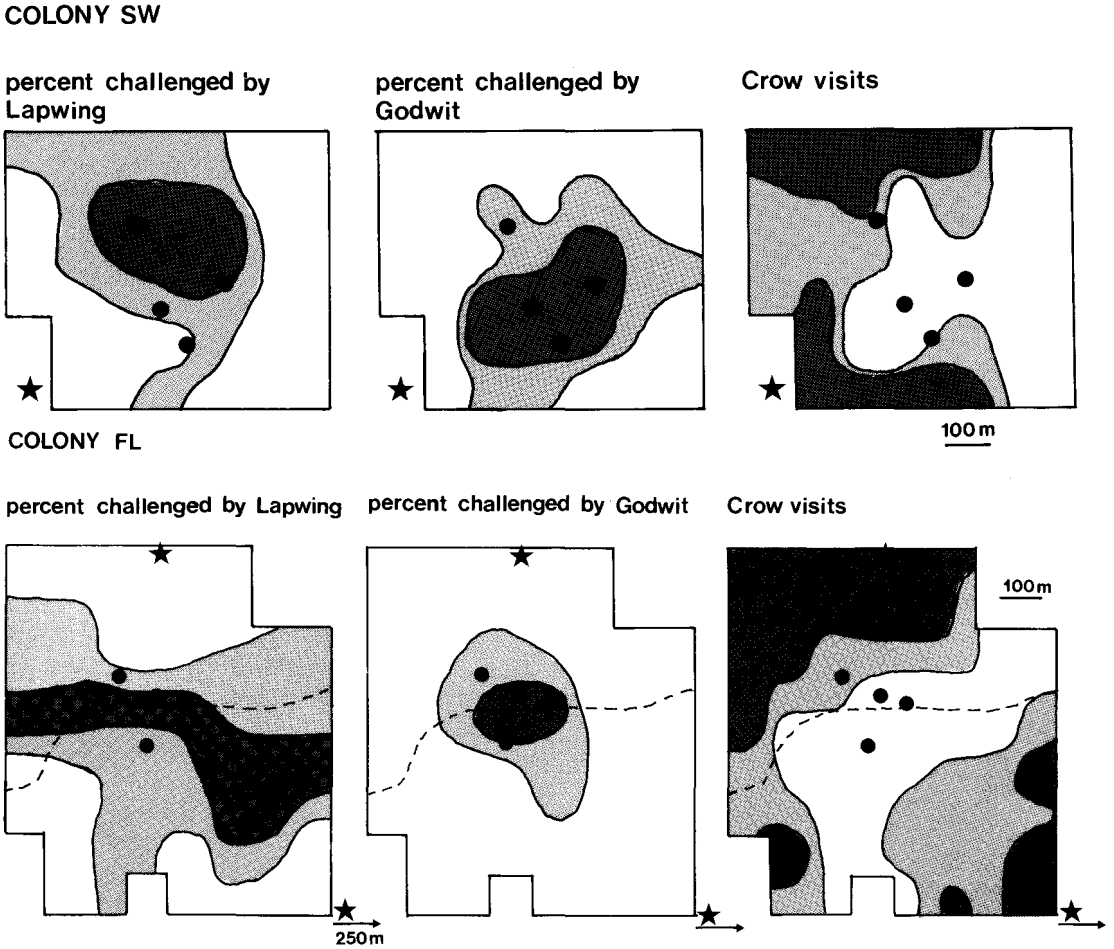

Fig. 2. Contour maps representing the frequency of visits of Carrion Crows to 100 x 100 m squares in the vicinity of two Black-tailed Godwit colonies and the proportion of visits challenged by Godwits and Lapwings. Stars show the positions of Crow nests and the dashed line shows a Crow territory boundary. Circles show the locations of Godwit nests. The frequency distribution of Crow visit rates to squares was divided into three. The most frequently visited third of squares are shaded dark, the least visited are shaded light and the middle third are intermediate. On the maps representing proportions of visits challenged by Lapwings and Godwits, dark shading represents >66% challenged, intermediate 34-66% and light 0-33%.

nies. During wader census visits in May, the average number of Lapwings counted per visit was 16 for area SW and 46 for FL (0.36 and 0.71 birds per ha respectively).

It was clear that Crow visit rate tended to be higher near to Crow nest sites. When visit rate was plotted against the distance of the centre of the 100 x 100 m square from the nest of the Crows in whose territory the square lay there was a tendency for visit rate to decline exponentially with increasing distance. Visit rates were transformed to logarithms before effects other than that of distance from the Crow nest were investigated in order to linearise the relationship between visit rate and distance and to remove a trend in the variance of visit rates with distance from the Crow nest. We considered that the chance of attack by Godwits and Lapwings might affect the use of parts of their territory by Crows so we related

Table. 1. Simple correlation coefficients between the frequency of visiting of 100 x 100 m squares by Carrion Crows, the distance from the Crows' nest and the proportion of visits challenged by Black-tailed Godwits and Lapwings.

variable	2. visits challenged by Lapwings	3. visits challenged by Godwits	Log Crow visits per hour
colony SW			
1. distance from Crows' nest	0.341	-0.184	-0.219
2. visits challenged by Lapwings		0.287	0.069
3. visits challenged by Godwits			-0.298
colony FL			
1. distance from Crows' nest	0.363	0.212	-0.717
2. visits challenged by Lapwings		0.294	-0.506
3. visits challenged by Godwits			-0.449

Table. 2. Multiple regression analysis relating log-transformed frequency of visiting of 100 x 100 m squares by Carrion Crows to the distance from the Crows' nest and the proportion of visits challenged by Black-tailed Godwits and Lapwings. Signed t values are tabulated for the effects of the three independent variables in a linear regression model in which all three are included (SW and FL refer to different areas).

	t-value		
variable	SW	FL	Pooled
1. Distance from Crows' nest	-2.26*	-4.69***	-5.38***
2. Visits challenged by Lapwings	1.81	-1.72	-0.01
3. Visits challenged by Godwits	-2.57*	-2.16*	-3.15**

* $P < 0.05$, ** $P < 0.01$, ***, $P < 0.001$

log Crow visit rate to the proportion of Crow visits challenged by these species. Simple correlation coefficients indicated negative relationships of log Crow visit rate to distance from the Crows' nest and the proportion of visits challenged by Godwits (Table 1). There appeared to be a negative effect of the proportion of visits challenged by Lapwings at the FL colony but not at SW. However there were correlations between some of the independent variables in this analysis so the data were analysed further by multiple regression analysis (Table 2). The analysis indicated negative effects of distance from the Crows' nest and Godwit challenge rate on Crow visit rate for both colonies. The effect of Lapwing challenge rate was not significant in either colony and the direction of the effect differed between colonies. In the analysis of the pooled data for the two colonies any effect of colony was removed by including a dummy variable representing the colony. The analysis was repeated with the independent variables transformed to logarithms but the conclusions were unchanged. We conclude that Crows made most use of areas near to their nests and that, after this effect was taken into account, they were less likely to visit areas in which there was a high risk of being attacked by Godwits.

Removal of eggs from artificial nests

The distributions of times between the start of the experiment and the first record of an egg having been removed from artificial nests varied significantly among the three groups of nests (Fig. 3, Kruskall-Wallis test $H_2 = 11.57$, $P < 0.01$). Times from setting out the nest to the first record of egg removal were classed as 1,2,3,4 and 5 or more days to overcome the problem of the shorter period of monitoring for nest group C. Pairwise comparisons of the three nest groups indicated that eggs began to be taken sooner from nests in groups A and C

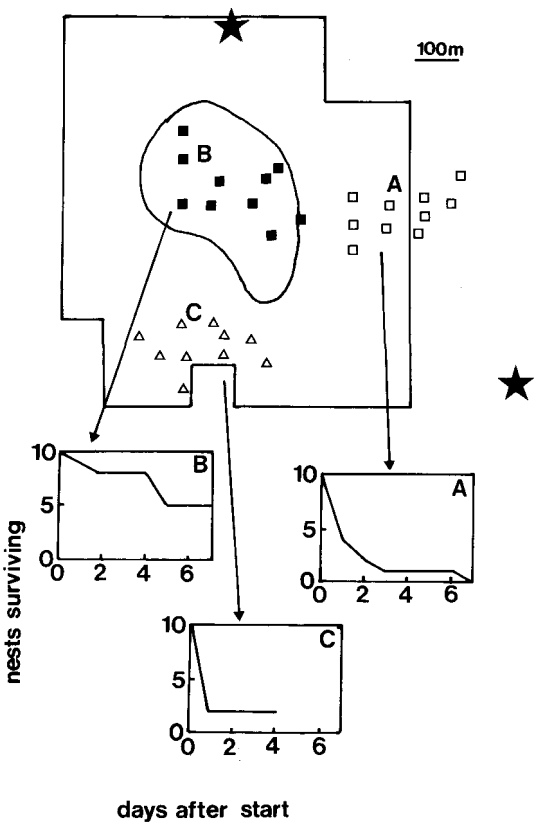

Fig. 3. Predation on artificial nests within and outside Black-tailed Godwit colony FL. The map shows the positions of artificial nests, Crow nests (stars) and the area within which >33% of Crow visits were challenged by Godwits. The graphs show the numbers of nests remaining intact at 24 hour intervals after the start of the experiment.

Table. 3. Speed of removal of hens' eggs from depredated artificial nests inside and outside Godwit colony FL. Numbers of nests from which all three hens' eggs were removed within one 24 hour period are compared with numbers which were partially robbed or where removal occurred over a longer period.

	All eggs taken within:	
Group	1 day	>1 day
A	7	3
B*	0	5
C	8	0

* within the Godwit colony

than from those in group B (Mann-Whitney U tests, A vs. B, $P < 0.005$, A vs. C, $P > 0.50$, B vs. C, $P < 0.005$). Another difference between nest groups was that in groups A and C the whole clutch had usually been removed when the first evidence of egg removal was observed whereas eggs disappeared more gradually from nests within the Godwit colony and all but one of the group B nests contained some eggs at the end of the experiment (Tab. 3). There was significant variation between nest groups in the speed of egg removal from depredated nests (Exact test for a 2 x 3 table (Kalbfleisch 1980), $P = 0.001$). Pairwise comparisons by means of Fisher exact tests showed that significantly more of the depredated nests were partially robbed or robbed over a period of more than one day in the nest group within the Godwit colony (A vs. B, $P = 0.026$, B vs. C, $P = 0.001$, A vs. C, $P = 0.216$).

Comparison of Fig 3 with Fig 2 shows that the areas covered by nest groups A and B were strongly defended against Crows by Lapwings. Nest group C was also defended by Lapwings, but to a lesser extent. Nest groups B and C were in areas of low to intermediate Crow use and nest group A was in an area of intermediate to high Crow use. Hence the rate of removal of eggs from artificial nests is related more strongly to proximity to the Godwit colony than to the degree of defence against Crows by Lapwings or to Crow visit rate.

Of the 61 eggs that disappeared from the arti-

ficial nests during the experiment the shells of nine (15%) were recovered from two shell dumps used by one of the pairs of Carrion Crows nesting near colony FL.

DISCUSSION

Black-tailed Godwits attacked Carrion Crows and Grey Herons that approached their nests or chicks, but were unlikely to attack Kestrels during the incubation period though they did so when caring for chicks. Carrion Crows were frequently seen to take both the eggs and chicks of waders and other birds. Examination of prey remains at Kestrel nest-boxes at the Ouse Washes (unpublished observations) showed that adult Snipe, wader and rail chicks and passerine birds were their main food. Kestrels do not commonly eat birds' eggs (Cramp & Simmons 1980), hence the tendency for Godwits to tolerate Kestrels during incubation and attack them during chick rearing and to attack Carrion Crows during both incubation and chick rearing can be seen as adaptive in relation to the threat of predation at each stage of breeding. In Poland, Dyrcz *et al.* (1981) found that harriers *Circus* spp., which were the main predators of wader eggs, were subjected to vigorous communal attacks by nesting Black-tailed Godwits. Therefore it seems that the response of Godwits to raptors during incubation may vary according to the feeding habits of the raptor species. It is difficult to interpret the Godwits' response to Grey Herons in adaptive terms because they were not seen to seek out the eggs or chicks of any field nesting species during this study though birds have been recorded as prey occasionally elsewhere (Cramp & Simmons 1977).

The activity of Carrion Crows appeared to be centred on their nests. Similarly Erikstad *et al.* (1982) found that predation on both the nests of Willow Grouse *Lagopus lagopus* and artificial nests declined rapidly with distance from the nests of Hooded Crows *C. corone cornix*. When the effect of distance from their nest was taken into account, the distribution of Crow activity was also affected by the likelihood of attack by Godwits. Elsewhere the nest defence activities of Lapwings have also been found to exclude Carrion Crows from their nesting areas and to protect artificial nests near their own (Goransson *et al.* 1975, Elliott 1985) but in the present study there was no evidence of exclusion of Crows from areas defended by Lapwings. Artificial nests in the area defended by Lapwings and not by Godwits (group A) were taken by predators more rapidly than those within the Godwit colony. A protective effect of attacks by Black-tailed Godwits on nearby nests of wader species which do not attack predators was described by Dyrcz *et al.* (1981).

The distance of the artificial nests used in the experiment from Crow nests was not standardised, but the mean distance of the protected artificial nests within the Godwit colony was intermediate between the mean distances for the other two nest groups. Hence it is unlikely that differences between nest groups in distance from Crow nests has produced a spurious effect of protection by Godwits.

Only 9% of hens' eggs removed from the artificial nests were recovered from Crow shell dumps. However, this must underestimate the proportion of the eggs taken by Crows because not all of the eggs removed by the Crows are taken to shell dumps (Loman & Goransson 1978). It is likely that some of the eggs removed from artificial nests were taken by predators other than Crows. Carrion Crows were the most abundant avian predator of eggs, but mammals such as Fox *Vulpes vulpes*, Stoat *Mustela erminea* and Hedgehog *Erinaceus europaeus* were also present. However egg shell remains at depredated nests of Snipe *Gallinago gallinago* and Lapwing at the Ouse Washes in 1982 and 1984 indicated that the majority of eggs were taken by avian predators (Green *et al.* 1987).

Godwits were more effective than Lapwings in excluding Crows and protecting artificial nests even though they attacked in smaller groups. This may have been because their larger size (about 30% heavier than Lapwing) made aerial attacks more difficult for Crows to tolerate. Contact between Godwits and Crows appeared to occur infrequently, but close swooping above or below a flying

Crow often appeared to interfere with its flight because of the turbulence produced by the attacking bird. Crows were seen on several occasions to return to Lapwing nests under attack from groups of Lapwings, remove the eggs one by one and carry them out of range of the attackers before consuming the contents. The failure of predators to remove all the eggs from depredated artificial nests within a Godwit colony suggests that Godwits could deter predators from returning to partially robbed nests in this way.

The possible effect of the body size of the attacking species on the effectiveness of aerial attacks on avian nest predators suggests some predictions about the evolution of nest defence strategies in relation to body size. Large species are better able to drive predators away, but their size relative to the height of vegetation may make it more difficult to conceal themselves on the nest. Small species are less likely to be effective in driving off predators and more likely to be small enough to conceal themselves and their nests in ground vegetation. Among the waders that nest on lowland grassland in north-west Europe this idea is supported. If the seven species are ranked according to mean body weight, the three smallest species (Snipe, Ruff *Philomachus pugnax*, and Redshank *Tringa totanus*) conceal their nests and either remain incubating or slip away when avian predators approach. The larger species (Lapwing, Black-tailed Godwit, Oystercatcher *Haematopus ostralegus*, and Curlew *Numenius arquata*) attack predators and tend to nest in more open habitats where they can see them approaching. A less obvious prediction is that where co-operative nest defence is the only function of colonial nesting we would expect it to occur only in medium sized species. This is because large species in which the pair are capable of repelling predators on their own would be expected to nest solitarily and thereby avoid the disadvantages of colonial nesting such as increased conspicuousness and competition for food. We have already considered the small species in which solitary nesting would be expected because they would be incapable of driving predators away even as a group. Among the seven grassland wader species it is two medium-sized species, the smallest of those which attack avian predators, Lapwing and Black-tailed Godwit, that nest in loose colonies. It would be interesting to know whether this pattern of nest defence strategy in relation to body size occurs in other groups of related species.

ACKNOWLEDGEMENTS

We thank Cliff Carson and Brian Cresswell for their help in carrying out the study and Drs Colin Bibby and Raymond O'Connor for commenting on a draft.

REFERENCES

Byrkjedal, I. 1985. Time budget and parental labour division in breeding Black-tailed Godwits *Limosa limosa*. Fauna norv. Ser. C, Cinclus 8:24-34.

Cramp, S. & K.E.L. Simmons (eds.) 1977. The birds of the western Palearctic, Vol. I. Oxford University Press, Oxford.

Cramp, S. & K.E.L. Simmons (eds.) 1980. The birds of the western Palearctic, Vol. II. Oxford University Press, Oxford.

Dyrcz, A., J. Witkowski & J. Okulewicz 1981. Nesting of 'timid' waders in the vicinity of 'bold' ones as an anti-predator adaptation. Ibis 123:542-545.

Elliott, R.D. 1985. The exclusion of predators from aggregations of nesting lapwings *Vanellus vanellus*. Anim. Behav. 33:308-314.

Erikstad, K.E., R. Blom & S. Myrbyrget 1982. Territorial hooded crows as predators on willow ptarmigan nests. J. Wildl. Mgmt. 46:109-114.

Goransson, G., J. Karlsson, S.G. Nilsson & S. Ulfstrand 1975. Predation on birds' nests in relation to antipredator aggression and nest density. Oikos 26:117-120.

Green, R.E., J. Hawell & T.H. Johnson 1987. Identification of predators of wader eggs from egg remains. Bird Study 34:87-91.

Kalbfleisch, J.G. 1980. Probability and Statistical Inference II. Springer-Verlag, New York.

Lind, H. 1962. Studies on the behaviour of the Black-tailed Godwit.- Monksgaard, Copenhagen.

Loman, J. & G. Goransson 1978. Egg shell dumps and crow *Corvus cornix* predation on simulated birds' nests. Oikos 30:461-466.

Pienkowski, M.W. 1984. Breeding biology and population dynamics of Ringed Plovers *Charadrius hiaticula* in Britain and Greenland: nest predation as a possible factor limiting distribution and timing of breeding. J. Zool., Lond. 202:83-114.

Snedecor, G.W. & W.G. Cochran 1980. Statistical Methods. Iowa State University Press, Ames.

SAMENVATTING

Dit artikel gaat over de verdediging door Grutto's en Kieviten van hun legsel en jongen tegen Zwarte Kraai, Torenvalk en Blauwe Reiger. Het onderzoek werd uitgevoerd op de Ouse Washes, aan de oostkust van Engeland ten noorden van Cambridge. In dit gebied nestelen de Grutto's in kleine kolonies van ongeveer 5 paren. De kans dat een Grutto een naderende predator zal aanvallen hangt af van de afstand tussen nest en predator. De aanvalskans is hoog op een afstand van 100 m, maar is erg klein als de afstand meer dan 200 m is (Fig. 1). Kraaien en reigers worden even vaak aangevallen in de periode dat er eieren zijn als in de periode dat er jongen zijn. Torenvalken worden vooral aangevallen als er jongen zijn. De regelmaat waarmee kraaien het gebied bezoeken hangt af van de aanvalskans van Grutto's, hoe groter de aanvalsbereidheid hoe minder kraaienbezoek (Fig. 2, Tabellen 1 en 2). Het aanvalsgedrag van Kieviten heeft geen aantoonbaar effect op de regelmaat van het kraaienbezoek.

Het Gruttogedrag leidt tot een verhoging van de overlevingskansen van de eieren in de kolonie. Dit bleek bij een experiment met kunstnesten waarin kippeëieren. Deze kunstnesten werden minder geplunderd in de Gruttokolonie dan in door Kieviten verdedigd gebied (Fig. 3, Tabel 3).

De verschillen in effectiviteit tussen de aanvallen van Grutto's en Kieviten worden vooral in verband gebracht met de lichaamsgrootte. JvR.