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Effects of leafing and position on nest predation in a Mediterranean fragmented forest.— Since Ricklefs' review (1969), it has been accepted that nest predation is a primary source of nesting mortality during the breeding season and is an important selective agent in the reproductive strategies of birds (Slagsvold 1982, Nilsson 1986). Hence, the choice of nest location could be a means of minimizing the effects of nest predation (Best and Stauffer 1980, Murphy 1983, Leonard and Picman 1987, Martin 1988a). Experiments using artificial nests have disclosed several factors affecting nest predation rates. In open nests and forest habitats, two of the main factors are vegetation cover and nest height. The former acts on the nest site and/or the nesting patch (e.g., Murphy 1983, Salathé 1987, Martin 1988a, Martin and Roper 1988) and may cause differences in predation rates among habitats. Likewise, Slagsvold (1982) has shown that in habitats with deciduous vegetation in which leaf phenology produces temporal changes in cover, the probability of nest predation varies throughout the reproductive season. Hence, species which breed after leafing (e.g., tran-Saharian migrants) should be less affected by nest predation than resident birds. With respect to nest height, higher positions have generally been found to be advantageous at temperate latitudes (Ricklefs 1969, Martin 1988b), although this advantage may be influenced by the cover in different vegetation layers (Slagsvold 1982, Yahner and Cypher 1987, Yahner and Scott 1988).

The present study is an experimental analysis of nest predation in a Mediterranean forest comprised of evergreen Holm oaks (*Quercus rotundifolia*), and deciduous Lusitanian oaks (*Q. faginea*). We hypothesized that the highest predation rates should be supported by nests with low cover, namely in Lusitanian oaks in early spring. Hence, nest predation should decrease in these trees after leafing, while it should be constant throughout the breeding season in the evergreen oaks. Holm oaks are thus controls which indicate variations in the predation pressure from causes other than cover such as variations of predator abundance or activity during spring (Slagsvold 1982, Smith and Andersen 1982, Yahner and Wright 1985). In this context, we also approached the influence of nest height on predation rates. We carried out our study in a fragmented forest. Recently, several authors have indicated that habitat fragmentation increases nest predation due to changes in the numbers and types of predators (e.g., Wilcove 1985, Martin 1987, Temple and Cary 1988). Cover and height advantages could thus be affected by fragmentation in our area, resulting in nesting patterns different from those evolved in more extensive habitats (Martin 1987).

Study area and methods.—The study area covers 525 ha in Villamayor de los Montes, Burgos province, in central Spain. The farming usage (dryland grain cropping and sheep grazing) has reduced the forest vegetation to a fragmented group of patches ranging from 0.1 to 90 ha, many of which are interconnected by small corridors. The arboreal vegetation has a mean height of 5.5 m and 35% coverage (22% Holm oaks and 12% Lusitanian oaks). The shrub layer (33% coverage and 0.7 m of mean height) is dominated by *Cistus* spp. The mean percentage of grassland is around 15%. Holm oaks and shrubby species are typical Mediterranean, evergreen plants, so their foliage cover is constant throughout the year, while the leaf phenology of Lusitanian oak causes the single cover differences among periods and sites in the study area. Hence, the foliage changes presumably do not affect ground cover, restricting to arboreal cover before and after Lusitanian oak leafing. Direct and indirect observations (footprints and feces), as well as trappings (Tellería et al. 1991), have shown that the area has a rich community of potential nest predators including corvids (Carrion Crow [*Corvus corone*], Black-billed Magpie [*Pica pica*], and Eurasian Jay [*Garrulus glandarius*], large and medium-sized mammals (wild boar [*Sus scrofa*], red fox [*Vulpes vulpes*], badger [*Meles meles*], weasel [*Mustela nivalis*], European Polecat [*M. putorius*] and western

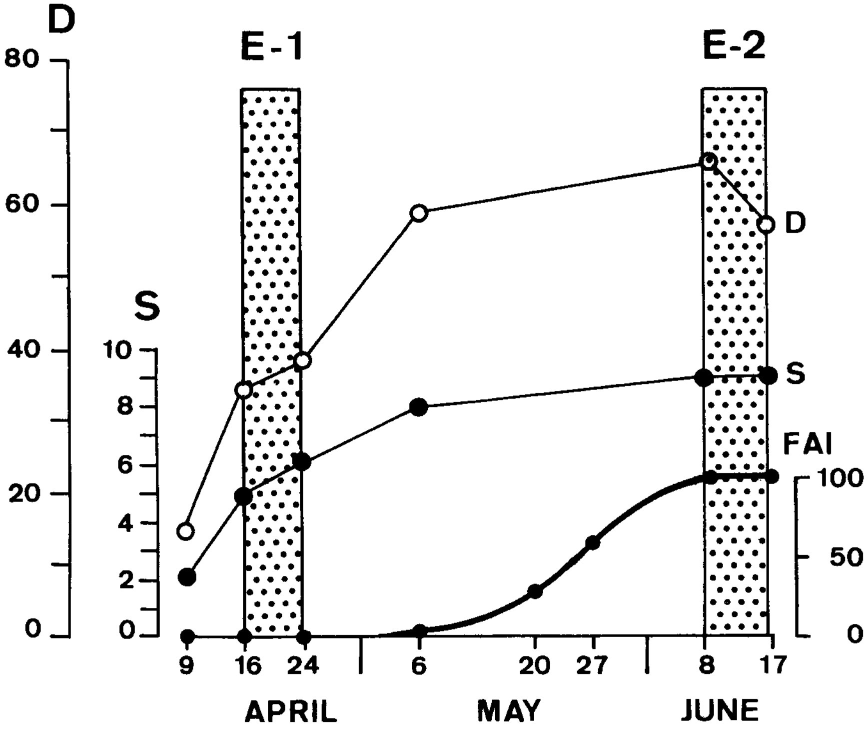

FIG. 1. Phenology of *Q. faginea* and summer passerines in the study area. D: density of summer passerines/density of passerines × 100. S: number of summer passerines. FAI: foliage area index, in percentages. E-1 and E-2 indicate dates of the first and second experiment, respectively. Migrant passerines: Subalpine, Orphean, and Bonelli's warblers (*Sylvia cantillans, S. hortensis,* and *Phylloscopus bonelli*), Common Nightingale (*Luscinia megarhynchos*), Brown Tree-Pipit (*Anthus trivialis*), and Ortolan Bunting (*Emberiza hortulana*). Resident passerines: Wood Lark (*Lullula arborea*), Common blackbird (*Turdus merula*), Robin (*Erithacus rubecula*), Great and European Blue tits (*Parus major* and *P. caeruleus*), Common Chaffinch (*Fringilla coelebs*), Common Serin (*Serinus serinus*) and Cirl Bunting (*E. cirlus*).

hedgehog [*Erinaceus europaeus*]), rodents (wood mouse [*Apodemus sylvaticus*] and garden dormouse [*Eliomys quercinus*]) and reptiles (ocellated lizard [*Lacerta lepida*]).

Lusitanian oak leafing phenology was monitored on eight occasions during spring 1988 (see Fig. 1 for dates), during each of which 2000 buds were sampled at random. The buds opened in May, after which time the number of leaves were counted, their length and width estimated, and an index of foliage area calculated by fitting the leaf form to an ellipse. Leaf cover was estimated for every date as the product of mean leaf surface by the number of leaves and further calculated as the percentage of the maximum value of full leafing (value 100%). Leaf growth accelerated in late May and was completed in early June when the Lusitanian oaks reached their maximum coverage (Fig. 1).

The arrival and settling of the migrant bird species was monitored along a 3.9-km transect six times during spring, using the line-transect method (Järvinen and Väisänen 1975). The study area has nine migrant species, six of which are passerines (Fig. 1). At the start of April only Subalpine Warbler (*Sylvia cantillans*) was present, but by 6 May all species had arrived and maximum densities were reached. These species made up approximately 60% of the passerine community during May and the first half of June (Fig. 1).

Two experiments, each lasting eight days, were carried out. The first began before the sprouting of the first Lusitanian oak leaves and coincided with the arrival of the earliest migrant bird species. The second experiment took place after the completion of leafing and the arrival of all migrant breeders. Artificial nests were used, with a diameter of 9–10 cm and a depth of 5 cm. Two Japanese Quail (*Coturnix japonica*) eggs were placed in each nest. The nests were muddied for camouflage (Martin 1987) and placed in two positions: on the ground at the base of tree trunks and above ground level in tree branches. In each experiment 80 nests were arranged in each tree species, 20 on the ground and 60 on the branches.

The nests were placed alternately in Holm oak and Lusitanian oak, at a distance of approximately 30 m from each other, to avoid the formation of food patches which might influence the searching activities of predators (Martin 1988b). The nests were visited eight days after their placement, with no intermediate interference in order to avoid any influence on predation rates by our activities (Best and Stauffer 1980, Salathé 1987). The nests were re-located by means of natural features for the same reasons (Göranson and Loman 1986). Each nest where one or two eggs had been broken or were missing was considered depredated. We identified the nest predators by means of their feces, footprints and toothmarks (Bang and Dahlström 1972, Green et al. 1987). Feces and toothmarks indicated predation by rodents. Depredated nests with a lack of marks (apart from the loss of eggs) or which had been moved but without identifiable marks were assigned to unidentified predators (reptiles, birds and great mammals; see Best and Stauffer 1980, Green et al. 1987). Because of the scarceness of reptiles, we assumed that in this predator group the nests with a lack of marks were predated by birds, especially the Carrion Crow (see Loman and Göranson 1978, Fjeld and Sonerud 1988), the most abundant bird predator in the study area.

Results and discussion.—Predation on Holm oaks was similar in both experiments, thus confirming the similar predation pressure throughout the study period (Table 1). The number of depredated nests in both tree species was similar in the first experiment (Table 1) in spite of the lack of leaf coverage for nests in Lusitanian oak (Fig. 1). Likewise, the Lusitanian oak nests were subjected to the same predation in both experiments, before and after the leafing. There was no difference between experiments when the data from both tree species were pooled (Table 1). Both trees also supported identical predation in the second experiment (Table 1), showing a lack of further differences with both species in full leaf (χ^2, $P > 0.1$ in all the tests).

The distribution of nest predation in the two positions (ground and tree; Table 1) showed higher depredation rates on the trees in the two experiments separately ($\chi^2 = 12.987$, $P < 0.001$ for the first experiment; $\chi^2 = 3.708$, $P = 0.0542$ for the second experiment) and pooled ($\chi^2 = 17.455$, $P < 0.001$)

Depredated nests showed one or more of the following signs: garden dormouse (28) and wood mouse (4) feces; rodent toothmarks (44); and moved nests (129). These traces indicated that rodents, mainly garden dormice, were responsible for most of the mammalian predation. Rodent predation (feces and/or toothmarks) as opposed to unidentified predators (depredated nests without signs of rodents) is shown in Table 2. The activity of each predator group was the same in both experiments (χ^2, $P > 0.2$ in the two tests). The distribution of depredated nests between the two groups did not differ between experiments (χ^2, $P > 0.3$). Hence, the predator community had a constant action throughout the reproductive season, accounting for the lack of differences in predation rate between experiments.

TABLE 1

PERCENTAGES OF DEPREDATED NESTS ACCORDING TO TIME OF SEASON (SEE FIG. 1), TREE SPECIES, AND NEST HEIGHT (G: GROUND, T: TREE). THE NUMBER OF NESTS ARRANGED IN EACH TREE AND PERIOD WAS 80, 20 ON THE GROUND AND 60 IN TREES

Time of season	Tree species	Nest position G	 T	 Totals
Before leafing	H Oak	65	90	83.75
	L Oak	60	88.3	81.25
	Totals	62.5	89.2	82.50
After leafing	H Oak	85	90	88.75
	L Oak	75	95	90
	Totals	80.0	92.5	89.38
Total	Both trees	71.25	90.8	85.90

The situation of depradated nests differed between both groups due to a greater rate of predation by rodents on the ground than in the trees compared with the unidentified predators ($\chi^2 = 6.5$, $P < 0.02$ for the first experiment and $\chi^2 = 9.9$, $P < 0.01$ for both experiments combined). Of the depredated nests attributed to birds, 16 were preyed upon on the ground and 92 in trees ($\chi^2 = 5.4$, $P < 0.02$ with respect to a random distribution in each situation).

These findings show that the increase in cover related to leaf phenology did not decrease the predation rates of the experimental nests, contradicting the importance it is generally given in temperate latitudes. The fragmented structure of the study area, however, could account for the high predation rate (e.g., Temple and Cary 1988, Møller 1989), which may decrease or nullify differences in predation due to leaf cover. Fragmentation leads to an increase in generalist predators (Janzen 1986, Temple and Cary 1988), forest remnants surrounded by agricultural matrices supporting high densities of corvids in temperate latitudes (Andrén et al. 1985, Angelstam 1986). In our area, crow abundance increases with

TABLE 2

PERCENTAGES OF NESTS DEPREDATED BY RODENTS AND OTHER PREDATORS ACCORDING TO TIME OF SEASON AND NEST HEIGHT (SEE TABLE 1). IN BRACKETS THE NUMBER OF NESTS PLACED IN EACH EXPERIMENT AND POSITION

Time of season	Height	Predator group Rodents	 Others
Before leafing	G (40)	27.5	35.0
	T (120)	15.8	73.3
	Totals	18.8	63.8
After leafing	G (40)	32.5	47.5
	T (120)	21.7	70.8
	Totals	24.4	65.0

fragmentation, very small fragments hosting the highest densities of crows. Differences in nest predation associated with cover could, therefore, emerge in larger fragments than those studied. In the conditions of our study, there is thus no apparent advantage in delaying breeding, at least with respect to the risk of nest predation. Likewise, resident birds do not gain any advantage from the greater Holm oak coverage in early spring. More work is necessary, however, to determine whether these results are typical of fragmented conditions. Similarly, studies designed on larger, less fragmented sites, are obviously needed to discriminate short-term effects caused by fragmentation from nesting patterns evolved through evolutionary time scales in extensive mixed forests (see Martin 1987).

The influence of nest position on the incidence of predators was, however, significant, in accordance with current ideas about its role in determining nest predation. In our study, predation was lower on the ground than at higher strata, perhaps indicating a lower incidence of mammals than in other studies where the opposite trend was found (see Ratti and Reese 1988, Yahner et al. 1989). The distribution of predation intensity between birds and mammals fitted, however, the general patterns found in other studies, where mammals mainly operated on the ground and birds were the primary predators on above-ground nests (e.g., Loman and Göranson 1978, Best and Stauffer 1980, Yahner and Cyper 1987, Møller 1988).

The observed differences in predation pressure between ground and tree nests could influence the organization of bird communities through the selection of nest position, according to Martins' ideas (Martin 1988b, c; see also Ricklefs 1989). If the fragmented structure of the studied forests was responsible for a part of the predation patterns found, however, we could expect changes in these patterns with respect to degree of fragmentation (Matthiae and Stearns 1981, Wilcove 1985, Martin 1987), via a variation in the predator community traits such as species composition and numbers and predator search tactics, which may be a source of local or more widespread variation (Slagsvold 1982, Martin 1987, Ratti and Reese 1988, Yahner et al. 1989). In this context, the dynamism of habitats and landscapes in temperate regions (Forman and Godron 1986, Yahner 1988) may induce a fast spatial and temporal turnover in predator communities and other factors affecting nest predation (e.g., habitat structure; see Wilcove et al. 1986).

As a consequence, we suggest that predation patterns and associated selective pressures are likely to be extremely dynamic and variable processes in many cases, operating on short time-scales (ecological time). Natural conditions, such as extensive and scarcely perturbed habitats, are hence required to investigate the importance of nest predation on evolutionary time.

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T. SANTOS AND J. L. TELLERIA, *Dept. Biología Animal (Zoología), Fac. Biología, Univ. Complutense, 28040 Madrid, Spain.* *Received 30 Oct. 1990, accepted 1 April 1991.*

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Pairbond formation in the Razorbill.—I report here the formation of a Razorbill (*Alca torda*) pairbond observed during a study of this species' mating system on Skomer Island, Wales, U.K., in the southern Irish Sea (51°40′N, 05°15′W) (Wagner 1991). Prior to egg laying, Razorbills that bred among boulders in the Basin study colony regularly attended two ledges near the entrance of the colony, which I refer to as "mating arenas." I observed color-banded individuals in the arenas on 44 mornings between 4 April and 24 May in 1988, for a total of 100 h in which birds were present, and for 52 mornings between 1 April and 26 May in 1989 for 125 h. In the same period, daily colony checks were made in which I recorded the attendance of individuals at numbered nest sites and their interactions with other Razorbills. I watched the arenas from a hide 25 m from the mating arenas with a 20–60 power spotting scope. Observations of the arenas began at first light, usually before any Razorbills had arrived from roosting at sea, and continued until most, or all, birds departed from the arenas or until their mating activities had virtually ceased.

Pairs performed 75% of their copulations in the arenas and the remainder in the nesting colony. Males frequently attempted extra-pair copulations, especially during the period in which females began to lay eggs, which began in the final week of April in 1988 and in the first week of May in 1989. For all copulation attempts I recorded the individuals involved, whether cloacal contact (and presumably insemination) was achieved, the number of cloacal contacts, and the duration of the mounting in seconds.

Almost all Razorbills that attended the arenas were paired, and mainly copulated with their mates, although 3% of successful copulations were with other individuals. Several unpaired males also attempted extra-pair copulations (EPCs) by copulating with paired