Patterns of artificial avian nest predation by introduced rats in a fragmented laurel forest (Tenerife, Canary Islands)

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Abstract

The importance of introduced rats as damaging factors on island biotas is globally recognized. The predation of artificial avian nests by Ship rats (*Rattus rattus*) in fragmented laurel forests in Tenerife (Canary Islands) was explored. The influence of road edge, patch type, and position (ground versus tree) on nest survival in two forest remnants differing in conservation degree, were assessed using failure-time analysis. Overall, nest predation was greater in the preserved than in the disturbed remnant. Nest predation also differed among and within patches, variation being greater within the disturbed remnant. The probability of nest failure was higher at the interior than along the road edge in both remnants, but the road edge effect on nest predation was more intense in the disturbed remnant. Predation pressure was higher in patches of mature, closed canopy or dense understorey with stump sprouting. Ground nests were predated at higher rates than tree nests at any location. These results contrast with other nest predation studies in fragmented landscapes where forest edges rather than the interior are more frequently used by predators. Predatory activity by rats seems negatively affected by forest disturbance and road edge effect. Overall, artificial nest predation patterns by rats confirm a potential predation risk for the avifauna of the Canarian laurel forest. This should be considered in implementing conservation management programmes.

Keywords: Artificial avian nest predation, disturbance, laurel forest, road edge effect, road fragmentation, Ship rats

Introduction

On oceanic islands, invasive predators have induced the extinction or reduction of populations of many endemic bird species (Atkinson 1985; Diamond 1987; Thibault et al. 2002). Native predators are often scarce or lacking on these islands, and exotic mammals rapidly assume the vacant role of generalist predators (Martin et al. 2000). Breeding birds

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are vulnerable to introduced nest predators depending on composition of the predator pool, and to the responses of both birds and predators to landscape configuration, fragmentation and edge type (Darveau et al. 1997; Dijak and Thompson 2000; Martin and Joron 2003). Nest predator impacts are related to habitat use of predators, and breeding success of birds is partly dependent on predator distribution and behaviour (Lahti 2001). Nest site location may influence vulnerability to predation (Martin 1988; Keyser et al. 1998), although evidence for this is not always clear (Hanski et al. 1996; Zanette 2002). Effects of roads on nest predation have been assessed at diverse spatial scales (Yahner and Mahan 1997; Bergin et al. 2000) and some researchers have evaluated road edge effects on nest predation (Burkey 1993; Lindenmayer et al. 1999; Miller and Hobbs 2000).

To our knowledge, no nest predation studies have been conducted in relation to roadtraversed landscapes on oceanic islands, where this form of fragmentation is specially damaging. Changes caused by roads in forest cover and vegetation structure affect native and alien predator abundance and behaviour (Bennett 1991; Forman and Alexander 1998). The road system creates corridors that favour predator dispersal and invasion (Vermeulen and Opdam 1995; May and Norton 1996). Mechanisms of predation by exotic animals, and effects of predator type, landscape, and road proximity on nest predation need, however, island-based research. To date, most nest predation studies that consider fragmentation and edges (including roads), have been performed in continental temperate and tropical forests and agricultural landscapes (reviewed in Lahti 2001). These studies, however, pose difficulties for assessing the contribution of specific predators to nest failure because of the abundance of predator species (e.g. Donovan et al. 1997; but see Schmidt et al. 2001). The simplicity of predator faunas on oceanic islands provides an opportunity to test road effects on a predator basis.

To explore predation patterns by an introduced species at several landscape scales, artificial avian nest predation experiments in the laurel forest (also known as laurisilva) of Tenerife, Canary Islands, were conducted. Advantage was taken of the presence of a single predator species, namely the Ship rat (*Rattus rattus* L.), to assess factors shaping nest predation on road-fragmented forests. Predation was studied in two contrasting forest remnants, and compared (1) among forest patches contrasting in their vegetation structure and the degree of disturbance caused by silviculture; (2) at the within-patch scale, where the effects of road proximity (edge effect) and nest position (ground versus trees) were assessed.

Predator species

The Ship rat probably colonized the islands in the 15th century with the arrival of Europeans (Rodríguez 2001) and is widely distributed in the Canary Islands, where native rodents are extinct (Michaux et al. 1996). Ship rats predate upon endemic bird nests in the laurel forest (Hernández et al. 1999) and are the main cause of decline of the endemic Laurel pigeon (*Columba junoniae* Hartert, 1916, ground nester) and Bolle's pigeon (*C. bollii* Godman, 1872, tree nester) (Martín et al. 2000). Ship rats were photographed in 99.5% of the predation events in a camera study (Hernández et al. 1999). They are also strong predators of endemic plants (Delgado 2000, 2002) and invertebrates such as molluscs (J. Delgado, personal observation). They exhibit maximum reproductive activity in spring and summer, with a resting period in winter (Contreras 1988). Some studies suggest that Ship rat populations reach higher densities in subtropical than in temperate forests (Hooker and Innes 1995). In the laurel forest, they reach densities of 8–33 rats ha⁻¹, and a biomass of

5.4-5.9 kg ha⁻¹ (Contreras 1988). In one study, Ship rats foraged more intensively along road edges than at the interior of laurel and pine forests (Delgado et al. 2001). However, their activity extends far from roads into mature forest (Hernández et al. 1999; Delgado 2002). Ship rats may be also more abundant in the laurel than in the Canarian pine forest, situated at higher altitude (Delgado et al. 2001). The Brown rat, *Rattus norvegicus* (Berkenhout, 1769), is extremely rare in laurel forests, as it mainly inhabits towns. As far as is known, no recent activity by avian nest predators (i.e. corvids), has been identified in laurel forests of Tenerife.

Study sites

The study was conducted in two laurel forest remnants in the north-east sector of Tenerife (Canarian archipelago), 12 km apart, namely Agua García-Paisaje Protegido de Las Lagunetas (hereafter Agua García; 28°27'N, 16°24'W) and Anaga (28°32'N, 16°17'W). Anaga is a mountainous massif with slopes up to 45%, whereas Agua García has only gentle slopes (<10%) at the study patches. Canopy height ranges from 5 to 20 m depending on slope, increasing from ridge to ravine beds through slopes. The canopy is formed mainly by Laurus azorica (Seub.) Franco, Myrica faya Aiton, Ilex canariensis Poir., Erica arborea L., E. platycodon (Webb and Berthel.) Rivas-Mart. et al., Prunus lusitanica L., and smaller proportions of other trees. The understorey is dominated by Viburnum rigidum Vent., Rubus spp., Daphne gnidium L., Hedera helix L., Asplenium onopteris L., and tree saplings. Since the remnants differ strongly in disturbance intensity, Agua García is treated as the disturbed and Anaga as the preserved area. Agua García has suffered sequential clearance of the original vegetation, planting of exotic species (mainly Pinus radiata D. Don and Eucalyptus globulus Labill.), followed by removal of these species and regrowth of native laurisilva under silvicultural regimes. Poles and branches (<5 cm diameter at breast height, dbh) of Erica, Ilex, Viburnum, and Laurus are harvested as vineyard supports. These intense cuttings favour stump sprouting with dense regrowth, leading to patch concealing. Main dividing elements of the remnant are a net of dirt roads (no paved roads are present), cleared areas, and regenerating stands. The maximum traffic is 90-130 cars per day in some areas.

Anaga includes tracks of the oldest and best preserved laurisilva on Tenerife. Thin pole harvesting is residual (mainly along road and footpath edges) and lighter than in Agua García, favouring greater forest integrity. The main dividing elements are paved and dirt roads. The maximum traffic is 620–2050 cars per day. Paved roads were selected instead of dirt roads because most of the available trails are limited by steep-slope forest, and this might preclude comparison between forest remnants that differ strongly in relief.

Methods

Nest predation in four replicate plots on each remnant was compared. The contrasting vegetation pattern was used to test for effects of road edge, nest position, and patch type on nest predation in Agua García and Anaga. The four Agua García plots represented a gradient from dense canopy, intermediate height, dense understorey (plot 1); dense tall canopy, sparse understorey, mature forest (plot 2); sparse and low canopy, sparse understorey, selective clearing (plot 3); and clearcut without canopy (plot 4). In the Anaga remnant, four unmanaged stands with \geq 50 years since the last human disturbance were studied.

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Artificial nest predation experiments were performed between March and May 2001, when most bird species and Ship rats reproduce in the Canarian laurel forest (Martín and Lorenzo 2001). On each plot and parallel to the road, two 100 m transects (one 1-5 m from the road edge and the other 50 m to the forest interior) were constructed. Transects were selected to avoid crossing with other contrasting vegetation types (i.e. plantations) or other road or clearcut edges. The selected road segments had some variation in width (Table I). Twenty nests were placed along each transect, 10 directly on the ground under bushes or trees, and 10 on the nearby vegetation at variable heights above ground (range 0.5-4.5 m; Anaga: 1.56 ± 0.37 (mean \pm SD); Agua García: 2.04 ± 0.85 ; N=80 nests per forest remnant). Artificial nests were arranged 10-15m apart on each transect to minimize spatial dependence on nest encounters in the study areas. Overall, 40 nests were used at every plot at both Anaga and Agua García (160 nests per forest remnant). Artificial nests were placed on 2 March in Agua García and on 30 April in Anaga, and were checked after 1, 3, 5, 10, and 20 nights of exposure to predators. Hardware mesh baskets were filled with litter and baited with three quail eggs, the average clutch size of bird species at the study sites (Martín and Lorenzo 2001). A nearby tree was marked with a plastic tape to facilitate nest detection in dense thickets. Broken egg shells, tooth marks, and droppings at or nearby the nests were noted every inspection day. In all cases they were caused by rats.

Statistical analysis

Nest survival between the forests, in the individual plots, and between road distances and nest positions were compared using survival analysis (Muenchow 1986). Nest survival rates were compared using Breslow chi-square tests in the Kaplan-Meier procedure (Fox 1993). When necessary, covariable effects were fixed for comparisons among different situations. This method calculates failure-time curves comparing the survivorship at each time step. The experiments lasted for 20 days. Nests surviving beyond this point entered the analysis as right-censored data (those for which real survival time is unknown) (Fox 1993). The nests were considered predated by rats (a predation event) when at least one egg had been removed or eaten *in situ*.

Results

Differences in nest predation among plots

Overall nest predation rates were significantly higher in Anaga (the preserved forest) than in Agua García (the disturbed forest) (Breslow χ^2_1 =136.18, *P*<0.001) (Table II). At the end

Remnant	Plot	Road type	Elevation (m)	Aspect	Corridor width (m)
Agua García	1	Dust trail	1010	NW	4.5
0	2	Dust trail	830	NNE	4
	3	Dust trail	1015	Ν	4
	4	Dust trail	1080	NW	3.5-9.5
Anaga	1	Asphalt road	910	SW	9.3
C	2	Dust trail	910	Ν	4.3
	3	Asphalt road	960	NE	6.4
	4	Dust trail	920	ESE	7

Table I. Description of the plots used in artificial nest predation by Ship rats in two laurel forests in Tenerife.

of the experiment, overall nest survival varied between 60 and 98% in Agua García and between 5 and 25% in Anaga. Survival was significantly different among the four plots in Agua García (Breslow $\chi^2_3=23.41$, P<0.001). In this forest, plot 3 (sparse and low canopy, sparse understorey) was highly disturbed by wood harvesting and experienced only one predation event (Table II). Survival was significantly lower on plot 1 (dense intermediate canopy, dense understorey), followed by plots 2 (dense tall canopy, sparse understorey, mature forest) and 4 (clearcut scrub). In Anaga, survival was significantly different among all plots (Breslow $\chi^2_3=32.71$, P<0.001). Plot 1 showed a significantly higher nest survival rate than plots 2, 3, and 4, but there were no significant differences between these three plots (Breslow $\chi^2_2=1.94$, P=0.379).

Nest predation and road edge effect

Overall, median survival times were higher for artificial nests along the road edge in both Agua García and Anaga forests. In Agua García, the number of predation events (final number of nests predated) was 13 along road edges and 21 in the forest interior. In Anaga there were 62 predation events along the road edge and 71 in the forest interior (Table III). Survival rates were significantly higher along the road edge than at the interior at plots 1, 2, and 4 in Agua García, but only at plot 3 in Anaga (Table III).

Predation on ground and tree nests

Survival probability was less for ground than for tree nests regardless of distance to road in both forests. Ground nests were predated at higher rates than nests placed on adjacent trees in both forests grouped (Breslow $\chi^2_1=34.73$, P<0.001) and apart (Agua García: Breslow $\chi^2_1=10.62$, P<0.01; Anaga: Breslow $\chi^2_1=48.46$, P<0.001). With proximity to road edge as a fixed effect, survival analysis revealed higher nest predation rates for ground nests than for tree nests (Table IV). All ground nests in Anaga were predated (0% censored data) at both edge and interior habitat (i.e. 40 predation events each). Tree nests in Anaga were more rapidly predated at interior (31 predation events, median survival time (MST)=11.27 days) than along the road edge (22 predation events, MST=17.65 days) (Table IV). For tree nests in Agua García, only three and six predation events (MST=24.63 and 22.38 days) took place at edge and interior habitat, respectively. For ground nests, 10 and 15 events (MST=22.1 and 19.27 days) were detected at edge and interior habitat, respectively, in Agua García.

	Agua García			Anaga			
Plot	No. of nests predated	No. of censored nests	MST±SE	No. of nests predated	No. of censored nests	MST±SE	
1	16	24	18.22 ± 1.46	31	9	17.68 ± 1.08	
2	5	35	23.65 ± 0.71	33	7	7.78 ± 1.37	
3	1	39	24.88 ± 0.12	31	9	9.35 ± 1.50	
4	12	28	22.63 ± 0.73	38	2	5.45 ± 0.89	
Overall	34	126	22.34 ± 0.49	133	27	10.06 ± 0.72	

Table II. Survivorship of artificial nests in the Agua García (disturbed) and Anaga (preserved) forests.

Numbers of predation events and censored nests (those that were not predated during the study, real survival time unknown) are shown. MST, mean survival time (days until predation).

	Road edge			Forest interior			
Plot	No. of nests predated	No. of censored nests	MST±SE	No. of nests predated	No. of censored nests	MST±SE	Breslow
Agua García							
1	5	15	21.9 ± 1.41	11	9	14.55 ± 2.29	5.36*
2	5	15	22.3 ± 1.35	0	20	_	5.55*
3	1	19	24.75 ± 0.24	0	20	_	1.00 ns
4	2	18	24.5 ± 0.34	10	10	20.75 ± 1.29	7.83**
Anaga							
1	15	5	18.8 ± 1.51	16	4	16.55 ± 1.52	1.14 ns
2	16	4	9.4 ± 1.99	17	3	6.15 ± 1.82	2.95 ns
3	13	7	13.3 ± 2.22	18	2	5.4 ± 1.57	7.73**
4	18	2	6.75 ± 1.54	20	0	4.15 ± 0.81	1.79 ns

Table III. Survivorship of artificial nests along road edges and forest interior in the Agua García (disturbed) and Anaga (preserved) forests.

Numbers of predation events and censored nests (those that were not predated during the study, real survival time unknown) are shown. MST, mean survival time (days until predation). N=20 nests at each situation (edge and interior) per plot. At the interior of plots 2 and 3 in Agua García all nests survived for 20 days. Significance levels for Breslow χ^2 (all tests with 1 df), *P<0.05; **P<0.01; ns, not significant.

Discussion

Artificial nest predation by Ship rats was greater at laurel forest interior than along road edges. This finding was consistent regardless of forest remnant, plot or foraging substrata (ground or trees). This result does not support the conventional hypothesis of higher nest predation along habitat edges (Paton 1994). Similarly, Lahti (2001) did not find conclusive evidence that higher nest predation rates take place near habitat edges. In fact, many studies have revealed that nest predation actually decreases near some borders, including forest trails (Miller and Hobbs 2000). Moreover, nest predation is frequently higher at forest interior than along edges in forest-dominated landscapes (Hanski et al. 1996; Heske et al. 1999; Dijak and Thompson 2000).

Table IV. Survivorship of ground and tree nests in the Agua García (disturbed) and Anaga (preserved) forests.

	Ground						
	No. of nests predated	No. of censored nests	MST±SE	No. of nests predated	No. of censored nests	MST±SE	Breslow
Agua García							
Edge	10	30	22.1 ± 0.98	3	37	24.63 ± 0.21	4.91*
Interior	15	25	19.27 ± 1.38	6	34	22.38 ± 0.72	6.04*
Overall	25	55	20.69 ± 0.86	9	71	24 ± 0.38	10.62**
Anaga							
Edge	40	0	6.48 ± 1.12	22	18	17.65 ± 1.28	36.40***
Interior	40	0	4.85 ± 0.94	31	9	11.27 ± 1.42	17.77***
Overall	80	0	5.66 ± 0.73	53	27	14.46 ± 1.02	48.46***

Numbers of predation events and censored nests (those that were not predated during the study, real survival time unknown) are shown. MST, mean survival time (days until predation). N=10 nests at each position (ground and tree) per plot and road distance. Significance levels for Breslow χ^2 (all tests with 1 df): *P<0.05; **P<0.01; ***P<0.001.

Nest predation effects can penetrate variable distances from road edges, as reported in mainland forests (e.g. 300–600 m, Wilcove et al. 1986; 30–500 m, Burkey 1993; 188.6–282.5 m, Keyser et al. 1998; 0–200 m, Lindenmayer et al. 1999). The highest nest predation rates are frequently found within the first 50 m of forest from a given edge (Paton 1994). Thus, the edge-interior trend presented here may illustrate only a partial trend that would not hold if transects penetrate further into the forest matrix (i.e. 100 m, Delgado et al. 2001). Ship rats extend their foraging areas considerably far from roads (Amarasekare 1993; Hernández et al. 1999). In addition, rats foraging at interior habitats would experience lower predation pressure by aerial raptors, such as *Tyto alba* (Scopoli, 1769) and *Asio otus* (Linnaeus, 1758), present at the study areas, than rats foraging along road edges.

Other nest predator species may be, however, differentially abundant along edges (Paton 1994), and higher predation rates may occur in relatively deforested landscapes compared to continuous forest (Hartley and Hunter 1998). Andrén (1995) found that nest predation along edges was higher in forests surrounded by farmland than within forest habitats. The results of this study differ from these findings in that the most forested landscape (Anaga) showed the highest rate of artificial nest predation by Ship rats.

Vegetation structure was more homogeneous in the preserved remnant than in the disturbed remnant. Years from the last major disturbance, such as cutting or thinning were also similar among the Anaga patches, but differ in the Agua García sample. Some authors have found a correlation between plot age and dummy nest predation rates. For instance, Yahner and Wright (1985) showed higher predation rates in mature plots (>55 yr) than in younger ones (≤ 4 yr). Similarly, we found that the older remnant (Anaga) suffered a heavier predation pressure by rats than the younger remnant (Agua García). Rats depleted more artificial nests on the ground than on trees in both forests, but arboreal nest predation was higher in Anaga (preserved forest) than in Agua García (disturbed forest). Canopy disturbance in Agua García may limit the use of the trees as substrata for nest-searching rats, as it may also limit real bird nesting.

Ship rat territory sizes have not been measured in the laurel forest, but in other areas home-ranges averaged 150–174 m in diameter, and territories overlapped greatly (Dowding and Murphy 1994; Hooker and Innes 1995). Spatial patterns of home ranges, along with high population densities, may influence nest predation on small spatial scales (Fenske-Crawford and Niemi 1997).

Roads probably play an important role in facilitating invasion by rats (May and Norton 1996; Downes et al. 1997; Delgado et al. 2001). Ship rats respond to road vicinity, topography, vegetation structure, food abundance, and native competitors and predators (Amarasekare 1993; Downes et al. 1997; Hernández et al. 1999; Delgado et al. 2001). The habitat surrounding roads can be more important than the mere road proximity for nest predation patterns (Bergin et al. 2000). Fragmentation intensity, disturbance level, and amount of edge area (and thus mean edge proximity) were relatively greater in the laurel forest of Agua García, where the edge effect in nest predation was also more intense. On the other hand, overall nest predation was greater, but intensity of edge effect was lower in the less-fragmented forest (Anaga). This strongly suggests that the degree of disturbance may affect habitat use of rats at forest-road ecotones (Fenske-Crawford and Niemi 1997). As in other islands where this predator dominates (e.g. Mauna Kea, Hawaii, Amarasekare 1993; French Polynesia, Thibault et al. 2002; New Zealand, Clout et al. 1995), Ship rats may largely determine the overall nest predation risk in the studied laurel forests. This study suggests that nest predation risk may be partly determined by the response of rats to different levels of habitat disturbance along road edges and forest interior.

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