

Trade-offs of Territory Choice in Male and Female Marsh Warblers

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Predation and food availability are two major ecological factors affecting reproduction in birds (Ricklefs 1969). Food availability may affect primarily the ease of raising offspring (Duckworth 1990, Westneat et al. 1990). For example, if food is abundant near the nest or is easily gathered, parental effort will be less than if food is located far away or hard to obtain. In this sense, food access is an important determinant for the necessity and amount of biparental care. One would expect that, in the process of territory choice and because of their high initial investment, females should be more selective than males for factors important for nest-site protection (e.g. vegetation density; Hoi and Winkler 1988, Martin 1988, Velarde 1992). Males, however, should be more selective regarding food availability. Since males generally have better options for desertion, food availability mainly influences their opportunities for further matings. However, male territory choice cannot be independent of female preferences. To partially fulfill male and female requirements the territory should have a high food supply and well protected nest sites.

High nest predation can also favor a male's propensity to become polygynous, due to the increased probability of survival for offspring in different nests (R. Montgomerie, J. Briskie, and T. Poldmaa, 1992 abstract Int. Behav. Ecol. Congress). Also, the propensity to become a secondary female can be greater under situations with high nest predation. For instance, the likelihood of a Great Reed-Warbler (*Acrocephalus arundinaceus*) female to choose an already mated male is higher under high predation risk. In this species males provide care only to chicks of their primary female and with predation risk the likelihood of nest losses for primary females increase and in turn the secondary female's chances to get a primary status (Bensch and Hasselquist 1991). Therefore, male and female territory choice might be influenced by different factors and the interrelations of them. The relationships between ecological factors in a territory are poorly known. Still less is known about how these relationships affect territory choice or the mating system of a species (Martin 1992).

Comparing two study areas of the Marsh Warbler (*Acrocephalus palustris*), we could show that in the area with high vegetation density, food abundance was low and vice versa. This indicates a negative relationship between the two ecological factors. Settlement of Marsh Warblers was earlier and reproductive success was higher in the area with higher vegetation density. Moreover, a difference in male feeding effort was indicated for the two areas (Ille and Hoi 1995). In this study, we want to elucidate the relationship

between food availability and nest-site cover in Marsh Warbler territories, its influence on territory choice and reproductive success and, finally, its importance for male and female reproductive strategies.

Methods.—Our study was conducted in a marsh area around Lake Neusiedl in eastern Austria (47°56'N, 16°45'E) for five breeding seasons (1989–1993). The study area consisted of a 1.5-km strip of land along a water ditch.

Birds were mist netted and color banded. To determine the time of territory occupation we used male singing behavior and the laying date (date of the first egg) of the females. Reproductive success was evaluated based on clutch size, chick development (calculated as deviations from mean mass in grams of a given chick age), and number of hatchlings and fledglings. Male and female feeding rates were recorded during 1-h periods from a mobile blind that was placed 5 to 10 m from the nest. Observations started the day after erecting the blind. Feeding protocols were carried out at about noon (1100–1500). On average, three observation periods were spent at each nest where chicks were four to nine days of age.

Insects were collected during the nestling phase with pitfall traps to obtain an index of insect abundance and activity. The traps had a diameter of 10.2 cm and were filled with 2% formaldehyde to a depth of 4 cm. At each nesting site, six traps were set for two days at a height of 10 cm above the ground within a radius of 5 to 10 m of the nest. A nutrition index (N) was calculated as:

$$N = n s / 100, \quad (1)$$

where n is the number of insects and s is insect size (mm, measured using a micro scale).

To characterize the habitat surrounding the nest, the following three habitat variables were recorded: (1) proportion of main vegetation types; (2) vegetation height; and (3) vegetation density at a height of 1.0 m. Six point samples were taken at distances of 5 m from the nest. The most important habitat types were: (a) stinging nettles; (b) reeds; (c) vegetation lower than 1 m, including grasses, sedges and tules; and (d) water. The proportion covered by these habitat types was estimated within a 5-m radius of the nest. Vegetation density was measured by means of a vegetation stratimeter (VSTRAT 901; see Oppermann 1989) and is given as percent of covered area. At the nest site, we measured nest height, vegetation density, vegetation height, distance to the water, and type of vegetation.

A discriminant analysis (Ludwig and Reynolds 1988) was used to evaluate the importance of different veg-

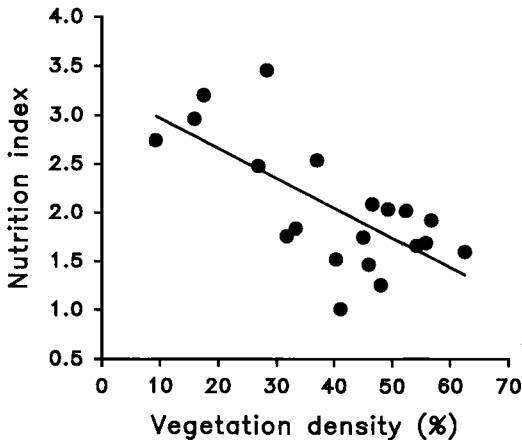


Fig. 1. Relation between vegetation density (percent of covered area within radius of 5 m of nest) and insect abundance (nutrition index within radius of 5 m of nest) for each Marsh Warbler territory.

etation parameters for nest predation. Vegetation parameters were compared between successful and depredated nests. Multivariate transformation procedures were applied to habitat variables (see Dunn 1981) to meet the requirements of the test. A multiple-regression analysis was used to control seasonal effects and number of chicks for the relation between male feeding component and nutrition index. Non-parametric statistical tests were used (Siegel 1956).

Results.—Vegetation density in Marsh Warbler territories was negatively correlated with their food abundance given as a nutrition index ($r = -0.69$, $P < 0.001$, $n = 24$; Fig. 1). Additionally, we found a negative correlation between food abundance and vegetation height ($r = -0.70$, $P < 0.001$, $n = 24$), whereas territories with high food supply had also higher proportions of low (vegetation lower than 1 m) vegetation ($r = 0.55$, $P < 0.001$, $n = 24$). On average, vegetation density was $40.98 \pm \text{SD of } 14.51\%$. Vegetation density was normally distributed among territories (Kolmogoroff-Smirnov goodness-of-fit test, $X^2 = 0.12$, $df = 23$, $P > 0.1$).

From territory establishment until the end of the breeding season there was a slight increase in food abundance ($r = 0.31$, $P = 0.04$, $n = 32$). However, it was not significant during the feeding period ($r = 0.25$, $P = 0.17$, $n = 32$). There is no evidence that food abundance around the nest site influenced reproductive success. We found no relation between the nutrition index and clutch size, number of nestlings, or chick development (Table 1).

No correlation was found between clutch size or number of nestlings and vegetation density when controlling for the seasonal variation in vegetation density (Table 1). Also, there was no correlation between vegetation and nestling development, yet when depredated nests are included, there was a significant

TABLE 1. Partial correlation coefficients between food availability (nutrition index) or vegetation density and different parameters of reproductive success (sample size in parentheses). For correlation between nutrition index and fledgling success, depredated nests were excluded.

	Nutrition index	Vegetation density
Clutch size	-0.28 (32)	0.09 (23)
No. fledglings	0.04 (32)	-0.19* (16)
Chick development	0.15 (12)	0.28 (12)

* If depredated nests included, correlation is 0.53 ($P = 0.01$, $n = 25$).

correlation with the number of fledglings (Table 1). Fledgling success increased with increasing vegetation density, which indicates the importance of nest predation. Twenty (32.3%) of 62 nests failed, and 14 of these 20 were depredated (70.0%). In three cases, cuckoo parasitism (15.0%) and weather were the cause. There were no partial nest losses due to starvation or other reasons. Comparing depredated and successful nests, vegetation variables significantly differed between depredated and successful nests (Table 2, Fig. 2). Nest predation showed a seasonal peak (Kruskall-Wallis test, $t = 15.2$, $df = 7$, $P = 0.03$; Fig. 3). There was a positive correlation between the weekly number of active nests and predation rate (percent nests depredated; $r = 0.37$, $P = 0.03$, $n = 59$).

Examining the relationship between both ecological factors and male territory choice, we found that males selected territories with higher vegetation cover. This is shown by the correlation of the rank of territory establishment with vegetation density and height (Table 3). The preferred territories also had a lower insect supply than those that were later occupied (Table 3). The male feeding component was not related to territory establishment ($r = 0.15$, $P = 0.74$, $n = 7$).

We found no correlation between the male feeding component and a measure of female choice—the start of egg laying ($r = 0.09$, $P = 0.64$, $n = 27$). However, the start of egg laying was highly correlated with the rank of territory establishment ($r = 0.79$, $P < 0.001$, $n = 22$) and to vegetation cover (Table 3). This indi-

TABLE 2. Correlations of four habitat variables (entered at significant level [$P < 0.05$] after univariate F -test) and first discriminant axis. Correlation coefficient (r) and univariate F - and P -values given (n of 25 for distance to edge and 26 for other variables).

	r	F	P
Distance to edge	-0.80	9.9	0.004
Percent open vegetation	0.70	4.5	0.04
Vegetation density	-0.90	14.6	0.001
Vegetation height	-0.78	9.6	0.005

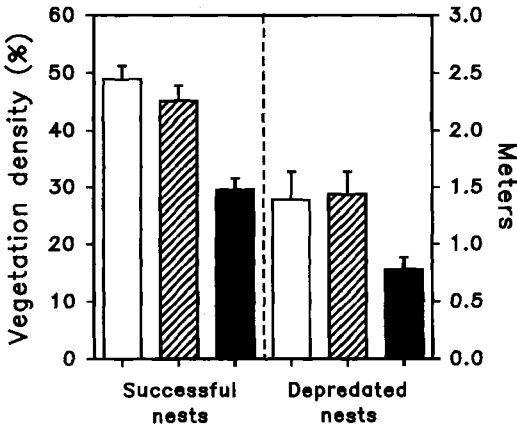


Fig. 2. Mean of vegetation density (percent; open bars), vegetation height (m; hatched bars) and distance to water (m; filled bars) in territories of males where nests were successful (all chicks fledged) and depredated. Whiskers indicate SE.

icates that female territory choice depends on vegetation cover rather than paternal quality.

There was considerable variation in the male feeding component ($\bar{x} = 37.71\%$, range 0.0–55.9%). The male feeding component was not correlated with the number of chicks ($r = 0.09$, $P = 0.62$, $n = 20$). The male feedings per chick actually decreased with the number of chicks ($r = -0.44$, $P = 0.02$, $n = 20$), but this decrease had no significant effect on chick development ($r = -0.28$, $P = 0.37$, $n = 7$). Since a male's opportunities for further matings partly depend on the date of first pairing, we controlled for this seasonal effect (using start of egg laying) and the number of chicks per clutch when examining the relationship

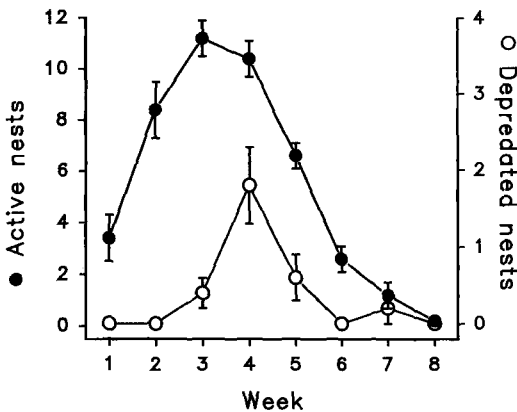


Fig. 3. Number (\pm SE) of depredated nests (open circles) in relation to active nests (nests containing eggs or nestlings; filled circles) throughout season (given as weeks from date of first egg laying). Five years (1989–1993) of data pooled.

TABLE 3. Correlation (with n in parentheses) between territory establishment or start of egg laying and four ecological factors.

	Territory establishment	Egg laying
Vegetation density	-0.43* (23)	-0.38 (24)
Vegetation height	-0.51** (23)	-0.47* (24)
Proportion low vegetation	0.46* (23)	0.58** (24)
Nutrition index	0.69*** (20)	0.68*** (31)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; others $P > 0.05$.

between the male feeding component and food availability around the nest site. Eliminating these effects, the male feeding component was negatively related to the nutrition index ($r_{\text{part}} = -0.52$, $P = 0.04$, $n = 17$), whereas there was no relation to feedings per chick ($r = -0.31$, $P = 0.22$, $n = 17$).

Discussion.—The timing of territory establishment by males and the start of egg laying by females indicate that in Marsh Warblers both sexes prefer territories with high vegetation density. However, female choice also can be based on male-quality features. Since territory quality often is interrelated with male quality (Heisler 1981, Reid and Weatherhead 1990), we cannot exclude that some factors of male quality might be interrelated with territory quality. Nevertheless, there is evidence that female choice is not based on male parental quality alone, supported by the fact that the timing of territory establishment was not related to later male parental effort. Therefore, territory establishment is not a good predictor for male parental quality.

Marsh Warblers selected territories with higher vegetation density, which revealed a significant effect on reproductive success, mainly due to reduced nest predation. Although there was considerable variation in food availability among territories, we found no influence of food availability in nest proximity on reproductive success (Table 1). This result can be explained partly by the fact that Marsh Warblers arrive very late in the breeding season (Schulze-Hagen 1991, Ille and Hoi 1995), and they use only a short breeding window (Schulze-Hagen 1991) concurrent with an optimal food supply (Schulze-Hagen et al. unpubl. manuscript). The variation of food supply at this time may be unimportant for nestling survival; food supply may already be above a critical threshold for affecting offspring development.

Our results show that food availability and vegetation density are negatively related. Territories, therefore, provide either a high food availability or good nest protection, making the preference of dense territories at least reasonable. Due to the fact that food availability does not appear to be influential for reproductive success, male Marsh Warblers may have the opportunity to emancipate themselves from pa-

ternal duties and become polygynous (Emlen and Oring 1977, Dowsett-Lemaire 1979, Wittenberger and Tilson 1980), a possibility supported by our results. We might expect food supply in the territory to determine the male feeding component. However, as mentioned above, females prefer territories with good nest protection. Therefore, we would expect contradicting interests between the sexes. To increase their mating chances, males may have been forced to occupy high-vegetation-density territories that when considering other factors may not have been optimal for the males. Male chances for a further mating depend on: (1) food supply (because this determines independency from parental care); (2) date of first mating (because this influences chances of obtaining second mate); and (3) the availability of territories with high food supply in relation to high-vegetation-density territories. For instance, a surplus of territories with well protected nest sites will decrease male mating chances because females will first select the well-protected territories. In our study area, most territories had a high vegetation density. In such situations, only few females were forced to settle in low-quality (low vegetation density) territories. Therefore, territory choice is under female control and male opportunities for polygyny are low. Territory choice would be under male control if only few well protected territories were available. This situation would enable a male to mate quite early in the season, even in less protected territories.

Under conditions of high predation pressure, spreading the chicks over several nests can be a strategy to increase the survival chances of at least some nestlings (R. Montgomerie, J. Briskie, and T. Poldmaa, 1992 abstract Int. Behav. Ecol. Congress). Thus, apart from habitat quality (see polygyny-threshold models), polygyny also may be favored by high nest predation (Bensch and Hasselquist 1991). In territories with poor food conditions where the necessity for male parental care is high, extrapair copulations might be an alternative strategy to spread chicks over several nests. At the moment, no information on extrapair paternity in Marsh Warblers is available.

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LITERATURE CITED

- BENSCH, S., AND D. HASSELQUIST. 1991. Nest predation lowers the polygyny threshold: A new compensation model. *Am. Nat.* 138:1297–1306.
- DOWSETT-LEMAIRE, F. 1979. The sexual bond in the Marsh Warbler, *Acrocephalus palustris*. *Gerfaut* 69: 3–12.
- DUCKWORTH, J. W. 1990. Parental care in the Reed Warbler. D. Phil. thesis, Univ. Cambridge, Cambridge.
- DUNN, J. E. 1981. Data-based transformations in multivariate analyses. Pages 93–102 in *The use of multivariate statistics in studies of wildlife habitat*. U.S. Department of Agriculture, General Tech. Rep. RM-87.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- HEISLER, I. L. 1981. Offspring quality and the polygyny threshold: A new model for sexy son hypothesis. *Am. Nat.* 117:16–328.
- HOI, H., AND H. WINKLER. 1988. Feinddruck auf Schilfbrüter: Eine experimentelle Untersuchung. *J. Ornithol.* 129:439–447.
- ILLE, R., AND H. HOI. 1995. Factors influencing fledgling survival in the Marsh Warbler *Acrocephalus palustris*: Food and vegetation density. *Ibis* 137: 586–589.
- LUDWIG, J. A., AND J. F. REYNOLDS. 1988. *Statistical ecology*. Wiley, New York.
- MARTIN, T. E. 1988. Habitat and area effects on forest bird assemblages: Is nest predation an influence? *Ecology* 69:74–84.
- MARTIN, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. *Curr. Ornithol.* 9:163–197.
- OPPERMANN, R. 1989. Ein Meßinstrument zur Ermittlung der Vegetationsdichte in grasig-krautigen Pflanzenbeständen. *Nat. Landschaft* 64:332–338.
- REID, M. L., AND P. J. WEATHERHEAD. 1990. Mate-choice criteria of Ipswich Sparrows: The importance of variability. *Anim. Behav.* 40:538–544.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithson. Contrib. Zool.* 9.
- SCHULZE-HAGEN, K. 1991. *Acrocephalus palustris*. Pages 377–433 in *Handbuch der Vögel Mitteleuropas* (U. N. Glutz von Blotzheim and K. M. Bauer, Eds.). Aula, Wiesbaden.
- SIEGEL, S. 1956. *Non-parametric statistics for the behavioral sciences*. McGraw-Hill, New York.
- VELARDE, E. 1992. Predation of Heermans Gull (*Larus haermanni*) chicks by Yellow-footed Gulls (*Larus livens*) in dense and scattered nesting sites. *Colon. Waterbirds* 15:8–13.
- WESTNEAT, D. F., P. W. SHERMAN, AND M. L. MORTON. 1990. The ecology and evolution of extra-pair copulations in birds. *Curr. Ornithol.* 7:331–369.
- WITTENBERGER, J. F., AND R. L. TILSON. 1980. The evolution of monogamy: Hypotheses and evidence. *Annu. Rev. Ecol. Syst.* 11:197–232.

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