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# Spatiotemporal patterns of egg predation in forest islands: an experimental approach

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Thirty holm oak *Quercus rotundifolia* forests, ranging from 0·1 to 350 ha, were studied in central Spain to analyse the spatial and temporal patterns of predation in relation to size of forest patches. During two springs (1988 and 1989), quail *Coturnix coturnix* eggs were placed in these forests to evaluate predation rates. Two trials (April and June) during each year were performed to study the intraseasonal and interyear constancy of predation. Results showed that predation rate tends to increase with forest fragmentation, although forest size was poorly related to predation rate. Predation rates seemed to be constant within spring seasons and between years. These results suggest that predators concentrate their search activities in some selected forests, thus accentuating their effect on prey species.

## INTRODUCTION

The reduction of forests affects the composition and structure of their animal communities (Harris, 1984; Wilcove *et al.*, 1986). This has been well illustrated with birds, where various studies have documented the loss of species as a consequence of progressive fragmentation of forests (see Robbins *et al.*, 1989 for a review). This phenomenon may result from several causes, including the elimination of certain microhabitats, depletion of food resources and reduction of populations (Wilcove *et al.*, 1986; Gilpin, 1987). Increased predation has been considered as another possible cause. Wilcove (1985) showed an increase in predation on artificial nests in small forests and Martin (1988*a*) attributed the disappearance of bird species with more accessible open nests in smaller forests to the same cause. Recent studies suggest an increase in predation on nests in ecotone forest areas (Yahner & Wright, 1985; Angelstam, 1986; Wilcove *et al.*, 1986; Andrén & Angelstam, 1988; Møller, 1988; Yahner & Scott, 1988), providing indirect evidence of the negative effect of forest reduction related to fragmentation (forest reduction increases the border/area ratio). Nevertheless, little is known about the generality of increases in predation as forest size is reduced, or the nature of its spatial and temporal patterns. Thus, we studied forest 'islands' in central Spain with the following objectives: (1) to corroborate the increase of predation rates as forest size decreases; (2) to test the strength of association between forest size and predation rate; and (3) to study the constancy of predation, with the aim of evaluating the persistence of this factor on the prey communities in each forest. If high predation is maintained over time on a limited number of forests, it should increase the probability of local extinction of prey species.

## METHODS

Thirty isolated holm oak *Quercus rotundifolia* forests between 0·1 and 350 ha in size were selected for study in a 250-km$^2$ area in Burgos Province, Central Spain (see Santos & Tellería, 1992). The zone sustains a rich community of potential egg predators such as corvids (*Corvus corone*, *Pica pica*), carnivores (*Vulpes vulpes*, *Mustela nivalis*, *Meles meles* and *Sus scrofa*) and lizards (*Lacerta lepida*). Commercial quail *Coturnix coturnix* eggs

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were used to evaluate the rate of predation. Single eggs were placed directly on the ground every 25 m along a transect from the edge through the middle of each forest beside any easily recognized natural feature to verify their presence or disappearance after the experimental period. In smaller forests in which a linear transect was too short to provide a minimum number (see below), they were placed as sparsely as possible. If there were no reliable natural features, the ground or a branch was marked with a small notch. We did not use artificial marks and spent less than one minute placing each egg in order to avoid the discovery of eggs through the activity of the researchers themselves (Yahner & Wright, 1985; Salathé, 1987). The number of eggs deposited varied according to the size of the forest, on a logarithmic scale, from six in forests smaller than 2 ha to 72 in forests over 200 ha. Densities of eggs were higher in small forest patches than in the larger ones (see Haila, 1988, for a review of the influence of plot size on density). This may affect predation rates, as some studies have shown that risk of nest predation increases with density of nests (e.g. Martin, 1988*b*). For this reason we included egg densities (number of eggs/ha in each forest patch) as an additional variable in our analysis. The eggs were in place for 48 h in each forest. After this period, we estimated the predation rate ($p$) in each forest by $p = m/n$, where $m$ = number of missing eggs after a 48-h period and $n$ = total number of eggs deposited.

Temporal constancy of egg predation was tested by trials run during late April and again during early June in 1988 and 1989. Given the largely perennial nature of the tree and shrub vegetation (Santos & Tellería, 1992), there was no change in forest cover between April and June tests that could substantially affect predation rates (Yahner & Wright, 1985; Andersen & MacMahon, 1986). A total of 1350 and 1334 eggs were placed during springs of 1988 and 1989, respectively.

Data were normalized by means of logarithmic (forest size, egg density) or arcsin-transformations (predation rates) before statistical analysis (Zar, 1984). Correlation coefficients are shown below as NS (not significant) when $p > 0{\cdot}05$, * when $p < 0{\cdot}05$, ** when $p < 0{\cdot}01$, and *** when $p < 0{\cdot}001$.

## RESULTS

Predation rate tended to decrease as forest size increased (Fig. 1), but no significant overall correlation between the two parameters was obtained (1988: $r = -0{\cdot}257$ NS; 1989: $r = -0{\cdot}354$ NS). High variability of predation rates in smaller forests, a pattern already illustrated by Wilcove (1985), seemed to be the main reason for this lack of relationship between forest area and predation rates.

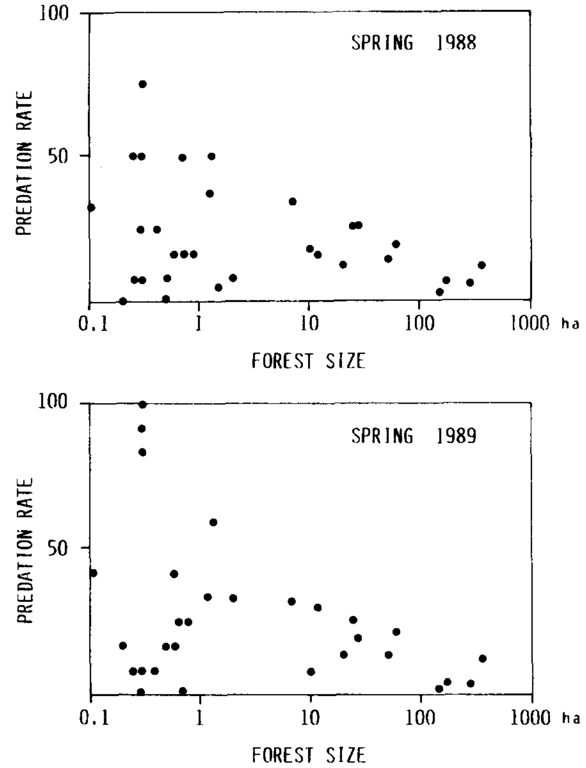

**Fig. 1.** Relationship between mean predation rates and forest size during the spring of 1988 and 1989.

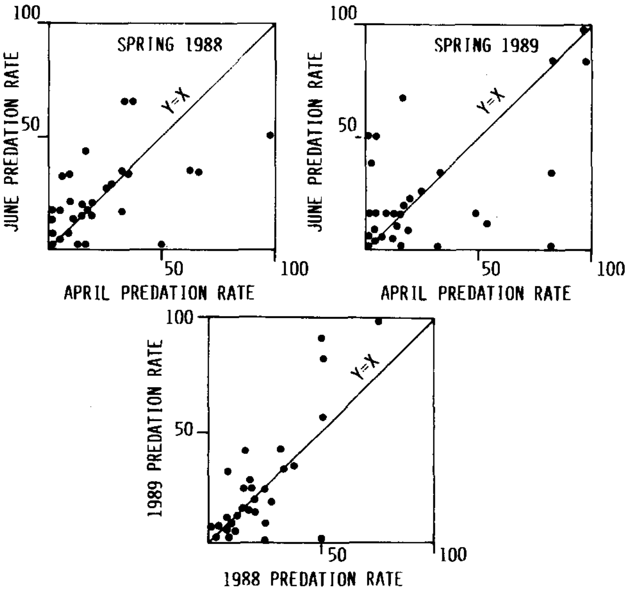

**Fig. 2.** Relationships between April and June predation rates in the spring of 1988 and 1989 (above) and between mean spring predation rates during 1988 and 1989 (below).

**Table 1. Predation according to month, year, and forest area and results of Chi-Square heterogeneity tests ($\chi^2$)**

| | Forest area | | | |
|---|---|---|---|---|
| | <10 ha<br>*p*/*n* (%)[a] | 10–100 ha<br>*p*/*n* (%) | >100 ha<br>*p*/*n* (%) | |
| 1988 | | | | |
| April | 38/126 (30·2) | 38/259 (14·7) | 16/272 (5·9) | 34·79 *** |
| June | 38/142 (26·8) | 67/279 (24·0) | 24/272 (8·8) | 22·32 *** |
| Total | 76/268 (28·4) | 105/538 (19·5) | 40/544 (7·4) | 52·23 *** |
| 1989 | | | | |
| April | 47/124 (37·9) | 40/262 (15·3) | 16/276 (5·8) | 54·58 *** |
| June | 37/126 (29·4) | 57/270 (21·1) | 16/276 (5·8) | 33·92 *** |
| Total | 84/250 (33·6) | 97/532 (18·2) | 32/552 (5·8) | 84·40 *** |

[a] *p*, No. of predated eggs; *n*, no. of deposited eggs; %, predation rate.
***, $p < 0{\cdot}001$.

There was also no significant correlation between egg density and predation rates (1988: $r$ = 0·235 NS; 1989: $r$ = 0·316 NS). Excluding the effects of bait density by means of partial correlation analysis, forest size still failed to reach significant correlation with predation rate (1988: partial $r$ = −0·101 NS; 1989: partial $r$ = 0·019 NS), and bait density, excluding the effect of forest size, was also not related to predation rate (1988: partial $r$ = −0·057 NS; 1989, partial $r$ = 0·019 NS).

Clearer trends, however, were shown when the results were grouped according to different-sized groups of forests: predation rates increased significantly in all four time periods as forest size decreased (Table 1). This seems to suggest that an increase in predation occurred with increasing fragmentation of landscape elements, although erratically in the smaller forest patches comprising this environment.

We found positive, significant correlations between April and June predation rates in each of the forests studied during both years (1988: $r$ = 0·457 *; 1989: $r$ = 0·517 **; Fig. 2). This suggests that the spatial distribution patterns of predation rates among forests are fairly constant over time. This is not a spurious relationship, caused by the influence of forest size and egg density (smaller forest patches will always tend to have a higher predation rate), since a significant correlation between June and April predation rates was maintained when these factors were removed by partial correlation. Thus, the June rate was influenced by that of April (1988: partial $r$ = 0·477 *; 1989: partial $r$ = 0·510 *) and not by the forest area (1988: partial $r$= −0·071 NS; 1989: partial $r$ = 0·204 NS) or bait density (1988: partial $r$ = −0·099 NS; 1989: partial $r$ = 0·242 NS).

Similar results were obtained by comparing the annual rates ($r$ = 0·615 ***; Fig. 2). Partial correlations also showed that the 1989 predation rate was correlated with the 1988 predation rate (partial $r$ = 0·569 **) but not with forest size (partial $r$ = 0·021 NS) or bait density (partial $r$ = 0·063 NS).

## DISCUSSION

These results corroborate the current hypothesis about the tendency of predation to increase in fragmented forests. However, the overall association between woodland size and predation rate was low, and there is a need to test such conclusions with more natural prey. The study also showed persistent levels of predation (at least at the temporal scale we studied), a fact that could considerably increase its negative effect on the prey communities of the affected forest patches: Stamps *et al.* (1987) considered that some forest patches may be bounded by a 'hard edge' which certain small vertebrates never cross to enter surrounding habitats. Under these conditions, populations of the prey species located in small forest patches could face an increasing risk of extinction because of the continuous predation pressure. In the case of forest patches with 'soft edges', permeable to migrants, constant predation could cause these to become sink areas for immigrants.

The increase of predation rates as forest fragmentation progresses may be attributed to the complementary occurrence of two phenomena. First, the division and reduction of forests is usually accompanied by a substantial change in the predatory fauna as certain highly abundant generalist predators increase (Andrén *et al.*, 1985;

Salathé, 1987). Second, a reduction in forest area produces a proportional increase in ecotone areas favouring the search strategies and increasing the predation rates of certain predators (Wilcove *et al.*, 1986; Andrén & Angelstam, 1988; Møller, 1988). Forest fragmentation thus may produce an overall increase in predation at a landscape scale, as our results suggest (Table 1; see also Wilcove, 1985). This fact does not imply, however, that the area of each forest patch in the resulting archipelago will determine its own predation rate. This rate could depend on the way predators make use of the space on a broader scale.

Environmental heterogeneity seems to drive animals to exploit the more productive sectors more intensively (see Stephens & Krebs (1986) for a review). Large predators with home ranges of over 200 ha such as crows, foxes, badgers, and wild boars are capable of systematically covering a wide area (Schoener, 1968; Harestad & Bunnell, 1979). Each small forest may be considered to provide some specific trophic resources and, together with other forest fragments, they make up a mosaic that is included in the routine movements of such predators. Studies on the home range of some predators in patchy habitats have shown preferential use of forest patches as hunting and breeding places (e.g. Stevenson & Major, 1982; Haroldson & Fritzell, 1984). This fact, together with the interyear home range fidelity of many of these species (Andelt, 1985; Arthur *et al.*, 1989), may explain the seasonal and interyear constancy of predation over some forest patches. Marginal forests, inaccessible or undesirable for some reason (e.g. very distant) in the view of one predator individual, may be visited less frequently and thus receive a low intensity of predation.

On the other hand, smaller predators (e.g. small mammals and lizards) with home ranges of <1 ha (Stamps, 1977; Harestad & Bunnell, 1979), will be established in these forests. Populations of these small vertebrates in each forest island may vary significantly because they too are subject to the inherent dangers of local extinction associated with insular environments (Wilcove, 1985). It is thus possible that the impoverishment or extinction of a small predator community may also lead to a subsequent reduction and uneven distribution of predation rates in forest fragments. Insofar as small predators continue to occupy certain forests, predation rates will again tend to remain constant within each.

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