Ornis Hungarica 7: 39-42. 1997

Distinction of solitary and colonial breeding in waders

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Hegyi, Z. and Sasvári, L. 1997. Distinction of solitary and colonial breeding in waders. – Ornis Hung. 7: 39-42.

Distances between neighbouring nests, antipredator attacks and foraging distances from the nests were recorded in Lapwing (*Vanellus vanellus*), Redshank (*Tringa totanus*) and Black-tailed Godwit (*Limosa limosa*) breeding on 380 ha of meadows in Kiskunság National Park, 50 km south of Budapest. We found a notable low level of simultaneous activities in antipredator behavior when distances between neighbouring nests were longer than 200 m, both in conspecific and heterospecific neighbourhoods and a lower proportion of simultaneous antipredator attacks in non-conspecific neighbourhoods than in conspecific ones. Parents foraged over distances greater than 200 m in most often when they nested closer than 200 m from each other and conversely, parents foraged closer than 200 m when they nested further than 200 m from each other. When the nearest neighbours were closer than 200 m there was a higher proportion of longer foraging distances in conspecific than in non-conspecific neighbourhoods. We suggest that an aggregation of Lapwing, Redshank and Black-tailed Godwit nests separated by less than 200 m may be considered as a single or mixed species colony of waders.

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1. Introduction

It has been showed that aggregation of waders in the breeding season is a strategy that reduces the risk of predation on eggs and chicks. Göransson *et al.* (1975) found that predation rate on artificial nests, exposed in habitats of ground-nesting birds, was lower within aggregations of breeding Lapwings than outside them. Field work focused on the costs and benefits of breeding aggregations in waders has been restricted to single species colonies (Elliot 1985a, 1985b, Berg *et al.* 1992). Only Byrkjedal & Kalas (1983) have reported studies of the adaptive value of mixed species colonies in breeding shore birds.

In this study our question was how the colonial and solitary breeding could be distinguished in waders. Berg *et al.* (1992) considered coloniality exists in Lapwings when neighbouring nests were closer than 200 m. We predicted that coloniality should be reflected in cooperative activities and longer foraging distances from the nests than the distances separating neighbouring nests. Hence we compared the proportion of simultaneous antipredator attacks of neighbouring parents which nested at various distances from each other and the proportion of foraging at distances longer than 200 m for parents whose nearest neighbours nested either closer or further than 200 m.

2. Study area and methods

The study area was chosen on a site where artificial fish ponds had been created in 1953 over 380 ha in Kiskunság National

Tab. 1. Proportions (%) of simultaneous antipredator attacks by neighbouring pairs of three wader species. Antipredator attacks were recorded when both parents of neighbouring pairs were closer than 50 m to their own nest. When one or both of the parents attacked, together with one or both of parents of neighbouring pairs, simultaneous attack was recorded.

Distance from neighbouring nest (m)	Neighbouring species	Lapwing			Redshank			Godwit		
		n	x̄	SD	n	x̄	SD	n	x̄	SD
<100	Conspecific*	12	96.3	10.7	12	78.7	9.3	7	97.8	8.4
	Non-conspecific**	17	86.4	7.6	13	71.1	6.3	15	78.7	10.2
100-200	Conspecific	10	84.0	7.9	11	66.7	5.2	8	83.7	9.4
	Non-conspecific	14	78.9	8.5	15	61.4	7.3	14	74.4	10.1
>200	Conspecific	7	12.0	2.1	14	7.6	2.7	7	10.5	3.1
	Non-conspecific	9	8.4	3.0	21	7.0	2.9	10	7.4	2.8

*There was not heterospecific nest closer than the nearest conspecific nest.
**There was not conspecific nest closer than the nearest heterospecific nest.

Park, 50km south of Budapest (19°07'E, 47°08'N), and where fish breeding was abandoned in 1966. The fish ponds had dried up and were first flooded artifically in 1987. Each August the ponds dried up and were re-flooded every autumn during the study period from 1988-1995.

Lapwing (*Vanellus vanellus* L.), Redshank (*Tringa totanus* L.) and Black-tailed Godwit (*Limosa limosa* L.) nests were detected by observing the incubating parents either from a car parked on the banks or from hides where suitable nesting sites were a long way from the banks. About 70-80 ha could be viewed from the hides and 130-160 ha from the banks. Nests were marked with sticks placed a few meters from them, and their arrangement in the study area was mapped. Nest identification started at the beginning of March.

Marking of birds was carried out using the technique suggested by Paton & Pank (1986). Dummy eggs were treated with a mixture of oil jelly and either Rhodamin B, anilin blue or xylinene orange. Beads of gel (5-10 x 3-5mm) were placed along the length of the eggs, which were then substituted in the nests while both parents were involved in the incubation. Combinations of the colours marked the birds in unique patterns on their abdomens and breasts so that they could be individually identified. Parents from 7-11 nests were marked in each species in each year.

We carried out 280 hours of observations through 8 years for records of

Tab. 2. Proportion (%) of foraging distances longer than 200m from the nests in three wader species. Number of nests indicate small and large aggregation where the neighbouring nests are closer than 200m. Distances were calculated in the aggregations where three species bred.

Distances from nearest neighbour further than 200 m				Distances from nearest neighbour closer than 200 m							
				number of nests		Only conspecific neighbours			Heterospecific neighbours*		
	Lapwing	Redshank	Godwit			Lapwing	Redshank	Godwit	Lapwing	Redshank	Godwit
n	16	35	17	3-4	n	8	9	8	8	7	6
x̄	15.5	8.1	11.2		x̄	79.4	68.9	84.4	66.4	62.2	75.7
SD	2.8	1.5	1.9		SD	8.9	8.3	7.3	8.1	9.0	5.2
				7-8	n	14	14	7	23	21	23
					x̄	82.3	78.2	85.6	71.4	65.2	81.3
					SD	9.7	9.1	6.6	7.5	6.1	5.9

*There was not conspecific nest closer than the nearest heterospecific nest.

antipredator attacks and foraging distance from the nests. To avoid differences due to diurnal fluctuations, the daily period was divided into five time units: 5.00-8.00, 8.00-11.00, 11.00-14.00, 14.00-17.00 and 17.00-20.00, and events were observed and recorded for one hour in each unit. The parents of several nests were observed simultaneously and observations on each type of activity were distributed equally between the first and second half of the incubation period. Observations in all five time periods were taken over one or two days. Magpie (*Pica pica* L.) and marsh harrier (*Circus aeroginosus* L.) represented the most frequent avian predators.

One antipredator attack was recorded when either or both sexes attacked the predator. Foraging distance was estimated by the distance travelled by the parents after leaving the clutch and first beginning to search for food. The distance was coded as 1 = less than 50 m, 2 = between 50 and 200, and 3 = greater than 200 m. Distances over the five hours were averaged for each individual.

Statistical analyses were carried out using the SPSS statistical package, percentage data were arcsine square root transformed for parametric testing.

3. Results and discussion

We found a notable low level of simultaneous activities in antipredator behaviour when distances between neighbouring nests were longer than 200 m, both in conspecific and heterospecific neighbourhoods (ANOVA conspecific and non-conspecific neighbours, Lapwing: $F_{2,26} = 10.43$ and $F_{2,37} = 14.20$; Redshank: $F_{2,34} = 9.16$ and $F_{2,46} = 11.83$; Godwit: $F_{2,19} = 11.35$ and $F_{2,36} = 13.09$; $p < 0.001$ in each occasion; Tab. 1). Pooled data, recorded for various distances showed a lower proportion of simultaneous antipredator attacks in non-conspecific neighbourhoods than in conspecific ones. (In conspecific and non-conspecific neighbourhoods Lapwing: $n = 29$, $\bar{x} = 71.7$, $SD = 6.2$ and $n = 40$, $\bar{x} = 66.2$, $SD = 5.8$, $t = 3.74$; Redshank: $n = 37$, $\bar{x} = 48.2$, $SD = 4.7$ and $n = 49$, $\bar{x} = 40.6$, $SD = 4.9$, $t = 7.31$; Godwit: $n = 22$, $\bar{x} = 65.0$, $SD = 5.0$ and $n = 39$, $\bar{x} = 58.9$, $SD = 6.1$, $t = 4.21$, $p < 0.001$ in each occasion.)

We found that parents foraged over distances greater than 200 m in most often when they nested closer than 200 m from each other and conversely, parents foraged closer than 200 m when they nested further than 200 m from each other (Tab. 2). This was recorded both when the number of close neighbours was low (3-4 pairs) and high (7-8 pairs). (ANOVA Lapwing: $F_{2,32} = 9.81$, $p < 0.001$ and $F_{2,51} = 12.37$, $p < 0.001$; Redshank: $F_{2,31} = 7.33$, $p = 0.001$ and $F_{2,53} = 11.09$. $p < 0.001$; Godwit: $F_{2,29} = 7.18$, $p = 0.002$ and $F_{2,45} = 10.46$, $p < 0.001$. Calculations made for small and large aggregation separately, include the same values of parents whose nearest neighbours were further than 200 m.) When the nearest neighbours were closer than 200 m pooled data showed a higher proportion of longer foraging distances (more than 200 m) in conspecific than in non-conspecific neighbourhoods. (In conspecific and non-conspecific neighbourhoods Lapwing: $n = 22$, $\bar{x} = 81.2$, $SD = 9.4$ and $n = 31$, $\bar{x} = 70.1$, $SD = 7.7$, $t = 4.55$, $p < 0.001$; Redshank: $n = 23$, $\bar{x} = 74.6$, $SD = 8.7$ and $n = 28$, $\bar{x} = 64.4$, $SD = 7.8$, $t = 4.36$, $p < 0.001$; Godwit: $n = 15$, $\bar{x} = 84.9$, $SD = 6.9$ and $n = 29$, $\bar{x} = 80.1$, $SD = 5.7$, $t = 2.62$, $p < 0.02$.)

A breeding colony is generally defined as a place where birds nest in a relatively

small areas and where foraging occurs outside that area. Field applications of the concept of a colony is often difficult, because there is a continuum from solitary breeding to semicolonial and colonial nesting. If, however, co-operative or mutual interactions operate among the individuals they may be regarded as an integrated group (Coulson & Dixon 1979). Nevertheless Alexander (1974) and Koenig (1982) argue that while co-operation and mutual interaction may or may not occur among the colony members, competitive interactions are always evident.

We found a higher level of simultaneous activities in antipredator behaviour for birds which nested within 200 m of each other than for birds nesting further apart. In addition we recorded longer foraging distances for the parents which nested within 200 m of each other than for parents which nested further apart. We believe that our findings support our decision to consider a single or a mixed species colony as an aggregation of Lapwing, Redshank and Black-tailed Godwit nests separated by less than 200 m.

Acknowledgements. We are grateful to Susan Totterdell, Department of Pharmacology, University of Oxford for her linguistic corrections. This work was supported by the Department of General Zoology of Eötvös University, and the Hungarian Scientific Research Fund.

Összefoglalás

Magányos és telepes fészkelés parti madaraknál

A bíbic (*Vanellus vanellus*), a piroslábú cankó (*Tringa totanus*) és a nagygoda (*Limosa limosa*) szomszédos fészkeinek a távolságát, ragadozó ellenes viselkedését, és a táplálkozás során a fészektől való eltávolodás nagyságát vizsgáltuk a Kiskunsági Nemzeti Park egy 380 ha-os vizes réti élőhelyén. Amikor a szomszédos fészkek távolsága 200 m-nél nagyobb volt, a szimultán ragadozó ellenes viselkedés ritka volt. Azonos fajhoz tartozó szomszédos fészkek esetében a szimultán ragadozóellenes viselkedés gyakoribb volt, mint a más fajhoz tartozóknál. A szülők gyakrabban táplálkoztak 200 m-nél távolabb, ha 200 m-nél közelebb fészkeltek egymáshoz, és általában 200 m-nél közelebb táplálkoztak, ha fészkeik 200 m-nél távolabb voltak. Ha a 200 m-n belüli legközelebbi szomszédok azonos fajhoz tartoztak, nagyobb volt a távolabb táplálkozások aránya, mint amikor más fajhoz tartozók fészkeltek egymás közelében. Szerintünk a bíbic, a piroslábú cankó és a nagygoda fészkeinek csoportosulása 200 m-n belül egy-, illetve többfajú kolóniának tekinthető.

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Received: Dec 10 1997, accepted: Feb 18 1998