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PATTERNS OF NEST PREDATION CONTRIBUTE TO POLYGYNY IN THE GREAT REED WARBLER

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Abstract. According to the polygyny threshold model, females are compensated for the cost of sharing a territory with other females by breeding in territories of higher quality than those of monogamously mated females. In the polygynous Great Reed Warbler (*Acrocephalus arundinaceus*), the variation in territory quality may be associated with nest site characteristics or food supply. In this study, we examined the probability of nest predation in Great Reed Warblers in relation to an indirect measure of territory quality (territory attractiveness rank as indexed by settlement order) and to several variables of nest site structure. Artificial nests with attached soft plasticine model eggs were placed in Great Reed Warbler territories of different attractiveness. Marks in the soft model eggs were compared to marks from possible predator species. Both inter- and intraspecific predators were found to prey upon eggs in artificial nests. Marsh Harriers (*Circus aeruginosus*) predominantly preyed upon artificial nests located in territories of low attractiveness, in low-density reed beds, and early in the season. Bitterns (*Botaurus stellaris*) and Water Rails (*Rallus aquaticus*) showed a preference for artificial nests located inside the reeds. When all types of predators of artificial nests were pooled, the probability of nest predation was lower in more attractive territories. This pattern was corroborated in an analysis of predation on real nests. In general, polygyny occurred in territories with a low rate of nest predation, whereas unmated males held territories where the risk of predation was high. The low rate of nest predation in attractive territories on average compensated secondary females for the cost associated with sharing a male (i.e., reduced male assistance when feeding nestlings). The polygyny threshold model has been around for several decades, however, only few studies have identified the factors that may compensate secondary females for the cost of sharing a mate. In the present study we were able to show that the patterns of nest predation can be an important territory quality parameter that compensate secondary females, and, hence, contribute to the occurrence of avian polygyny.

Key words: Acrocephalus arundinaceus; *mating system; Great Reed Warbler; nest predation; nest site selection; polygyny; territory quality.*

INTRODUCTION

In polygynous species in which males provide parental care, females mated to already-mated males often receive a low share of the males' assistance. Therefore, females pairing with polygynous males often pay a cost in terms of lowered reproductive success (e.g., Alatalo et al. 1981, Catchpole et al. 1985, Urano 1990, Veiga 1990, Bensch and Hasselquist 1991*a*). However, quality differences among male territories (e.g., in food supply or predation risk) may make particular territories attractive to females even if other females have already settled in them. The polygyny threshold model states that if the reduction in reproductive success of a female breeding monogamously on a low quality territory exceeds the benefit of paternal care, females are expected to settle with polygynous males on high quality territories (Verner 1964, Verner and Willson 1966, Orians 1969). In addition, several other mechanisms may compensate females for the potential cost of polygyny or lower the polygyny threshold (Searcy and Yasukawa 1989, Bensch 1997). For example, nest predation may cause switches in harem status of females between the time of settling and when nestling feeding occurs that on average decrease the relative difference in reproductive success of females settling as primary and secondary (Bensch and Hasselquist 1991*a*).

The Great Reed Warbler (*Acrocephalus arundinaceus*) is a polygynous passerine. At our study site, territories differ in attractiveness as measured by male settlement order (Bensch and Hasselquist 1991*b*). The pattern of territory settlement order is remarkably similar in successive years despite the fact that individual males frequently change territories between years (Bensch and Hasselquist 1991*b*). This suggests that territory attractiveness is determined by some physical characteristics of the habitat, e.g., food abundance or nest site quality. Territory attractiveness rank as indexed by settlement order correlates with both male and female lifetime reproductive success (Bensch et al. 1998, Hasselquist 1998), and therefore can be used as

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an indirect measure of territory quality. Females in this population have been shown to actively choose already-mated males on attractive territories, even if unmated males are available close by (Bensch and Hasselquist 1991*b*, 1992) and by doing so they receive less male assistance (Bensch and Hasselquist 1994). The polygynous mating system seems best explained by the polygyny threshold model because females simultaneously settling with mated and unmated males enjoy similar reproductive success and survival (Bensch 1996).

To investigate whether rates of nest predation differ in relation to the attractiveness of Great Reed Warbler territories, and thus might explain why females choose already-mated males, we carried out an experiment with artificial nests. The nests were collected real Great Reed Warbler nests to which we had attached model eggs. These were made of soft plasticine in which predators would leave marks, making it possible to distinguish between different predator species (Møller 1989, Bensch and Hasselquist 1994, Hansson et al. 1997). Artificial nests were placed in territories of different attractiveness, mimicking the location of real nests, and their fate as well as particular nest site characteristics were documented. Real Great Reed Warbler nests at the study site were monitored in the same manner. We first examined which species were the predators of the eggs in the artificial nests. Second, we analyzed whether territory attractiveness and/or nest site characteristics were associated with the probability of predation of artificial nests. To examine whether the predation of artificial nests reflected the situation with real nests, we also analyzed predation of real nests. Third, we investigated whether differences in predation rates among territories of different attractiveness may compensate females for the cost of sharing a territory with other females (in accordance with the polygyny threshold model; Verner 1964, Verner and Willson 1966, Orians 1969). The polygyny threshold model has been around for several decades; however, to date only few studies have identified the variable that gives secondary females a fitness compensation for the lower male assistance in polygynous territories (Pleszczynska 1978). We found that in Great Reed Warblers the rate of nest predation was lowest in territories of high attractiveness (inhabited by polygynous males) and highest in territories of low attractiveness (inhabited by monogamous and unmated males). The present study shows that nest predation could be the fitness link explaining why secondary females settle with already mated males despite the potential cost of lower male assistance, and hence that the spatial distribution of nest predation can contribute to the occurrence of avian polygyny.

METHODS

Study population and general methods

The Great Reed Warbler breeds in reed beds of eutrophic lakes and marshes over much of the Palearctic temperate region (Cramp 1992). It migrates to tropical Africa and returns to breed in northern Europe beginning in early May (Bensch and Hasselquist 1991*b*, Hasselquist and Bensch 1991, Cramp 1992). At Lake Kvismaren (59°10′ N, 15°25′ E), in south-central Sweden, the population of Great Reed Warblers consists of ∼60 breeding adults, and it has been studied from early May to late July in 1985–1998. For a detailed description of the field methods, see Bensch and Hasselquist (1991*b*, 1994). Color-ringed birds' social activities were recorded during daily observations and their locations plotted on detailed maps of the study site. Males hold territories throughout the breeding season, and the first date a male sang was regarded as the first day of territory occupancy. By following each nest-building female, we were able to locate >95% of the nests in the area. Nests were checked at intervals of 1–4 d, with daily visits around the expected hatching date. This enabled us to estimate various breeding parameters, and if and when nests were depredated.

To measure nest site quality, in 1993–1995 we measured five nest characteristics: (1) distance (m) from the nest to the nearest reed edge to open water (could be a lagoon or a canal); (2) water depth (cm) under the nest; (3) density of reed stems, i.e., number of reed stems in one square meter with the nest in the center; (4) maximum reed height (cm) from the water surface to the tip of five of the longest reed stems within the square; and (5) reed diameter (mm) at water surface level of the same five reed stems. Of a total of 113 nests recorded during 1993–1995, 26 nests were depredated during the egg stage, 21 during the nestling stage, whereas the remaining 66 nests were successful.

Experimental methods

To identify the nest predators of Great Reed Warblers and the pattern of nest predation we carried out an experiment in 1994–1995. We tried to mimic the natural breeding situation as closely as possible (cf. Major and Kendal 1996). We placed four model eggs made of plasticine in old Great Reed Warbler nests collected in previous years. The model eggs were carefully made with real Great Reed Warbler eggs as prototypes. Predators leave marks in the model eggs (Møller 1989, Bensch and Hasselquist 1994). To prevent predators from removing the eggs, we attached each egg to the nest with a thin nylon string.

Using data on territory boundaries from previous breeding years (Bensch and Hasselquist 1991*b*), we chose 24 experimental territories before the arrival of males in 1994. Two artificial nests were put up 20–130 m apart in each experimental territory, 12 pairs of nests in the middle of May (early period) and 12 at the beginning of June (late period) each year, for a total of 96 artificial nests. Within a territory one nest was placed close to the edge and one 5–10 m inside the reeds, both nests at 25–50 cm above the water level and in dense reeds, similar to real Great Reed Warbler nests. We documented the location and reed quality of the artificial nests in the same manner as used for real nests. We checked the artificial nests every second day during the experimental period of 16 d, i.e., corresponding to the mean period from start of egg laying to hatching in real nests. When predation took place we noted the day and the depredated model eggs were collected. If the depredated eggs showed only small marks (indicating intraspecific predation), we replaced the pecked eggs and the experiment was continued. The rationale for this was that we wanted to quantify the rate of interspecific predation also on territories where intraspecific nest predation occurred. Therefore, some nests ($N = 9$) were depredated by both intra- and interspecific predators. However, if the eggs in an artificial nest showed large marks (indicating interspecific predation) we finished the experiment after the predation event. Because of fixed dates of experimental initiation, occupation status (e.g., no Great Reed Warbler present; occupied by a male only, etc.) changed for many of the experimental territories as Great Reed Warblers settled.

We analyzed the model eggs under a stereo microscope (10–30×) and compared the marks with reference marks of potential predators. The reference collection of marks consisted of imprints in model eggs of the bills of all possible avian predators that occur regularly in or close to our study area: Bittern (*Botaurus stellaris*), Water Rail (*Rallus aquaticus*), Marsh Harrier (*Circus aeruginosus*), Cuckoo (*Cuculus canorus*), Hooded Crow (*Corvus corone cornix*), Great Reed Warbler, and Reed Warbler (*Acrocephalus scirpaceus*). For detailed information about the mark pattern by each of the reference species, see Hansson et al. (1997). We did not find any marks from mammalian predators, such as mink (*Mustela vison*) or mouse (*Mus musculus*). Mouse is a frequent egg predator in Spain, as shown by bite marks from this species in clay eggs placed in artificial nests (R. Pinheiro, *personal communication*).

Data analyses

Male settlement order of territories in our study area is remarkably similar in successive years; the same territories are always occupied early despite low male territory fidelity between years (only 6% of the males settle in the same territory as in the previous year; see Bensch and Hasselquist 1991*b* for a detailed description of territory settlement order and male territory infidelity). We used data on annual territory settlement order to construct an index of territory attractiveness. For each territory we defined its yearly attractiveness rank according to male settlement order; rank 1 was given to the territory chosen by the first arriving male, etc. We calculated the mean attractiveness rank of the experimental territories for 1993 to 1996 (i.e., the two experimental years and their flanking years), and this value was used as our measure of territory attractiveness in the present analyses. A low rank value corresponds to a highly attractive territory. In the statistical analyses we used experimental period as a two-state variable: early period = 1, late period = 2. Of the nest site variables, reed height and reed diameter correlated significantly (artificial nests: $r = 0.48$, $N = 96$, $P < 0.001$; real nests: $r = 0.40$, $N = 113$, $P < 0.001$). Therefore, we computed a size measure of the reed (PC1) using principal component analysis (Sokal and Rohlf 1995), which replaced the two original variables in the analyses. We pooled the data from the two experimental years in the analyses because there was no difference in predation rate between years (total predation: 38 nests in 1994 and 35 in 1995, $\chi^2 = 0.12$, $P > 0.5$; different predators separately: $P > 0.5$ in all cases). Predation events by different predator types were examined both separately and pooled. A few artificial nests ($N = 9$) were depredated by both an intra- and an interspecific predator, and in these cases only one predation event was counted (the first predation event, i.e., predation by intraspecific predators, in analyses of total predation; the second predation event, i.e., predation by interspecific predators, in analyses of interspecific predation). We performed the corresponding analyses for real nests except that we used the laying date of the clutch, instead of experimental period, as the independent factor accounting for any seasonal effect. For real nests we examined total predation rate as well as predation rate at the egg and nestling stages separately. Because territory attractiveness may be determined by one or several of the investigated nest site variables, we investigated the relationship between predation risk and territory attractiveness, and predation risk and nest site characteristics, separately.

Statistical methods used are according to Sokal and Rohlf (1995) and Crawley (1993), and statistical tests were performed with SYSTAT 7.0.1 (SYSTAT 1997). The statistical significance of independent variables in the logistic regressions was assessed by the change in deviance, G, which is approximated by a χ^2 distribution with corresponding degrees of freedom (Crawley 1993). In multiple analyses, we used a stepwise procedure and independent variables entered the model if $P < 0.1$. No interaction term increased the models' explanation significantly (Tables 1 and 2). Two-tailed tests were used in all analyses.

RESULTS

Comparison of nest site characteristics of artificial and real nests

Artificial nests were located in significantly less dense reeds than real nests (mean ± SD: 242 ± 76.7 vs. 270 ± 83.6 stems/m^2; $t = 2.45$, df = 205, $P < 0.05$). Other parameters of nest site characteristics (i.e., distance to reed edge, water depth, size of reed) did not differ significantly between artificial and real nests.

TABLE 1. Probability of predation of artificial nests in relation to experimental period and territory attractiveness estimated by logistic regression.

Type of predator	Final logistic regression model (and variables not entering this model)	Estimate	df	G	P†
a) Marsh Harrier	Final model‡		93		
	Constant	4.56	1		
	Experimental period§	−6.10	1	35.3	<0.001
	Territory attractiveness rank‖	0.33	1	18.2	<0.001
b) Long-billed predator	Final model‡		94		
	Constant	−3.21	1		
	Experimental period§	1.05	1	3.6	<0.1
	(Territory attractiveness rank)‖	−0.01	1	<0.1	NS
c) Interspecific	Final model‡		93		
	Constant	2.24	1		
	Experimental period§	−2.13	1	13.8	<0.001
	Territory attractiveness rank‖	0.11	1	5.7	<0.05
d) Inter- and intraspecific	Final model‡		93		
	Constant	3.16	1		
	Experimental period§	−2.11	1	13.8	<0.001
	Territory attractiveness rank‖	0.09	1	4.1	<0.05

† NS indicates $P > 0.1$.
‡ No significant first-degree interaction.
§ Mid-May or early June.
‖ Low rank value corresponds to highly attractive territory.

TABLE 2. Probability of predation of artificial nests in relation to experimental period and nest site variables estimated by logistic regression.

Type of predator	Final logistic regression model (and variables not entering this model)	Estimate	df	G	P†
a) Marsh Harrier	Final model‡		92		
	Constant	5.50	1		
	Experimental period§	−3.23	1	34.1	<0.001
	Density of reed‖	−0.01	1	5.7	<0.05
	(Distance to reed edge)	0.02	1	<0.1	NS
	(Size of reed; PC1)	−0.17	1	0.4	NS
	(Depth of water)	0.03	1	1.7	NS
b) Long-billed predator	Final model‡		93		
	Constant	−3.93	1		
	Distance to reed edge	0.18	1	5.7	<0.05
	Experimental period§	0.98	1	3.6	<0.1
	(Density of reed‖)	0.01	1	2.0	NS
	(Size of reed; PC1)	−0.06	1	<0.1	NS
	(Depth of water)	0.02	1	1.3	NS
c) Interspecific	Final model‡		93		
	Constant	1.84	1		
	Experimental period§	−1.88	1	13.8	<0.001
	Distance to reed edge	0.24	1	11.6	<0.001
	(Density of reed‖)	−0.01	1	1.2	NS
	(Size of reed; PC1)	−0.19	1	0.7	NS
	(Depth of water)	0.03	1	1.6	NS
d) Inter- and intraspecific	Final model‡		93		
	Constant	2.93	1		
	Experimental period§	−1.80	1	13.8	<0.001
	Distance to reed edge	0.14	1	3.9	<0.05
	(Density of reed‖)	0.01	1	0.3	NS
	(Size of reed; PC1)	−0.14	1	0.4	NS
	(Depth of water)	0.01	1	<0.1	NS

† NS indicates $P > 0.1$.
‡ No significant first-degree interaction.
§ Mid-May or early June.
‖ One nest with missing value.

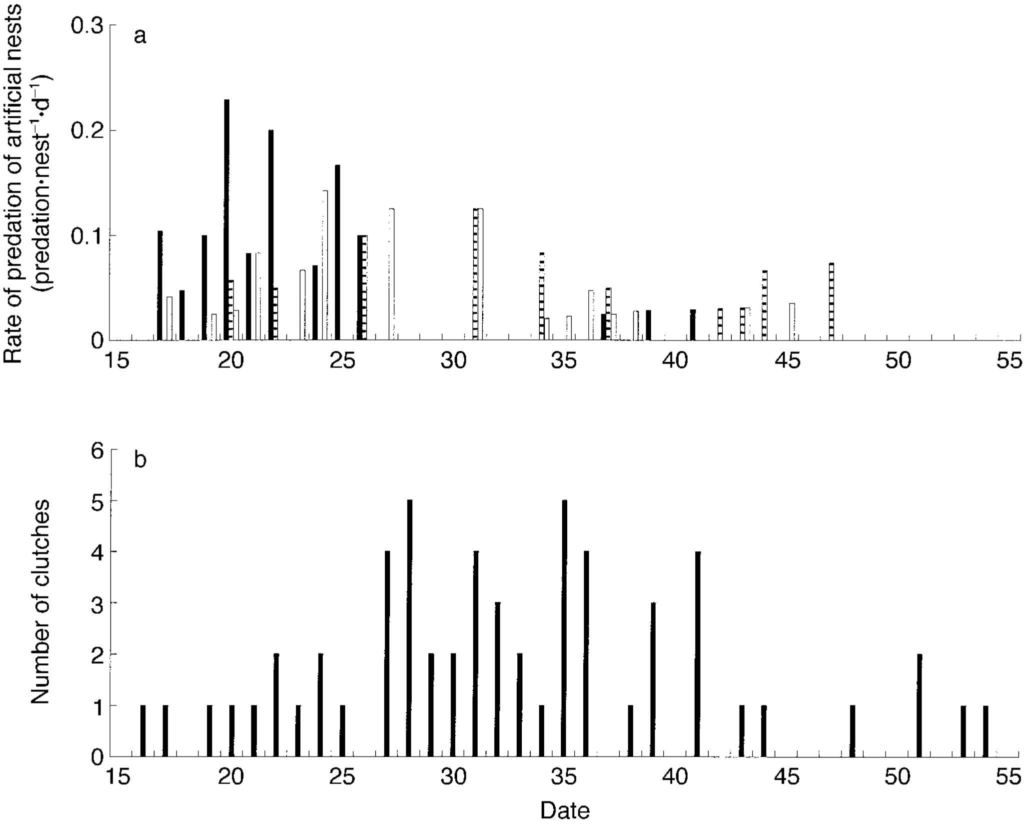

FIG. 1. (a) Daily rate of predation of artificial nests by Marsh Harriers (solid bars), long-billed predators (striped bars), and intraspecific predators (open bars). (b) Laying date of the first egg in first clutches of female Great Reed Warblers in the two experimental years. Date 1 = 1 May.

Predation of artificial nests

We were able to assign each nest to one of three predator categories: 33 artificial nests were depredated by Marsh Harriers, 17 by long-billed predators, and 23 by small-billed predators. Of the nests depredated by long-billed predators, 8 were preyed upon by Bitterns and the remaining 9 by either Bitterns or Water Rails.

Peckmarks made by small-billed predators closely resembled those of a Great Reed Warbler. Moreover, the temporal and spatial distribution of this type of predation correlated with the settling of Great Reed Warbler females on the territories, and with the proximity to the nests they initiated (Hansson et al. 1997). This provides strong indirect evidence of infanticide, evaluated in detail in a previous paper (Hansson et al. 1997). Therefore, nests affected by intraspecific predators are only included in analyses of total nest predation. The daily rate of predation of artificial nests by Marsh Harriers, long-billed predators, and intraspecific predators is shown in Fig. 1a. To illustrate the temporal association between predation events and real breeding attempts of Great Reed Warblers, we also show the laying date of first clutches in the two experimental years (Fig. 1b).

Probability of nest predation in relation to territory attractiveness

Marsh Harrier predation was significantly higher in the early period ($P < 0.001$), and on less attractive territories ($P < 0.001$) (Table 1a). The latter relationship held also when the experimental periods were treated separately (logistic regression, $N = 48$; early period: $G = 16.8$, df = 1, $P < 0.001$, late period: $G = 2.8$, df = 1, $P < 0.1$). When we reanalyzed the model in Table 1a including only territories occupied by Great Reed Warblers, the probability of Marsh Harrier predation was still significantly correlated with experimental period and territory attractiveness rank (logistic regression, $N = 73$; experimental period: $G = 17.6$, df = 1, $P < 0.001$; territory attractiveness rank: $G = 12.5$, df = 1, $P < 0.001$).

The probability that artificial nests would be depredated by long-billed predators tended to be higher in the late experimental period ($P < 0.1$), and was not related to territory attractiveness rank (Table 1b). When nest depredations by interspecific predators were pooled, the predation probability was higher in the early experimental period ($P < 0.001$) and on territories of low attractiveness rank ($P < 0.05$) (Table 1c). This

TABLE 3. Probability of predation of real Great Reed Warbler nests in relation to laying date and territory attractiveness estimated by logistic regression.

Status of nest at predation	Final logistic regression model (and variables not entering this model)	Estimate	df	G	P†
a) Egg stage	Final model		111		
	Constant	−1.85	1		
	Territory attractiveness rank‡	0.09	1	2.9	<0.1
	(Laying date)	0.02	1	2.1	NS
b) Nestling stage	Final model		86		
	Constant	1.15	1		
	(Laying date)	0.02	1	1.5	NS
	(Territory attractiveness rank‡)	0.08	1	1.7	NS
c) Total	Final model		111		
	Constant	−1.01	1		
	Territory attractiveness rank‡	0.10	1	4.4	<0.05
	(Laying date)	0.02	1	2.1	NS

† NS indicates $P > 0.1$.

‡ Low rank value corresponds to highly attractive territory.

was also true when all types of predators were pooled, i.e., when also including intraspecific predators (Table 1d).

Probability of predation in relation to nest site characteristics

Together with experimental period, the probability of Marsh Harrier predation was explained by density of reeds around the nest ($P < 0.05$), with less predation of nests surrounded by high density reed (Table 2a). Long-billed predators were significantly more likely to attack nests located far from the reed edge ($P < 0.05$) and tended to attack more nests in the late experimental period ($P < 0.1$) (Table 2b). For interspecific predation pooled, more nests were attacked in the early experimental period ($P < 0.001$) and when nests were located far from the reed edge ($P < 0.001$) (Table 2c). This pattern remained when we analyzed total predation rate, i.e., also considering intraspecific predation (Table 2d).

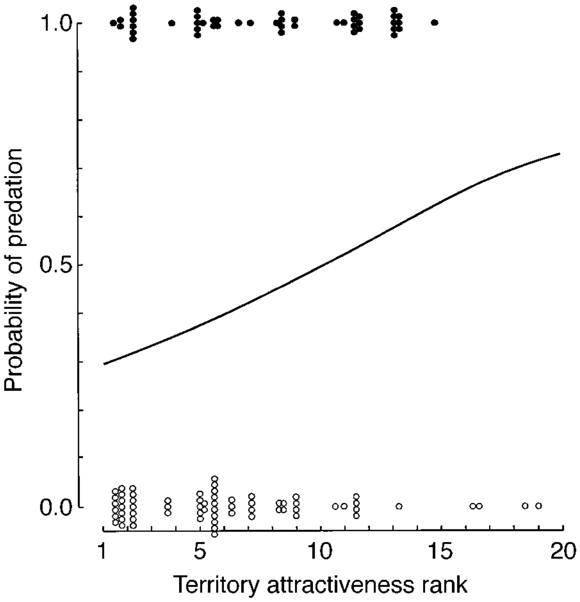

FIG. 2. Successful (open circles) and depredated (solid circles) real nests and associated territory attractiveness rank. Low rank value corresponds to highly attractive territory. Also shown is the fitted logistic regression line of the probability of predation in relation to territory attractiveness rank of these nests (from Table 3c).

To examine whether territory attractiveness rank could explain nest predation probability when nest site characteristics were taken into account, we simultaneously tested the significant predictors from Tables 1 and 2 in logistic regression analyses. Territory attractiveness rank still explained nest predation probability in the analyses (significant values as in Table 1). Nest site characteristics explained nest predation probability as in previous analyses (Table 2), with the exception of the analysis of total predation (i.e., both inter- and intraspecific predators included) where distance to reed edge did not enter the model. The correspondence with the analyses where territory attractiveness and nest site characteristics were investigated separately may be explained by the lack of correlation between territory attractiveness rank and reed density ($r_s = -0.02$, $N = 95$, NS), and between territory attractiveness rank and distance to reed edge ($r_s = 0.09$, $N = 96$, NS).

Predation of real nests

Territory attractiveness tended to explain the occurrence of nest predation at the egg stage ($P < 0.1$; Table 3a), but not during the nestling stage (Table 3b). When we pooled egg and nestling predation, the probability of predation was significantly lower in territories of high attractiveness rank than in territories of low attractiveness rank ($P < 0.05$; Table 3c; Fig. 2). Therefore, the analyses of real nests (Table 3c) corroborated the pattern of nest predation among territories found in the experiment (Table 1d).

Of the examined nest site characteristics, only size of reed (PC1) tended to explain the occurrence of predation of real nests; with a lower probability of predation in large reeds (logistic regression, $N = 113$; $G = 3.6$, df $= 1$, $P < 0.1$).

DISCUSSION

In our study population of Great Reed Warblers, territories can be ranked with respect to their attractiveness to settling males (Bensch and Hasselquist 1991*b*). Males in highly attractive territories often become polygynous, whereas males in less attractive territories often remain unmated (Bensch and Hasselquist 1991*b*, 1992, Hasselquist 1999). The main result of the present study is that the frequency of nest predation is lower on more attractive than less attractive Great Reed Warbler territories.

Our experiment with artificial nests was initiated before the males arrived from their wintering grounds. Because the males arrived asynchronously in time, attractive territories were more often occupied by males during the experiment than less attractive territories. Hence, one possibility is that male territory defense against predators, which occurs in some other avian species (e.g., Cresswell 1997), could explain the low predation rate of artificial nests on attractive territories. In fact, in Great Reed Warblers the males often increase their singing intensity and deliver continuous song when a Marsh Harrier is approaching. This change in singing behavior suggests that the males are aware of the predation risk posed by the Marsh Harriers, and may also act as a warning signal to females present on the territory. However, when the analysis of the data from the experiment was restricted only to those territories that were occupied by male Great Reed Warblers, the significant correlation between territory attractiveness and predation rate by Marsh Harrier remained. In addition, the analysis of real nests, of which all were located in territories with males and females present, showed that more attractive territories had a lower rate of predation than less attractive territories. Hence, it appears that particular territories rather than territorial defense caused the correlation between rate of nest predation and territory attractiveness (cf. Ezaki 1990, Searcy and Yasukawa 1995).

We can think of two processes that can explain the mechanistic link between consistent attractiveness of certain territories and nest predation. One or several characteristics of the territory may act as cues both for settling birds and hunting predators, and hence determine both territory attractiveness and probability of nest predation. None of the five nest site characteristics that we measured could explain the probability of predation of real nests. Therefore, at least these nest site characteristics are probably not involved in linking attractiveness of certain territories and probability of nest predation; however, we can not exclude that other, unexamined, characteristics may do so. There may also be differences in the degree of spatial overlap between Great Reed Warbler territories and the most frequently used hunting areas of the predators, so that some Great Reed Warbler territories are located outside the predators' main domains. This may arise in two ways. Great Reed Warblers may directly assess the distribution of potential predators in the focal year. At our study site, most predators are already present when the Great Reed Warblers arrive in spring, which may enable the warblers to settle in territories with low predator encounter rate. In this scenario, the link between consistent territory attractiveness and nest predation is primarily an effect of the spatial preference of the predators and the warblers' response to this. Another possibility is high territory site fidelity in response to distribution of nest predation in previous years. In our study population this explanation is not likely because there is an overall low between-year territory fidelity of both sexes (males 6%, females 18%; Bensch and Hasselquist 1991*b*). A related idea that may apply, however, is that an arriving bird with previous breeding experience may choose one of several territories that all had similar frequency of nest predation during previous breeding seasons. This may result in a correlation between attractiveness and nest predation, even when the actual territory fidelity is weak.

The experiment showed that Marsh Harriers attack bird nests, and that they are more likely to attack artificial nests located in less attractive territories, in less dense reeds and early in the breeding season. Real Great Reed Warbler nests were predominantly located in attractive territories, in dense reeds and temporally later than the peak of Marsh Harrier predation. Moreover, the Marsh Harrier is a large bird and should, in most situations, damage a Great Reed Warbler nest and the reed surrounding it. Only occasionally do we see such signs of nest predation in our study area. Therefore, Marsh Harriers almost certainly depredate nests less frequently in real breeding situations than indicated by the experiment. The decreased rate of Marsh Harrier predation on artificial nests over the breeding season may be a result of increased shelter from the broad leaves of the new reed that develops in June, or a switch by the harriers to other prey items as the season progresses. In real breeding situations the incubating females conceal the eggs, which probably further decreases nest detectability and, hence, the predation risk by Marsh Harriers. That real nests were located in denser reeds than artificial nests suggests that females actively choose dense reeds as nest sites. This is adaptive as it lowers the risk that the nest will be detected by Marsh Harriers and, possibly, by other predators. However, the experiment clearly demonstrated that there is a high potential for Marsh Harrier predation of nests on territories of low attractiveness, and this may partly explain the higher predation rate of real nests on less attractive territories. Bitterns and Water Rails spend most of their life inside reed beds (Cramp and Simmons 1977), which is in accordance with our finding that long-billed predators were more prone to depredate artificial nests far from the reed edge. Also, when pooling all predator types, a nest's location in relation to the reed edge was an important predictor of its risk of being depredated. The temporal distribution of artificial nests depredated by Bitterns and Water Rails coincided with the peak of laying and incubation of female Great Reed Warblers. Therefore, Bitterns and Water Rails probably quite frequently depredate Great Reed Warbler eggs at Lake Kvismaren, especially at nests located well inside reed beds. Female Great Reed Warblers frequently built their nests inside reeds at distances which, according to the experiment, would increase the risk of predation by Bitterns and Water Rails. This may be explained if other predator species, not detected by our experiment because they mainly prey upon nestlings, prefer reed edges for hunting. In accordance with this possibility, we found no correlation between predation and distance to reed edge for real nests. We have a few confirmed cases of mink depredating nestlings (direct observations or bite marks in remnants of killed nestlings), and many more cases when we strongly suspect mink without clear evidence. The mean distance from the reed edge to nests evidently preyed upon by mink was 1.7 ± 0.94 m (mean ± SE, $N = 6$), indicating that minks mainly attack nests located close to the reed edge. Hence, nest site location in relation to the reed edge may be determined by a trade-off between avoiding minks on the one hand and avoiding Bitterns and Water Rails on the other. It is important to emphasize that even if some predators were not revealed in the experiment, our main conclusion (i.e., low rate of predation in highly attractive territories) was corroborated from the data on real nests, which include nest predation by all types of predators.

According to the polygyny threshold model, differences in quality between territories is the factor that explains the occurrence of polygyny (Verner 1964, Verner and Willson 1966, Orians 1969). The Great Reed Warbler is a polygynous species in which females actively mate with already-mated males on attractive territories even if unmated males are available close by (Bensch and Hasselquist 1992). Within a harem, the first female to hatch eggs often receives all or most of the male's assistance with feeding young whereas the second female to hatch eggs gets limited or no assistance (Bensch and Hasselquist 1994). Therefore, females in a harem differ in reproductive success (Bensch and Hasselquist 1994, Bensch 1996). These characteristics of the mating system are in accordance with the polygyny threshold model (Bensch 1996).

To examine whether the lower risk of nest predation in attractive territories may compensate secondary females for the loss of male assistance, we calculated the expected probability of predation and the reproductive success of successful nests of (1) females of different harem status on territories of polygynous males, (2) females on territories of monogamous males, and (3) hypothetical females settling as the only female on territories of unmated males (Table 4). Territories occupied by polygynous males were on average more attractive than territories of monogamous males which in turn were more attractive than territories of unmated males. To calculate the probability of predation of nests located in different territories, we used the estimated logistic regression model for real nests (Table 3c; Fig. 2) and entered mean attractiveness ranks corresponding to territories of polygynous, monogamous and unmated males. By definition nests never occur on territories of unmated males, therefore, the regression model based on observations of real nests necessarily excludes these territories. This may limit the model as a predictor of the probability of nest predation on territories of unmated males. However, in the experiment artificial nests were evenly distributed in territories of different attractiveness. To examine the accuracy of the calculated probability of predation on territories of unmated males based on real nests, we also calculated the probability of nest predation in different territories using the regression model for artificial nests (Table 1d). The difference in estimated probability of nest predation between territories of monogamous and unmated males was very similar for the two regression models based on real and artificial nests (0.10 vs. 0.11; Table 4). The average relative reproductive success of successful nests for females of different harem status during nestling feeding is also shown in Table 4. The hypothetical reproductive success a female would get if settling on the territory of an unmated male was set to be equal to that of monogamous females, because unmated males are expected to provide full parental assistance and their territories are likely to be rather similar with respect to food supply to territories of monogamous males.

From Table 4, we can estimate the expected relative reproductive success of females in different breeding situations by multiplying the relative reproductive success of successful nests by the corresponding probability of escaping nest predation. The expected relative reproductive success of secondary females (0.54) was similar to that of females of monogamous males (0.55) and higher than if females had settled on territories of unmated males (0.44; Table 4). This was a result of differences in probability of predation among territories of different attractiveness. Moreover, the average success of secondary females is expected to be even higher because sometimes secondary females reach primary status when the nest of the primary female fails. When this occurs, males often redirect their assistance to the former secondary females, and this enhances the expected reproductive success of females settling with already-mated males (Bensch and Hasselquist 1991*a*; Bensch and Hasselquist 1994; Hansson et al. 1997). Previous analyses have shown that secondary females on average reach primary status in 29% of breeding attempts, due to the combined effect of inter- and in-

TABLE 4. Expected reproductive success of female Great Weed Warblers in different breeding situations.

Territory status and female status at the nestling-feeding stage	Territory attractiveness rank†	Probability of nest predation estimated from:		Relative reproductive success of successful nests‖	Expected relative reproductive success¶
		Real nests‡	Artificial nests§		
Polygynous territory					
Primary female	5.9	0.40	0.53	1.09	0.65
Secondary female	5.9	0.40	0.53	0.90	0.54
Monogamous territory	8.1	0.45	0.59	1.00	0.55
Territory of unmated male	12.4	0.56	0.69	1.00#	≤0.44

† Mean territory attractiveness rank in the experimental years (polygynous territories $N = 21$; monogamous $N = 19$; territories of unmated males $N = 15$). Low rank value corresponds to highly attractive territory.

‡ Estimated from the formula in Table 3c, by entering mean territory rank (see Fig. 2).

§ Estimated from the formula in Table 1d, by entering mean territory rank and late experimental period (in correspondence with the laying date of the majority of females). Because the experiment covered only the egg-laying and incubation period (16 d), the calculated predation probability was recalculated to include the whole breeding cycle of 26 d, using the formula $1 - (e^{\ln(1-P)/16})^{26}$; where P is the predation probability estimated from the formula in Table 1d.

‖ Fledgling success in successful nests relative to that in nests of monogamous females. Data from real nests in the two experimental years ($N = 38$ nests) and from 1985–1989 (Bensch and Hasselquist 1991a).

¶ Reproductive success × survival probability of real nests (i.e., 1 − predation probability estimated from real nests) (e.g., primary females: $1.09 \times (1 - 0.40) = 0.65$).

The hypothetical reproductive success of females at territories of unmated males is expected to be equal to that of monogamous females (see *Discussion*).

traspecific nest predation (Hansson et al. 1997). Inclusion of the probability of reaching primary status in the analyses of Table 4, increases the expected reproductive success of secondary females from 0.54 to 0.57 ($0.65 \times 0.29 + 0.54 \times 0.71$), i.e., higher than the expected reproductive success of monogamous females (0.55; Table 4).

To conclude, due to differences in the probability of nest predation on territories of different attractiveness, females settling with already-mated males are expected to get similar reproductive success as females of monogamous males, and higher success than if they would have settled with unmated males. Thus, the spatial pattern of nest predation is an important territory quality parameter that can give secondary female Great Reed Warblers compensation for the cost of sharing territories with other females, and hence explains the occurrence of polygyny.

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