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Habitat selection by breeding curlews (*Numenius arquata*) on farmland: the importance of grassland

Jari Valkama, Pete Robertson & Dave Currie

Valkama, J. & Currie, D., Section of Ecology, Department of Biology, University of Turku, FIN-20014 Turku, Finland
Robertson, P., Central Science Laboratory, Sand Hutton, York YO4 1LZ, UK

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We examined habitat composition of territories, habitat use during foraging, and nest-site selection in the curlew *Numenius arquata* in two arable farmland areas in western Finland 1996–1997. Tall vegetation types, especially grassland, occurred more frequently within territories than expected by their availability. Habitat utilisation during foraging was significantly non-random in one of the two study areas where tillage was preferred to taller vegetation while in the other area curlews appeared to prefer tall vegetation. In both areas curlews showed a marked preference for taller vegetation types and avoided short vegetation (tillage) when selecting their nest-sites. Individuals also appeared to avoid nesting close to forest edges and ditches although this pattern was not significantly consistent between years. Breeding dispersal (the extent of movements between years) was high in the study area where curlew density was low and nest predation was frequent. In this area, breeding dispersal was higher among pairs that had failed in their previous breeding attempts than among successful pairs. Curlews preferred habitats which are relatively uncommon in an intensive agricultural regime, and we suggest that lack of suitable habitats in intensively cultivated farmland areas may be one reason for poor reproductive success and decline of curlew populations in Finland.

1. Introduction

When choosing between different environments an individual is expected to try to maximise its survival and reproductive success (e.g., Morris 1987, Orians & Wittenberger 1991). For species which utilise an all purpose territory (Hinde 1956), the chosen area must contain sufficient resources to meet the individual's requirements, for example sufficient food, suitable nest-sites and protection from predators. As a result, selected areas are likely to comprise a variety of different habitat types and vary in size as resources are not evenly distributed in time and space (Southwood 1977). The choice of a habitat is therefore likely to be a consequence of the abundance, availability, and use of specific resource(s) by the individual.

Farmland typically consists of a wide number of vegetation types and is potentially highly variable between years due to rotational use of fields (e.g., Berg *et al.* 1992, Berg 1993). There can be large differences between agricultural habitats in prey abundance, risk of predation and nest destruction due to farming practices (O'Connor & Shrubb 1986, Berg 1992a). Consequently, habitat selection by ground-nesting farmland birds is expected to be strong (Berg *et al*. 1992).

The curlew *Numenius arquata* is a large monogamous wader characteristic of farm- and moorland. It is a highly territorial species, since breeding and the majority of foraging occurs within the territory which is also defended rigorously against conspecifics by breeding adults (Cramp & Simmons 1983). We studied habitat selection of curlews on two farmland areas in western Finland which differed with respect to landscape characteristics, intensity of nest predation, food availability, and breeding densities (Currie & Valkama 1998, J. Valkama *et al*., unpubl.). In particular, we examined habitat preferences by curlews with respect to (i) territory composition, (ii) foraging, and (iii) nest-site selection.

2. Material and methods

2.1. Study area

Our study was carried out during 1996–1997 in two arable farmland areas in western Finland: Vammala (18 km^2; 61°22´N, 22°50´E) and Kauhava (6 km^2; 63°05´N, 22°56´E; approx. 200 km north from Vammala). Vammala comprises five small agricultural areas (each less than 5 km^2) separated by woodland, farms and small villages, while Kauhava is a part of a larger uniform and flat farmland area (100 km^2) characterised by long and narrow fields separated by ditches (for more details *see* Korpimäki & Norrdahl 1991, Norrdahl *et al*. 1995). During 1996–1997, the proportion of tillage fields was about 69% in both areas; the rest of the fields were covered by hay (managed and harvested yearly; 14%), stubble (9%) and fallow/meadow (fallow fields were usually mown once at the end of the summer whereas meadows were totally unmanaged areas; 8%). Curlew breeding density was low in Vammala (1.6 pairs per km^2) and high in Kauhava (6.7 pairs per km^2).

Curlews arrived in both areas from mid-April onwards and the first eggs were usually laid during the first two weeks of May (mean 7 May). Searching for nests was initiated soon after the onset of incubation. A total of 42 and 60 first-clutch nests were found in Vammala and Kauhava respectively (replacement clutches were excluded).

2.2. Habitat composition of territories

In both areas, different habitats were marked on detailed maps (scale 1:10 000) prior to spring farming practices, and therefore the maps reflect habitat types which were available to curlews at the time of their arrival. Four habitat types were distinguished: tillage (no vegetation), hay (vegetation height 10–15 cm), stubble (20–30 cm) and fallow or meadow (25–45 cm). Tillage fields and some of the stubble fields were cultivated during the first two weeks of May. Other habitats remained undisturbed until June when silage was harvested from hay fields.

Boundaries of curlew territories were obtained by plotting the outermost observations for each pair on a map and connecting these points to form a minimum convex polygon (MCP, *see* Mohr 1947, Berg 1992b). Proportions of different habitat types within territories were measured for 29 territories in both Vammala and Kauhava. These territories fullfilled two criteria: (i) visibility on the territory was good, and (ii) at least one of the adults was colour-ringed. To determine any non-random habitat use by curlews, habitat compositions of observed territories were compared with habitat composition of the total study area. Since proportions of habitat types always sum to 1 and are therefore not independent, we used the log-ratio analysis of compositions in our analyses. In brief, compositional analysis renders the proportions independent and approximately normally distributed by log-ratio transformation based on one of the proportions as denominator, after replacing zero values with 0.01. The available (total study area) and utilised (MCP territory) habitat compositions were transformed to log-ratios y_A and y_U, and the difference $d = y_U - y_A$ was calculated. If the habitat types are used randomly the pairwise differences (d) follow a multivariate normal distribution such that d = 0. This hypothesis was tested using Analysis of Variance (Wilk's Lambda) on all log-ratios simultaneously (for more details *see* Aitchison 1986, Aebischer & Robertson 1992, Aebischer *et al*. 1993). Since some territories were replicated between years, data were analysed separately for each year. Significant differences in habitat use by birds from different areas were also tested for, and when significant differences were found further analyses present results for each area separately.

We combined hay, stubble and fallow/meadow to avoid numerous missing cells in the analyses. This division (tillage vs. other habitats) allowed us to compare habitats with and without vegetation cover. Water areas were not considered in the analyses because water only occurred in 11% of territories, and then only in small quantities (1% of those containing any).

In 1997, we measured the habitat heterogeneity of 23 mapped territories by dividing the number of blocks of different habitats within a territory by its size (ha). To examine whether curlew territories were more heterogeneous than expected by chance, we compared them with 23 randomly selected sites. Habitat compositions of these random 'territories' were obtained by drawing a circle around each site. Radii of these circles were equal to mean curlew territory sizes in each area in 1997 (mean ± SE, 21.8 ± 1.8 ha in Vammala (n = 11) and 10.9 ± 1.1 ha in Kauhava (n = 12)), i.e. radii of 260 m in Vammala and 190 m in Kauhava.

2.3. Foraging habitat data

Foraging observations were made separately for both sexes on focal territories in both areas between 20 April and 12 May in 1996 (prior to laying through the first week of incubation). Observations were made on 12 territories in Vammala and 11 territories in Kauhava. Individuals of either sex were observed for between 30 and 60 minutes from 05:00 to 21:00 (for more details *see* Currie & Valkama 1998). Mean number of minutes of observation (per territory, ± SE) was 108.5 ± 27.8 ($n = 23$) and mean number of minutes of foraging data (per territory, ± SE) was 47.3 ± 8.8 ($n = 23$). We calculated the proportion of time each pair spent foraging in each habitat type (tillage, hay, stubble and fallow/meadow), and compared these with proportions of each habitat within territories to determine whether individuals showed any habitat preferences when foraging. We compared foraging habitats with those available within each territory by calculating the log-ratio differences between each pair of utilised and available log-ratios, and tested for non-random use when foraging. In this case the mean of all log-ratio differences should not differ from zero. We also tested for significant effects of area and sex on curlew selection of foraging habitats. Hay, stubble and fallow/meadow were combined to avoid missing cells in the analyses.

2.4. Nest-site characteristics

To compare whether nest-site characteristics at real nests ($n = 42$ in Vammala and 60 in Kauhava) differed from those that would be expected randomly, we selected 102 sites from a random grid system (42 in Vammala and 60 in Kauhava). Habitat features were measured at both curlew nests and random sites to examine the effect of nest-site characteristics on nest-site selection. These features were considered as (i) factors associated with increased predation risk: distance to closest forest edge (predation risk is assumed to be high in the vicinity of forest edges; *see* Stroud *et al.* 1990, Berg 1992a), and distance to closest ditch (mammalian predators use ditches as pathways, e.g., Korpimäki *et al.* 1994), (ii) factors associated with human disturbance: distance to nearest road (since roads are used as walkways in addition to vehicular traffic), and (iii) nest-site characteristics: nest habitat (tillage, hay, stubble, fallow/meadow) and distance to other agricultural habitat. Nest habitat was classified as short vegetation (tillage) or tall vegetation (other habitat types) to avoid redundancies in the subsequent logistic regression analyses.

Within each area and year the data were analysed using logistic regression, in which distance variables and habitat type were entered as independent variables and type of the nest (real vs. random) as the dependent variable. All variables that had a univariate p-value < 0.25 were entered in the multivariate model with their first-order interactions (*see* also Hosmer & Lemeshow 1989). Non-significant interactions and main-effects were then gradually removed from the model starting from the least significant variable. Thus, only significant main-effects and interactions were present in the final model.

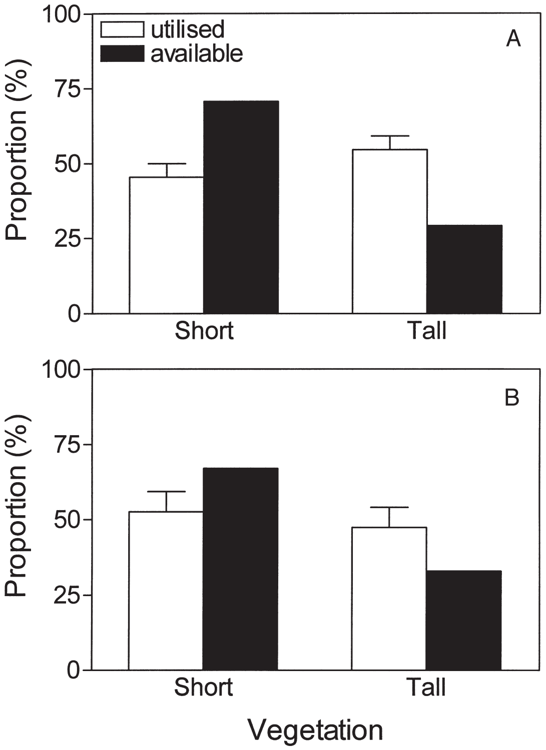

Fig.1. Proportions (%) of short (tillage) and tall (hay, stubble, fallow/meadow) vegetation in curlew territories (utilised; mean + SE) and in the total study area (available) in (A) 1996 and (B) 1997. Habitat use from MCP territories compared to habitat availability in the study area was significantly non-random in 1996 ($\Lambda = 0.74$, $F_{1,34} = 11.76$, $p = 0.002$) and marginally non-random in 1997 ($\Lambda = 0.87$, $F_{1,22} = 3.27$, $p = 0.084$).

Data were analysed using SAS (SAS Institute Inc. 1990) and SPSS (Norusis 1993) statistical packages.

3. Results

3.1. Habitat composition of territories

In both 1996 and 1997, there were no significant differences in territory composition between areas (1996: $F_{1,33} = 2.64$, $p = 0.113$; 1997: $F_{1,21} = 1.74$, $p = 0.201$), and therefore, the data were combined across areas within years. In both years, tall vegetation types occurred more frequently and tillage less frequently within territories than expected by their availability in the landscape (Fig. 1A and B). The majority of tall vegetation within curlew territories consisted of grassland (hay and fallow/meadow; 82% in 1996 and 83% in 1997).

Habitat heterogeneity index (number of blocks of different habitats/territory size) was marginally higher in Kauhava than in Vammala, but did not differ significantly between real and random territories (Table 1).

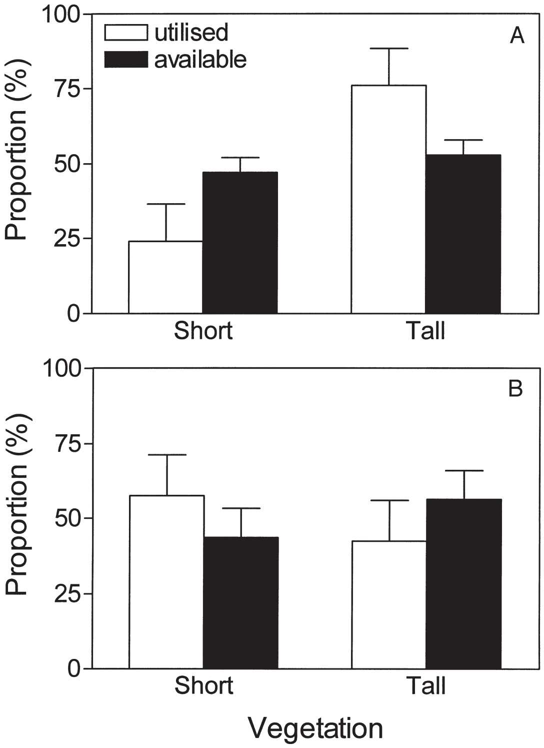

Fig. 2. Proportion of time (%) curlews spent on short (tillage) and tall (hay, stubble, fallow/meadow) vegetation during the bouts of foraging (utilised; mean + SE) and the habitat composition of curlew territories (available; mean + SE) in (A) Vammala and (B) Kauhava. Habitat use during foraging compared to habitat availability within the territories was marginally non-random in Vammala ($\Lambda = 0.73$, $F_{1,10} = 3.68$, $p = 0.084$) and significantly non-random in Kauhava ($\Lambda = 0.62$, $F_{1,9} = 5.54$, $p = 0.043$).

Table 1. Habitat heterogeneity indices (no. of blocks of different habitats / territory size; mean ± SE) for real and random territories in Vammala ($n = 11$) and Kauhava ($n = 12$) in 1997. Differences between the study areas and territory types (real or random) were tested with two-way ANOVA (heterogeneity index was log-transformed).

	Real territories	Random territories	
Vammala	0.32 ± 0.03	0.21 ± 0.04	
Kauhava	0.59 ± 0.28	0.38 ± 0.05	
	df	*F*	*p*
Area	1	3.98	0.053
Territory type	1	1.35	0.252
Area × type	1	2.28	0.138

3.2. Habitat utilisation during foraging

We found no significant difference between the sexes in their selection of foraging habitats within territories ($F_{1,28} = 0.06$, $p = 0.815$), but there was a significant difference between areas ($F_{1,28} = 10.28$, $p = 0.003$). In Vammala, curlews preferred taller vegetation when foraging (Fig. 2A; 99% of the foraging in tall vegetation took place on hay), while in Kauhava, tillage was the most preferred habitat (Fig. 2B).

3.3. Nest-site selection

Factors affecting nest-site selection of curlews varied between areas and years (Table 2). However, there were also some consistent patterns, as curlew nests were significantly closer to patches of other agricultural habitat (Vammala in 1996 and Kauhava in 1997) and closer to ditches (Vammala and Kauhava in 1997) than were random sites (Table 2). When the distance to other agricultural habitat was analysed with respect to nest-site habitat (short or tall vegetation), curlew nests were significantly closer to patch edges than random sites if the nest was in short vegetation (mean ± SE; curlew nests: 69.6 ± 17.9 m, $n = 21$ vs. random sites: 126.9 ± 18.5 m, $n = 36$; Mann-Whitney *U*-test, $z = -2.24$, $p = 0.025$), but not when the nest was in tall vegetation (44.6 ± 8.1 m, $n = 26$ vs. 49.4 ± 11.3 m, $n = 17$; $z = -0.15$, $p = 0.871$).

Curlew nests were further away from forest edges than random sites (Kauhava in 1997). Curlews also avoided placing their nest on tillage (short vegetation) in Kauhava in 1996 (Table 2) and the same trend was obvious also in the complete dataset since only 33% of curlew nests but as much as 59% of random sites were in short vegetation.

3.4. Breeding dispersal

Breeding dispersal (i.e., the extent of movements between years; *see* Greenwood and Harvey 1982) was significantly higher in Vammala than in Kauhava (mean distance ± SE; Vammala: 235.6 ± 32.2 m, $n = 36$; Kauhava: 102.2 ± 23.2 m, $n = 18$; $z = -2.91$, $p = 0.004$). In Vammala, breeding dispersal was higher among those pairs that had failed in their previous breeding attempt than among successful pairs (at least one hatched young produced) (mean distance ± SE; failed: 281.7 ± 40.5 m, $n = 24$; successful: 143.3 ± 43.2 m, $n = 12$; $z = -2.04$, $p = 0.042$). In addition, failed pairs changed their nest habitat more frequently than successful pairs between years (63% vs. 25%, $\chi^2 = 4.50$, df = 1, $p = 0.034$). However, this was partly an effect of moving further after failure, because the chance of the nest occurring in the same habitat was related to distance (same habitat: 161.1 ± 32.6 m, $n = 18$; different habitat: 310.0 ± 50.5 m, $n = 18$; $z = -2.09$, $p = 0.036$). There were too few failed nests in Kauhava to quantify breeding dispersal between failed and successful breeding attempts.

4. Discussion

4.1. Territory composition

Curlews showed a marked preference for tall vegetation (especially hay and fallow/meadow) within their territories, while there was no preference for tillage even though it was the most common of available habitat types. High preference for fields with taller vegetation is expected since these fields can be both good foraging areas (hay) and provide curlew nests and chicks with shelter from predation (hay, stubble and fallow/meadow) (Berg 1992a, 1992b, Currie & Valkama 1998).

Both curlew territories and randomly selected non-occupied territories were more heterogeneous in Kauhava than in Vammala, but the heterogeneity indices did not differ significantly between real and random territories (Table 1). The difference between areas was expected as in Kauhava the fields were longer and narrower and usually owned by different farmers whereas in Vammala shape of fields was more irregular and large patches of one habitat were typical. Skeel (1983) suggested that nesting success of whimbrels *Numenius phaeopus* was higher in complex habitats due to enhanced crypticity of the nest and incubating bird. Due to small sample sizes, we were unable to test directly whether habitat complexity affected breeding success of curlews, but we know that hatching success is significantly higher in Kauhava (Currie & Valkama 1988, J. Valkama *et al.*, unpubl.).

4.2. Foraging habitat selection

We found that use of foraging habitats was marginally non-random in Vammala, where taller vegetation, especially hay, was preferred by curlews

Table 2. Summary statistics of logistic regression analyses comparing habitat characteristics of curlew nests and random sites (only the final models are shown). Descriptive statistics (mean ± SE) are also presented. Sample sizes are the same for curlew nests and random sites.

	Curlew nests	Random sites	χ^2	df	*p*
Vammala 1996 ($n = 21$)					
Distance (m) to other habitat	81.9 ± 16.9	169.1 ± 25.9	5.64	1	0.018
Vammala 1997 ($n = 21$)					
Distance (m) to ditch	35.2 ± 5.4	19.8 ± 3.1	4.88	1	0.027
Kauhava 1996 ($n = 28$)					
Nest habitat (% nests on short vegetation)	28.6	67.9	8.17	1	0.004
Kauhava 1997 ($n = 32$)					
Distance (m) to ditch	23.2 ± 3.3	16.9 ± 2.2	3.33	1	0.068
Distance (m) to forest	782.8 ± 85.3	533.1 ± 55.4	4.81	1	0.028
Distance (m) to other habitat	34.7 ± 7.7	58.1 ± 9.8	4.99	1	0.026

(Fig. 2A). In Kauhava, however, the use of foraging habitats was clearly non-random, and tillage was the most preferred habitat. Berg (1992b, 1993) observed that curlews in a mixed farmland site in Sweden preferred grassland habitats when foraging due to their higher availability of earthworms. We have found that in Kauhava earthworm biomass was highest in tillage (Currie & Valkama 1998, also unpubl.), which may account for the preference for this habitat. Tillage fields could also be preferred as foraging habitat because prey species, especially surface invertebrates, were probably more conspicuous due to the lack of concealing vegetation (Galbraith *et al.* 1993). Thus, our results suggest that curlews foraged in relation to prey abundance or availability, not crop type *per se* (*see* also Berg 1993). Our data were collected prior to laying through the first week of incubation, and the observed patterns of foraging are likely to be different during late incubation or chick rearing (Berg 1993).

4.3. Nest-site selection

In general, the majority (67%) of curlew nest-sites were on habitats with tall vegetation (especially fallow/meadow and hay fields). Breeding in sheltered habitats can result in lower risk of nest predation, although some studies have not found any obvious connection between vegetation cover and nest survival (Götmark *et al.* 1995, Hatchwell *et al.* 1996). We have not detected any significant differences in predation rates of curlew nests between habitat types in the same areas (J. Valkama *et al.*, unpubl.), but the lack of difference in nest survival between habitat types does not necessarily mean that the ease of nest detection by predators is the same between different habitats.

There are additional reasons that may explain the observed preference for taller vegetation. First, tall vegetation can provide shelter for young chicks, especially against avian predators e.g., kestrels *Falco tinnunculus*, short-eared owls *Asio flammeus* and hooded crows *Corvus corone cornix* (Norrdahl *et al.* 1995, and pers. obs.). Secondly, during spring farming practises most nests located on tillage are likely to be destroyed (Berg 1992a, also pers. obs.) and therefore avoidance of tillage as nest habitat may be beneficial. Since curlews are long-lived birds with strong breeding-site fidelity (Berg 1994), they may have previous experience of high-risk habitats and consequently learn to avoid them. However, a relatively large proportion of nests in both study areas was on tillage (33%), although other options were frequently available within territory boundaries, and moreover, the nest habitat of a given pair seemed to vary between years. Adult curlews are probably most camouflaged against avian predators (e.g., goshawk *Accipiter gentilis*) on tillage (Berg 1992a). However, there may be a potential trade-off between nest survival and adult survival: nests on tillage are exposed to spring farming practises but breeding on other habitats with taller vegetation may be dangerous for the incubating adults as predators can approach the nest undetected.

Curlew nests were also closer to patch edges (indicated by distance to other agricultural habitat) than random sites. Since tillage was the most common habitat with largest patches in both study areas, nest–other-habitat distances were likely to be longer at nests on tillage than at nests on other habitats. Most curlew nests were on tall vegetation where patch size was smaller, and therefore the nest-site was unavoidably close to other habitat. In contrast, the majority of random sites was on tillage and therefore the distance to patch edge was high. Proximity to habitat edge has been considered as a threat to nest survival, although the threat only appears to be strong in forested landscapes (Andrén 1995). Predation of curlew nests is not affected by the distance to the habitat edge (J. Valkama *et al.*, unpubl.), and in this study, there was no evidence that curlews avoided habitat edges when selecting their nest-sites. In fact, curlew nests in short vegetation were closer to habitat edges than random sites which indicates that even if individuals did not directly utilise tall vegetation when selecting nest-sites, they preferred to breed close to it. Breeding in the vicinity of taller vegetation may be beneficial for example when the chicks are small and their risk of being preyed upon by avian predators (listed above) is highest. On the other hand, this behaviour may be beneficial because curlews prefer hay fields that are close to the nest as foraging habitats (*see* also Berg 1993).

Curlew nests were also located further away from ditches (both areas in 1997) and forest edges (Kauhava in 1997) than random sites. This may be an adaptation to reduce the risk of nest predation which can be higher in the vicinity of ditches and forest edges due to increased exposure to predators. Ditches are used as pathways by mammalian predators (Korpimäki *et al.* 1994) and forest edges are frequently associated with increased density of avian and mammalian generalist predators (Stroud *et al.* 1990, Berg 1992a).

Breeding dispersal of curlews was significantly higher in Vammala than in Kauhava. There are two reasons to explain this pattern: first, density was lower in Vammala and therefore birds were able to move over larger areas and had more to choose from. Secondly, nest predation has been more intense in Vammala than in Kauhava (70% vs. 10%; J. Valkama *et al.*, unpubl.), and thus curlews may avoid breeding close to the site where they have failed in the previous year, because predators may revisit those sites where they have been previously successful (*see* Jackson 1994, Marjakangas *et al.* 1997). This was supported by our data from Vammala, where breeding dispersal was higher among pairs that had failed in their previous breeding attempts.

In conclusion, curlews exhibited a strong preference for tall vegetation (especially grassland, i.e. hay and fallow/meadow) within their territories and also nested more frequently on these habitats than on tillage. Grassland is important to many wader species, because it is the habitat where breeding density and reproductive success are frequently highest (Berg 1992a, 1992b, Berg 1993, Kooiker 1990, Grant 1997). In our study areas, grassland was relatively uncommon in the agricultural landscape (22% of the total field area). Modern intensive agriculture is associated with the highly efficient use of fields, and has frequently led to the creation of uniform and large patches of one habitat (primarily tillage) and to the loss of marginal, uncommon habitats (hay, fallow and meadow) (Solonen 1985, Hanski and Tiainen 1988, Pain and Pienkowski 1997). Agricultural practices can also cause drastic changes in the composition of territories between years, and this together with high breeding-site fidelity may reduce opportunities of pairs to find enough suitable habitat. In such conditions, the lack of preferred habitat may force individuals to breed on less suitable and also high risk areas where nests are frequently destroyed by farming practices or predators. Continuous nest losses are likely to reduce reproductive success and/or force individuals to move elsewhere (Wilcove 1985) and can result in population decline observed in Finland and elsewhere in Europe (Ylimaunu *et al.* 1987, Baines 1988, Berg 1994, Bednorz & Grant 1997, Beintema *et al.* 1997).

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