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Differences in the intensity of nest predation in the curlew *Numenius arquata*: A consequence of land use and predator densities?¹

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Abstract: We quantified the intensity of nest predation in the curlew in two arable farmland areas in western Finland, as well as nest-site characteristics associated with nest predation using data on real nests (1995-1997) and artificial nests (1996). Predation on real curlew nests was consistently higher in the area of mixed farm/woodland than in the area of continuous farmland (64% versus 5% of nests depredated, respectively). There was no evidence that any of the measured nest-site characteristics was associated with high risk of nest predation and, therefore, area differences in predation on curlew nests probably were due to differences in predator density and landscape structure between the two areas. Predation on artificial nests was far higher than on real nests (79% versus 31% of nests depredated, respectively), but there was no difference in nest losses between areas. In both areas, the likelihood of predation on artificial nests was highest in the vicinity of forest edges. The majority of identified predators on real nests were mammals, whereas those on artificial nests were birds. As a result, we were unable to use artificial nests to estimate the threat of predation or to reliably identify factors related to predation risk on real nests in this study.

Keywords: curlew, farmland, nest predation.

Résumé : Nous avons quantifié l'intensité de la prédation de nids de courlis cendrés dans deux régions agricoles de l'ouest de la Finlande, ainsi que les caractéristiques des sites de nidification associés à la prédation, en nous basant sur des nids réels (1995-1997) et artificiels (1996). La prédation des nids réels de courlis était généralement plus élevée dans les régions agroforestières que dans les régions purement agricoles (64 % versus 5 % des nids attaqués). Les caractéristiques des sites de nidification n'étaient aucunement associées à la prédation des nids, ce qui suggère que les différences entre les taux de prédation étaient plutôt attribuables aux différences de densité des populations de prédateurs et de structure des paysages entre les deux régions. Le taux de prédation des nids artificiels était nettement plus élevé que celui des nids réels (79 % versus 31 %), mais il n'y avait aucune différence dans les pertes de ces nids entre les régions. Dans les deux régions, la probabilité de prédation des nids artificiels atteignait un maximum à proximité des lisières des forêts. La majorité des prédateurs identifiés aux nids réels étaient des mammifères, alors que ceux attaquant les nids artificiels étaient des oiseaux. En conséquence, nous étions incapables d'utiliser les nids artificiels afin d'estimer le risque de prédation ou d'identifier de manière fiable les facteurs liés au risque de prédation des nids réels.

Mots-clés : courlis cendrés, régions agricoles, prédation de nids.

Introduction

Nest predation is generally accepted as a major factor accounting for failed breeding attempts of birds (Ricklefs, 1969; Martin, 1993), and is likely to be an important factor in the structuring of communities and in modifying life-history traits (Andrén & Angelstam, 1988; Martin, 1995). As a result, there have been numerous studies, using data on both real and artificial nests, that have attempted to identify factors influencing nest predation (Andrén *et al.*, 1985; Wilcove, 1985; Andrén, 1992; Angelstam, 1986; Huhta, 1995; Huhta, Mappes & Jokimäki, 1996; Møller, 1989; Berg, Nilsson & Boström, 1992). Specific landscape features that favour nest predators, *e.g.*, distance to nearest perch and forest edge, as well as the type and density of predators, may determine the intensity of nest predation on farmland (Page, Stenzel & Ribic, 1985; Møller, 1989; Andrén, 1992).

Many ground-nesting, and particularly open-nesting, birds have evolved a variety of strategies to minimise the risk of nest predation. These include (i) avoidance of landscape features that may favour nest predators, (ii) (semi-) colonial nesting, and (iii) cryptic coloration of plumage and eggs (Dyrce, Witkowski & Okulewicz, 1981; Butcher & Rohwer, 1989; Green, Hiron & Kirby, 1990; Berg, Lindberg & Källebrink, 1992; Larsen & Moldsvor, 1992). But the effectiveness of such anti-predation traits may be limited, particularly in man-made and man-influenced landscapes, where land-use practises and resulting habitat characteristics may benefit predators and/or increase predator densities. For example, habitat fragmentation, which typically results in an increase in the amount of edge-habitat, may cause an increase in edge-dependent predation as predators may use the habitat-edge as both hunting areas and transitory zones (Gates & Gysel, 1978; Wilcove, 1985; Small & Hunter, 1988; Møller, 1989). Furthermore, edge- and patch size-related predation may be particularly acute in agricultural landscapes as open-land predators can better use the

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agriculture-forest boundary (Andrén, 1995; Huhta, Mappes & Jokimäki, 1996). Intensive agricultural practises may reduce habitat heterogeneity and complexity (a consequence of the enlargement of arable fields, a reduction in the variety of crops, and removal of areas covered with natural vegetation), in turn increasing predation by aiding predator search strategies and/or making the nest more visible (Bowman & Harris, 1980; Skeel, 1983).

The curlew *Numenius arquata* is a large ground-nesting wader species characteristic of farm- and moorland in northern Europe (Cramp & Simmons, 1983) in which nest predation is an important factor determining breeding success (Berg, 1992; Grant, 1997). Hence nest predation could be a contributory factor in explaining localised population declines (Grant, 1997; Valkama & Currie, 1999). In this paper, we quantify the intensity of nest predation during

incubation in two arable farmland areas that differ in their respective landscape characteristics; one was interspersed by forests and habitations, whereas the other was part of a larger expanse of continuous farmland. The second objective is to identify nest-site characteristics associated with an increased risk of nest predation, using data on real and on artificial nests.

Material and methods

This study was conducted during 1995-1997 in two arable farmland areas in western Finland; Vammala (18 km²; 61° 22' N, 22° 50' E) and Kauhava (6 km²; 63° 05' N, 22° 56' E). Vammala was the more heterogeneous area consisting of five small agricultural areas (each less than 5 km²) separated by forests, farms, and small communities (Figure 1), whereas

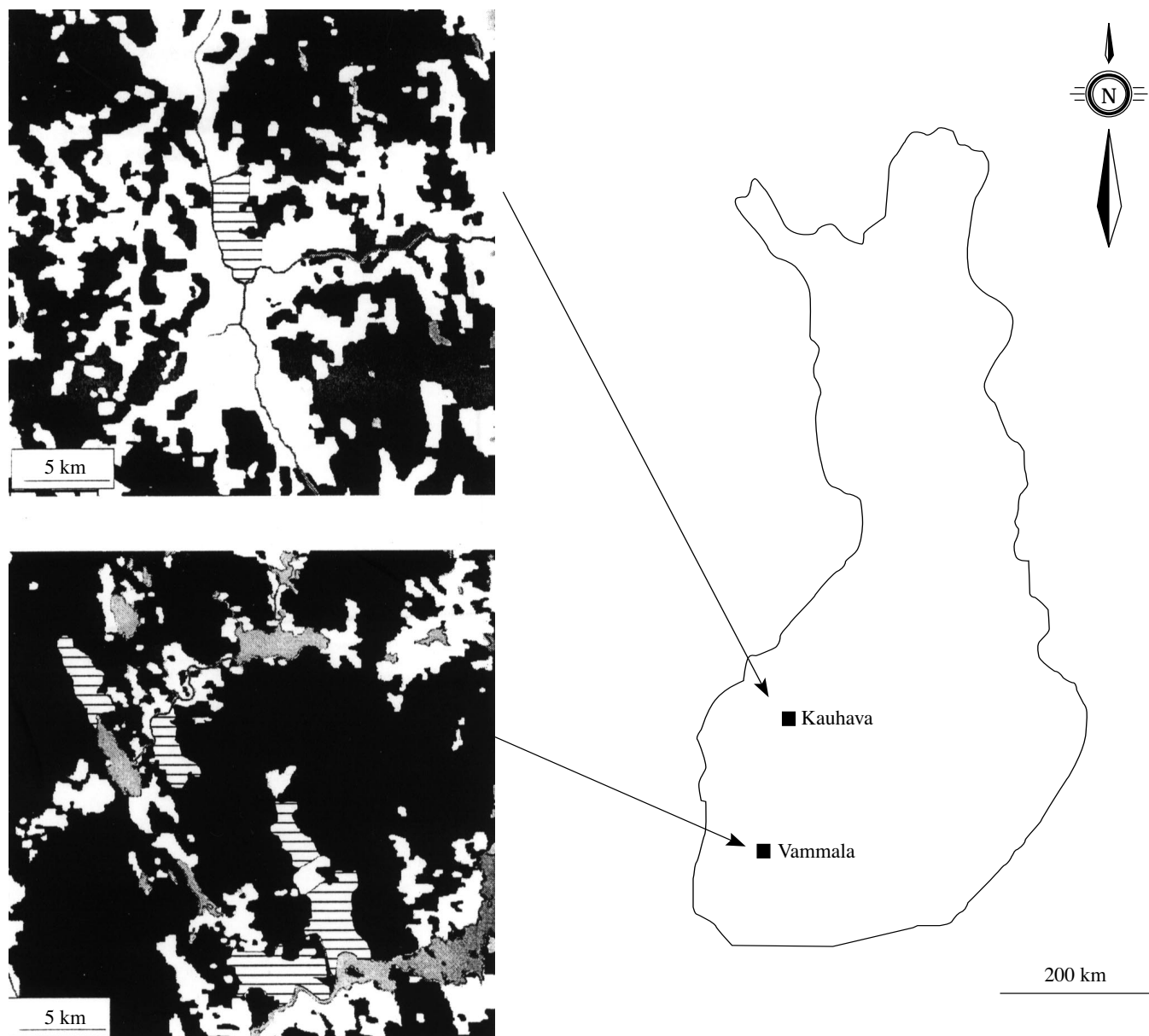


FIGURE 1. Map of Finland showing the location of the study areas. Enlarged maps show their exact location (hatched) and land use (black = woodland, white = farmland, and grey = water areas).

in contrast, Kauhava was part of a larger continuous area of farmland (size 100 km², Figure 1; for more details see Korpimäki & Norrdahl, 1991; Norrdahl *et al.*, 1995; Valkama, Robertson & Currie, 1998). The breeding density of curlews was lower in Vammala (1.6 pairs/km²) than in Kauhava (6.7 pairs/km²), as was the breeding density of other ground-nesting waders, namely lapwings (*Vanellus vanellus*), and whimbrels (*Numenius phaeopus*; O. Hemminki, pers. comm.). Agricultural practices were similar in both areas in all years and most fields were tillage (66%) and hay (15%), the remainder comprised stubble and meadow/fallow.

Curlews arrived in both areas from mid- to late April onwards, and usually the first eggs were laid during the first two weeks of May. Nests were found after the onset of incubation and clutch size was recorded. Sixty-five and 76 first-clutch nests were found in Vammala and Kauhava, respectively. To minimise nest losses during spring farming activities (the first two weeks in May) we marked 80% of these nests with wooden sticks (0.5–1.5 m high, 1 cm thick) in both areas. The sticks were placed two metres from the nest such that they were easy to detect from any approaching tractor. We did not detect any difference in daily predation rate (defined below) between marked and unmarked nests in Vammala where nest predation was most intensive (daily predation rate \pm SE; marked nests: 0.0445 ± 0.0095 ; unmarked nests: 0.0695 ± 0.0186 ; $z = 1.20$, n.s.; see also Galbraith, 1987). Too few nests were preyed upon in Kauhava to perform a similar analysis.

Habitat features were measured at each nest to determine the effect of nest-site characteristics on nest survival. These features were: (i) factors frequently associated with increased predation risk, *i.e.*, distance to forest edge (Stroud, Reed & Harding, 1990; Berg, 1992), distance to perch (Berg, Lindberg & Källebrink, 1992), and distance to ditch (Korpimäki, Norrdahl & Valkama, 1994); (ii) factors associated with human disturbance, *i.e.*, distance to nearest road (as roads are also used as walkways and for recreational purposes in both study areas); and (iii) other nest-site characteristics, *i.e.*, nest habitat (tillage, hay, stubble, fallow/meadow) and distance to other agricultural habitat. Many waders that breed close to each other exhibit communal nest defence against predators (“the protective umbrella”; Göransson *et al.*, 1975; Dyrce, Witkowski & Okulewicz, 1981; Elliot, 1985; Green, Hirons & Kirby, 1990). Therefore, we also counted the number of nests of ground-nesting birds (curlew, whimbrel and lapwing, all of which exhibit aggressive nest defence behaviours; Cramp & Simmons, 1983) within a 100-m radius of focal nests. Ground-nesting birds may also benefit from breeding close to kestrels *Falco tinnunculus* via the additional nest defence they provide from avian nest predators (Norrdahl *et al.*, 1995) and, therefore, the distance from focal nests to the nearest kestrel nest was also recorded.

ARTIFICIAL NESTS

A series of artificial nest experiments was conducted in 1996. The experiments were started on 20 May in both Vammala and Kauhava, and coincided with the middle of the curlew incubation period. In both areas, 70 nests with three brown hen *Gallus domesticus* eggs were assigned to

seven transects (10 nests per transect, interval between nests 50 m). Transect sites and directions were selected randomly and proportion of nests on different habitat types reflected the availability of these habitats in the landscape. Nests were made at dusk, to reduce attracting the attention of avian predators, and were marked with < 5 cm high sticks positioned at least 5 m from the nest. Nest contents were checked by quickly walking past them two, five, nine, and 18 days after the start of the experiment. If eggs were missing or broken, the nest was regarded as depredated, and the predator was identified whenever possible. Predators were identified by tracks on the ground or by tooth/beak marks on the egg. At the end of the experiment (day 18), the same nest-site characteristics were measured as for real nests.

STATISTICAL ANALYSES

All analyses for real nests refer to first broods and exclude nest losses incurred due to farming practises ($n = 18$) and nest desertions ($n = 4$). During the study period, we did not find any evidence of partial nest predation. To explore whether artificial nests were independently depredated within a transect we randomly selected one pair of adjacent nests (1–2, 3–4, etc.) and remote nests (1–10, 2–9, or 3–8), and compared their success. There was no indication that two adjacent nests within a transect had the same fate (depredated/non-depredated) more frequently than nests farther away from each other (86% of the pairs had the same fate in both groups) and, therefore, we assumed nests on transects to be independent data points (see also Møller, 1989; Huhta, 1995).

Daily predation rate ($P = \text{number of failed nests/number of observation days}$) for both real and artificial nests was calculated after Mayfield (1961; 1975). Standard errors and z -tests for comparison of daily predation rates were calculated after Johnson (1979) and Hensler & Nichols (1981).

Data were analysed using the SAS (SAS Institute Inc., 1990) and SPSS (Norusis, 1993) statistical packages. We used logistic regression analysis to examine the effects of nest-site characteristics on the survival (depredated/non-depredated) of real and artificial nests (separate analyses). Due to the low number of depredated curlew nests in Kauhava (three), the effects of nest-site characteristics on survival of real nests was analysed only in Vammala where nest predation was most acute. Distances (m) to nearest forest edge, perch (*e.g.*, tree, pole, stick etc), ditch (including small streams and rivers), patch of other agricultural habitat, and road were entered as continuous variables. Nest habitat type (tillage, hay, stubble, and fallow/meadow) and presence of wader nests (0 or ≥ 1) within a 100-m radius of focal nests were entered categorically. Distance to kestrel nest was also entered categorically as ≤ 500 m or > 500 m, because kestrels concentrate most of their nest defence within a 500-m radius of the nest (Tolonen & Korpimäki, 1995 and unpublished data). Nest-site characteristics (listed above) were only entered into the multivariate model if their univariate significance had a P -value < 0.25 (Hosmer & Lemeshow, 1989). Non-significant factors were removed, starting with the least significant, until only significant factors remained. Due to relatively small sample sizes we were unable to consider interactions in these analyses.

There were no significant between-year differences in daily predation rates of real nests during 1995-1997 within areas (Table I), and therefore data were grouped for all years in each area. This resulted in the replication of some territories because the breeding site fidelity of curlew is high (Berg, 1994; M. C. Grant, pers. comm). However, there was no indication that predation was limited to specific territories; data presented for Kauhava consist of 66 breeding attempts from 53 territories (data for 14 same territories), whereas data for Vammala represent 53 breeding attempts from 32 territories (data for 19 same territories); however, only four of the 33 replicated territories were consistently depredated between years. It therefore seems likely that nest-site/area characteristics as opposed to territory and/or adult characteristics *per se* were probably more important in accounting for nest predation, and that the replication of territories caused minimal bias in the analyses.

Results

REAL NESTS

The marked difference in nest-site characteristics between the two areas reflected the differences in landscape features between Vammala and Kauhava (summarised in

TABLE I. Daily predation rates of curlew nests in Vammala and Kauhava 1995-1997 (calculated after Mayfield, 1961; 1975). Standard errors and *z*-tests for comparison of daily predation rates and hatching success were calculated after Johnson (1979) and Hensler & Nichols (1981). Hatching success is the probability of surviving 30 days (the duration of incubation; $P^{30 \times 100}$). Daily predation rates were significantly higher in Vammala than in Kauhava within years (1995, $z = 2.55$, $p < 0.05$; 1996, $z = 2.81$, $p < 0.01$; 1997, $z = 3.91$, $p < 0.001$), but did not differ significantly within areas between years (*z*-test, all tests not significant)

	Predated	Non-predated	Number of nest days	Daily predation rate (\pm SE)	Hatching success
VAMMALA					
1995	9	9	202.5	0.044 \pm 0.0145	25.6
1996	10	7	252.5	0.040 \pm 0.0123	29.7
1997	15	3	204.0	0.074 \pm 0.0183	10.1
1995-1997	34	19	659.0	0.052 \pm 0.006	20.0
KAUHAVA					
1995	1	16	185.0	0.005 \pm 0.005	86.0
1996	1	21	419.5	0.005 \pm 0.002	86.6
1997	1	26	627.5	0.002 \pm 0.002	95.3
1995-1997	3	63	1232.0	0.003 \pm 0.001	91.0

TABLE II. Nest-site characteristics (mean \pm SE) of real and artificial nests in Vammala and Kauhava. Wader and kestrel show the proportion of nests that had at least one wader nest within 100-m radius or one kestrel nest within 500-m radius. Tillage shows the proportion of nests that were on tillage. Differences between areas were tested using Mann-Whitney *U*-tests (distance variables) and Chi-square tests

	Real nests			Artificial nests		
	Vammala ($n = 53$)	Kauhava ($n = 66$)	<i>P</i> -value	Vammala ($n = 70$)	Kauhava ($n = 70$)	<i>P</i> -value
Distance (m) to						
Ditch	33.1 \pm 4.2	19.8 \pm 2.1	< 0.05	48.6 \pm 6.4	19.6 \pm 2.13	< 0.05
Forest edge	239.9 \pm 27.1	761.7 \pm 64.8	< 0.0001	336.2 \pm 25.4	575.1 \pm 36.8	< 0.0001
Other habitat	81.8 \pm 8.9	42.0 \pm 7.2	< 0.0001	139.1 \pm 15.1	49.0 \pm 5.4	< 0.0001
Perch	74.3 \pm 6.5	70.8 \pm 5.2	n.s.*	73.9 \pm 7.8	68.9 \pm 5.2	ns
Road	195.9 \pm 21.7	475.2 \pm 41.7	< 0.0001	158.4 \pm 15.0	251.1 \pm 22.1	< 0.01
Wader	1.9	16.7	< 0.01	21.4	21.4	ns
Kestrel	20.8	30.3	ns	4.3	50.0	< 0.0001
Tillage	41.5	30.3	ns	75.7	77.1	ns

* n.s.: not significant.

Table II). Nests in Vammala were significantly closer to the forest edges and roads, whereas nests in Kauhava were closer to ditches and patches of different agricultural habitat (a consequence of narrow fields separated by ditches; the mean length of ditches in Vammala was only 73 m/hectare but in Kauhava it was as much as 184 m/hectare; Valkama & Currie, unpubl. data). Curlew nests in Kauhava were also closer to other wader nests (curlew, lapwing, or whimbrel) than in Vammala.

The difference in landscape characteristics is further highlighted by comparing 50 random plot - forest edge distances (m), measured in each area, which were significantly larger in Kauhava than Vammala (mean \pm SE; Vammala = 180.1 \pm 19.7 m, Kauhava = 619.0 \pm 63.2 m, Mann-Whitney *U*-test, $z = 5.41$, $p < 0.0001$).

Daily predation rate of real nests differed significantly between areas within years, being consistently higher in Vammala than in Kauhava (Table I). As a result, hatching success was also lower in Vammala than in Kauhava (Table I).

None of the measured nest-site characteristics affected survival of curlew nests in Vammala (Table III) and therefore it was likely that some other factor(s) explained the poor hatching success in that area (*e.g.*, lower wader density, higher predator density, and/or generally more fragmented landscape, see Figure 1, Tables II and V).

For the 12 out of 38 (32%) cases for which we were able to identify the nest predator (either avian or mammalian), the majority were depredated by mammals (10 out of 12; identified by tracks and egg remains as either fox (*Vulpes vulpes*) or raccoon dog (*Nyctereutes procyonoides*). Predator identification was based primarily on data from Vammala due to the low predation rate in Kauhava (Table I).

ARTIFICIAL NEST EXPERIMENTS

In general, area differences in nest-site characteristics of artificial nests were similar to that of real nests (Table II). However, predation on artificial nests was far higher than that on real nests, and after only two days, 77% of nests in Vammala and 80% in Kauhava were depredated. Furthermore, unlike real nests, there was no significant difference between areas in the daily predation rate of artificial nests: daily predation rate (\pm SE) was 0.267 \pm 0.021 in Vammala and 0.256 \pm 0.017 in Kauhava; $z = 0.41$, not significant).

TABLE III. Nest-site characteristics (\pm SE) for depredated and non-depredated curlew nests in Vammala. Wader and kestrel show the proportion of curlew nests that had at least one wader nest within 100-m radius or one kestrel nest within 500-m radius. Tillage shows the proportion of curlew nests that were on tillage. None of the measured nest-site characteristics differed significantly between depredated and non-depredated nests

	Depredated ($n = 34$)	Non-depredated ($n = 19$)
Distance (m) to		
Road	188.2 \pm 24.9	209.7 \pm 41.9
Forest edge	210.4 \pm 30.8	292.6 \pm 50.6
Ditch	33.4 \pm 5.0	32.5 \pm 7.6
Other habitat	75.7 \pm 10.6	92.6 \pm 15.9
Perch	71.6 \pm 7.0	79.2 \pm 13.4
Wader	2.9	0.0
Kestrel	17.6	26.3
Tillage	44.1	36.8

At the start of the experiment (two days), artificial nests close to the forest edge were more likely to be depredated in both areas (Table IV). In Vammala, depredated artificial nests were also closer to perch-sites and further from patch edges (as indicated by distance to other agricultural habitat). By the end of the experiment (day 18), almost all artificial nests were depredated (93% in Vammala, 90% in Kauhava), and we could not compare nest-site characteristics for depredated and successful nests.

At the majority of depredated artificial nests there were no egg remains or tracks (when nests were located on tillage) with which to identify predators, and as a result we were only able to identify the predator (avian *versus* mammalian) at 31% (44/140) of nests, 91% (40/44) of which were preyed upon by birds.

Discussion

This is one of the few studies to simultaneously examine nest predation using real and artificial nests in the same areas (see also Berg, 1996; Guyn & Clark, 1997; Valkama & Currie, 1999). There was a consistent yearly difference in predation on real nests between areas as, on average, 80% of curlew nests in Vammala were depredated, whereas only 9% of nests were depredated in Kauhava (similar to 8% previously observed in this area; Norrdahl *et al.*, 1995).

However, there was no inter-area difference in predation on artificial nests, albeit only one year's data were available. Predation on artificial nests was far higher than on real nests (see also Martin, 1987; Storaas, 1988; Willebrand & Marcström, 1988; but see Götmark, Neergaard & Åhlund, 1990), although this was expected due to their increased vulnerability—a consequence of the lack of parent birds to provide nest defence and incubate the eggs (Storaas, 1988; Willebrand & Marcström, 1988; Berg, 1996). The majority of real nests were obviously depredated by mammals, whereas birds appeared to be the main predators on artificial nests (see also Andrén *et al.*, 1985; Angelstam, 1986; Sugden & Beyersbergen, 1986; Andrén, 1992; Nour, Matthysen & Dhondt, 1993; Valkama & Currie, 1999).

FACTORS AFFECTING NEST PREDATION

The survival of real nests in Vammala (where nest predation was most acute) was not associated with any of the measured nest-site characteristics. For example, although proximity to forest edge or road is often associated with an increased threat of nest predation (Møller, 1989; Stroud, Reed & Harding, 1990; Tüllinghoff & Bergmann, 1993) nest survival in this study was not related to the distance from the nest to nearest forest edge or road. It is possible that curlews had few options when selecting their nest-sites in Vammala due to the fragmented landscape (Figure 1), *i.e.*, individuals were unable to avoid nesting close to forest edges and roads, and this resulted in nests being more vulnerable to predation (Andrén, 1992). However, proximity to forest edge *per se* cannot explain the observed difference in predation rate between the study areas, because in Vammala 26 out of 37 nests (70.3%) that were at most 300 m from the forest edge were depredated, whereas in Kauhava only 1 out of 18 (5.3%) was depredated. Therefore, it is likely that other factors facilitated nest predation in Vammala. These may include (i) higher predator density (Table V), (ii) lack of communal nest defence due to low wader density (Table II), and (iii) more fragmented landscape structure (Table II). Moreover, all these factors may act in concert.

Long-term data on mammalian predator numbers in Finland (Helle & Kauhala, 1991; Helle *et al.*, 1996; Lindén, Hario & Wikman, 1997; Kurki *et al.*, 1997) indicate that the

TABLE IV. Nest-site characteristics (\pm SE) for predated and non-predated artificial nests (after two days) in Vammala and Kauhava. Wader and kestrel show the proportion of artificial nests that had at least one wader nest within 100-m radius or one kestrel nest within 500-m radius. Tillage shows the proportion of artificial nests that were on tillage. Summary statistics of logistic regression analyses comparing nest-site characteristics of depredated and non-depredated nests are also shown

	Vammala		Kauhava	
	Depredated ($n = 54$)	Non-depredated ($n = 16$)	Depredated ($n = 56$)	Non-depredated ($n = 14$)
Distance (m) to				
Perch	65.2 \pm 8.3	103.4 \pm 18.0	68.5 \pm 6.0	70.9 \pm 10.4
Forest edge	305.3 \pm 28.9	440.6 \pm 45.4	464.6 \pm 27.4	1017.1 \pm 65.9
Ditch	44.1 \pm 7.5	63.9 \pm 11.2	18.5 \pm 2.4	24.1 \pm 5.1
Other habitat	152.0 \pm 18.8	95.6 \pm 14.9	49.3 \pm 6.5	47.9 \pm 7.5
Road	142.2 \pm 16.6	213.1 \pm 31.3	283.9 \pm 25.0	120.0 \pm 25.4
Wader	25.9	6.3	17.9	35.7
Kestrel	1.9	12.5	39.3	92.9
Tillage	77.8	68.8	80.4	64.3

Forest: $\chi^2 = 7.03$, $df = 1$, $p < 0.01$; other habitat: $\chi^2 = 4.26$, $df = 1$, $p < 0.05$; Forest: $\chi^2 = 10.46$, $df = 1$, $p < 0.01$.
Perch: $\chi^2 = 4.56$, $df = 1$, $p < 0.05$.

TABLE V. Relative density indices of mammalian predators 1988-1996 (from Lindén, Hario & Wikman, 1997). Indices of avian predators (crows and black-billed magpies) are not comparable with the mammalian predator densities

	Vammala	Kauhava
Red fox (<i>Vulpes vulpes</i>)	10 - 20	4.1 - 6
Raccoon dog (<i>Nyctereutes procyonoides</i>)	0.6 - 1.5	0.1 - 0.5
Mink (<i>Mustela vison</i>)	0.3 - 0.6	0.3 - 0.6
Stoat (<i>Mustela erminea</i>)	0.6-1.0	2.1-3.0
Avian predator index ¹ (\pm SE)	5.5 \pm 1.3	2.4 \pm 0.6

¹ Avian predator indices were calculated in 1996 from five-minute observations of curlew territories made every 2-3 days on 12 territories in Kauhava and 13 in Vammala prior to laying through to the first week of incubation. The number of potential avian nests predators observed within 500-m of focal territories were noted (mean number of observations per territory \pm SE = 2.3 \pm 0.4). Avian predator indices were higher in Vammala than in Kauhava, Mann-Whitney *U*-test, $z = 1.77$, $p = 0.076$.

density of predators is considerably higher in the southern (Vammala) than in the northern area (Kauhava; Table V). The density of potential avian predators (black-billed magpie [*Pica pica*] and hooded crow [*Corvus corone cornix*], counted in 1996) in the study areas also followed a similar latitudinal pattern (Table V; see also Andrén *et al.*, 1985). On the basis of higher predator densities, we would also expect nest predation to be more frequent in Vammala than in Kauhava.

There are contrary findings between studies examining the effect of breeding density on the intensity of nest predation; in some there is a positive correlation between breeding density and rate of predation (Dunn, 1977; Page *et al.*, 1983), whereas in others there is no correlation (Galbraith, 1988). A positive correlation is expected between predation and the breeding density of farmland wader species when most predators are mammals, as wader nest defence behaviours are thought to be most effective against avian predators (Berg, 1992; Berg, Lindberg & Källebrink, 1992). In this study, nest predation was lowest in the area that had the highest density of breeding waders (Kauhava). This correlates with low mammalian (and avian) predator density (Helle *et al.*, 1996; Lindén, Hario & Wikman, 1997; Table V) and may account for reduced nest predation at a high breeding density in this study.

The size of agricultural areas (suitable breeding habitat for curlew) was much smaller in Vammala (< 5 km²) than in Kauhava (part of 100 km² of continuous farmland; Figure 1), and as a result there was proportionately more farmland-forest edge habitat in Vammala (reflected by the shorter random plot - forest edge distances). Furthermore, the density of roads and farms within the agricultural areas were higher in Vammala than in Kauhava (Valkama & Currie, unpubl. data). Therefore it seems likely that area differences in nest-site characteristics (a consequence of landscape characteristics and the size of the study areas) at least partly explained the higher level of predation in Vammala due to increased exposure to potentially higher predator densities at the field-forest edge and increased human disturbance.

We observed an edge-related increase in predation pressure for artificial nests in both study areas (Table IV). Although not measured in this study, the densities of avian

and mammalian nest predators have been shown to be high at the forest edge (Andrén *et al.*, 1985; Angelstam, 1986; Lindström, 1989), which may result in a higher risk of nest predation (see Möller, 1989; but see Berg, 1992; Vickery, Hunter & Wells, 1992). In Vammala, predation of artificial nests was also higher in the vicinity of perch-sites, which suggests that birds may have been common predators on these nests. Artificial nests close to patch edges were also more likely to be depredated, possibly because most patch edges also have perches and the visibility from these perches decreases with increasing distance.

Data from the artificial nest experiments have shown that intensity of nest predation frequently increases along a north-south gradient in Scandinavia (Andrén *et al.*, 1985; Berg, Nilsson & Boström, 1992; but see Huhta, Mappes & Jokimäki, 1996). In this study, data on real nests were consistent with this pattern. However, this was not the case in our artificial nest experiment, as there was no difference in predation rate of artificial nests between areas. The marked difference in the types of nest predator (avian or mammalian) and patterns of predation between and within areas for real and artificial nests indicate that artificial nests cannot be used (using the current experimental design) to estimate the threat of predation or to identify factors related to predation risk (see also Berg, 1996 and references therein).

In conclusion, our results suggest that the area differences in predator density and landscape features were probably important in determining the intensity of nest predation in the curlew. Since we marked many nests, it was not possible to quantify exactly the influence of nest predation on breeding success; our nest-marking procedure probably underestimated the destructive effects of spring farming practises (Berg, 1992). However, it is clear that breeding success in Vammala was much lower than in Kauhava, much of which can be attributed to nest predation. The curlew population has decreased significantly in northern Europe over the last 20-30 years (Cramp & Simmons, 1983; Bednorz & Grant, 1997), and intensive nest predation may be one reason for the curlew decline observed in southern Finland (Ylimaunu *et al.*, 1987; Valkama & Currie, 1999). It is important for future studies to accurately identify nest predators and measure their densities in an attempt to quantify their impact on breeding success in the curlew.

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