The effects of forest edge and nest height on nest predation in two differing New Zealand forest habitats

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Abstract

Research in many parts of the world suggests avian nest predation may be higher at forest edges. This could have conservation implications for avian communities and may explain why some species are absent or rare in fragments. In the first study of its kind in New Zealand, we tested the generality of edge effects on nest predation in two forest habitat types. First, predation levels were measured in a mountain beech forest using experimentally-placed nests containing wax eggs, which allowed identification of predators by bite-marks. Second, predation levels were measured on natural nests in a kanuka/broadleaf forest fragment. As many of New Zealand's extinct or threatened birds are ground-nesters, we also compared predation rates on experimentally-placed ground versus arboreal nests. Although predation rates varied significantly with distance from edge in both habitat types, edge effects on nest predation were not detected. Instead, predation was patchy and idiosyncratic, with highest predation rates recorded at intermediate distances from the edge. Possums were the major predator of the experimental nests. Ground nests experienced significantly higher predation rates than arboreal nests. The predation pattern recorded in this study suggests that pest control in fragmented landscapes should extend greater distances into the forest interior to control introduced mammals beyond the edge zone. This study also supports the theory that ground nesting may have been a life history trait that increased the vulnerability of native species to predation by introduced mammals.

Introduction

Fragmentation is the breaking up of continuous habitat into smaller and more isolated patches. Fragmentation results in the formation of new habitats and increases the amount of forest edge in the landscape, with smaller fragments having

proportionally greater amounts of edge (Ewers & Didham, in press). The forest edge can differ from the forest interior in terms of abiotic and biotic factors, which can lead to differences in species distributions, abundance and behaviour between the forest edge and interior (Murcia 1995). For example, edges can affect nest predation rates, which can differ between the forest edge and interior (Hartley & Hunter 1998, Söderström 1999, Lahti 2001, Chalfoun *et al.* 2002).

Many studies have recorded higher levels of nest predation at the forest edge than the interior (Gates & Gysel 1978, Brand & George 2000, Flaspohler *et al.* 2001, Piper & Catterall 2004). Nest predation rates may be higher at the forest edge due to such factors as nest density being greater at the edge (Gates & Gysel 1978), or a high rate of incursion of generalist predators from the surrounding matrix habitat (Chalfoun *et al.* 2002). Predators may be more active at forest edges, or use edges as travelling lines, resulting in opportunistic predation (Chalfoun *et al.* 2002). For example, brushtail possums (*Trichosurus vulpecula*) in New Zealand move to the forest edge to feed on vegetation (A. Byrom pers. comm.). However, other studies have shown no edge effect on nest predation (Ratti & Reese 1988, Flaspohler *et al.* 2001, Purger *et al.* 2004). A review by Lahti (2001) concluded that the edge effect on nest predation hypothesis has been rejected more often than it has been supported. The variation in results of edge effect studies are considered to stem from differences among studies in factors such as landscape structure, predator and prey species composition, temporal and spatial variation, and experimental design (Hartley & Hunter 1998, Lahti 2001, Chalfoun *et al.* 2002).

If nest predation is greater at forest edges, this may explain why many songbird species are absent or low in abundance in small fragments (Zanette 2000). Predation has been identified as an important factor limiting the nesting success of many species of birds (Martin 1995), contributing to population declines in some species (Winter *et al.* 2000). For example, in New Zealand one of the main reasons for the decline of the kakapo (*Strigops habroptilus*) is considered to be predation by introduced mammals (Elliot *et al.* 2001). Across the New Zealand avifauna as a whole, predation has been strongly implicated in population declines and extinctions of a large number of species (Holdaway 2001, Duncan & Blackburn 2004).

Research on edge effects on nest predation has rarely been conducted in habitats south of 40° N (Lahti 2001) and never in New Zealand. Forest cover in New Zealand has decreased substantially over the course of human settlement. Clearance has progressively reduced forest cover from 78 to 23 percent (Clout & Saunders 1995), and now small fragments dominate in an otherwise largely pastoral landscape (Craig *et al.* 2000). For many avian species in New Zealand, population persistence at a regional scale is becoming increasingly dependent on populations within isolated remnants. Consequently, the factors which limit individual growth, reproductive fitness and mortality in fragments are critically important for conservation management in heavily fragmented landscapes. Therefore, it is important to determine whether patch-level processes, such as edge effects on nest predation, may play a synergistic role in the decline of many New Zealand bird species. Already, pest control is commonly focussed on forest edges in the most

heavily fragmented landscapes in New Zealand, primarily to control the movement of the vectors (possums and stoats, *Mustela erminea*) of bovine tuberculosis (*Mycobacterium bovis*; Tb) into pasture, where they can infect livestock. Therefore, the results from this study may highlight areas where pest control should be targeted, or confirm the usefulness of current techniques.

The main objective of this study was to test whether edge effects on nest predation occur in New Zealand forests and to test the generality of these trends in two differing forest habitat types. It was hypothesised that nest predation would be greater at the forest edge in both habitats and would decrease with increasing distance into the forest interior. The first study site was located in a continuous area of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest where predation rates on experimentally placed, natural nests, containing microcrystalline wax eggs were measured. These experimental nests were placed at set distances from the forest edge into the forest interior and were used as a surrogate measure of predation trends in relation to distance from the forest edge. The second study site was located in a lowland riparian forest fragment where predation rates were measured by monitoring naturally occurring bird nests. Predation rates at these nests were then analysed in relation to distance from the nearest forest edge.

Many studies of edge effects have failed to adequately describe predator species composition, which may affect the detection and interpretation of edge effects (Söderström 1999, Lahti 2001). Some studies have shown that certain predator species have an affinity to edges, such as corvids, which may explain the occurrence of edge effects in some habitats (Yahner & Scott 1988, Lahti 2001). Therefore, in this study the identity of each predator was also ascertained, through bite marks left on the microcrystalline wax eggs in the experimental nest study.

In pre-human New Zealand, predators of nests were typically other birds, until the introduction of mammalian predators (Holdaway 1999). Consequently, New Zealand birds evolved in the absence of mammalian predators, which may have left them maladapted to defend themselves against introduced mammals (Holdaway 1999). Species that have evolved in the absence of mammals tend to have a relatively limited range of defensive responses to mammalian predators and nest in easily accessible sites (Newton 1998). Many of New Zealand's extinct (e.g., bush wren, *Xenicus longipes*) or threatened birds (e.g., kakapo) are ground nesters and as such this life history trait may have increased their vulnerability to introduced mammals. Consequently, a second objective of the study was to test the predation rate of arboreal versus ground nests, using the experimental nests. This is the first study in New Zealand to address this question and it was hypothesised that predation rate would be greater on ground nests compared to arboreal nests.

Methods

Study sites

The first study site was located in a monodominant mountain beech forest near Cass, in Arthur's Pass National Park, South Island, New Zealand (42° 59' S, 171° 46' E) (Figure 1). The site consisted of a 500 x 244 m area at the edge of continuous forest, bordered on the south
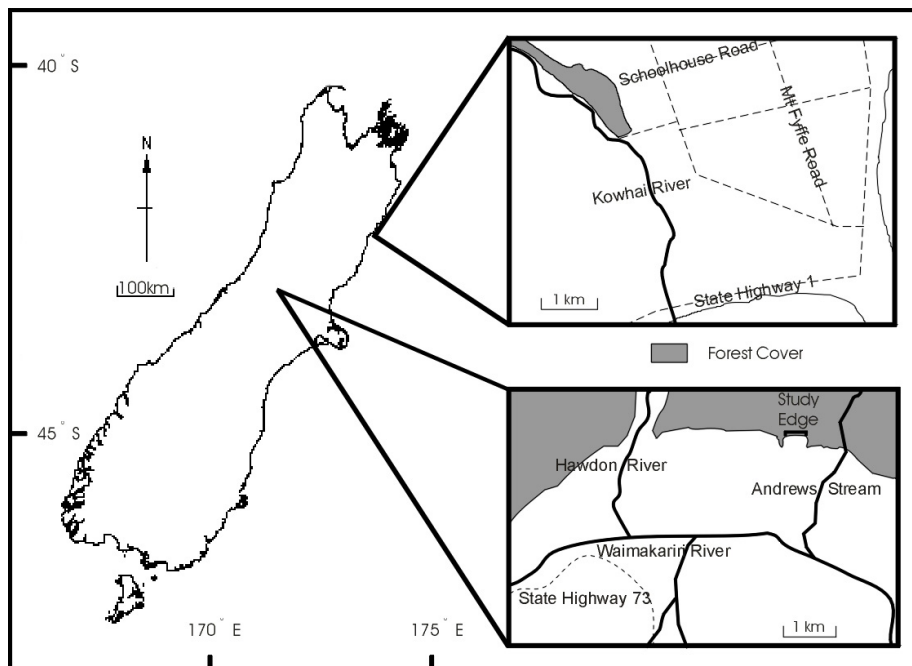
Figure 1. Map of the South Island of New Zealand showing the location of the two study sites at Cass and Kowhai Bush.

side by managed tussock grassland and pasture. No predator control had been carried out in the area in recent years.

The second study site was located at Kowhai Bush, a 240 ha remnant of lowland forest bordered by pasture in Kaikoura, South Island, New Zealand (42° 23' S, 173° 37' E) (Figure 1). The dominant tree species at Kowhai Bush was kanuka (*Kunzea ericoides*), although some areas were dominated by broad-leaved trees (*Melicytus ramiflorus*, *Myrsine australis*, *Pittosporum eugenioides*, *Carpodetus serratus* and *Hedycarya arborea*). Poisoning for possums was carried out by the Animal Health Board for five years prior to the study using feratox cyanide capsules, with the most recent application during May and August 2001 directly at the forest edge. Trapping for ferrets also occurred at the same locations from January – April 2001.

Materials and Methods

Mountain beech site

For experimental estimation of nest predation rates in the beech forest, natural song thrush (*Turdus philomelos*) and blackbird (*Turdus merula*) nests, which are very similar in appearance, were collected from Kowhai Bush, Kaikoura after the November – December 2001 breeding season. Two microcrystalline wax eggs were placed in each nest. Microcrystalline wax is reasonably malleable at room temperature and therefore allows identification of predator species from bite marks left on the eggs (Thomas *et al.* 1999). Moreover, microcrystalline wax is of low palatability, so bite marks can be retrieved without the predator consuming the evidence (Thomas *et al.* 1999). Eggs were made using commercially available chocolate moulds and were approximately

4 cm long by 3.2 cm wide by 2 cm high, and off-white in colour. The purpose was not to mimic the size of song thrush or blackbird eggs specifically, but rather to obtain a standard experimental egg equivalent in size to that of a small to medium-sized bird. After the eggs were made, they were left outside for a few days to allow human scent and the scent from the wax itself to dissipate. Reference bite marks were identified using skulls and live animals, and were compared to bite marks of known predator species in other studies (M. Thomas pers. comm.). In addition, eggs were placed in tracking tunnels so bite marks could be matched to predators that were identified by ink footprints (Ratz 1997). Using artificial nests to measure predation on natural nests may have potential biases (Zanette 2002). These potential effects were minimised in this study by using transplanted natural nests and preventing human scent on the nests and eggs. Furthermore, the measurement of relative predation patterns with respect to distance from the forest edge was the aim of the study and not actual predation rates.

To examine relative predation levels at varying distances from the forest edge, nests were placed at eight distances on a $\log_{2.5}$ scale, which allowed the analysis of distances close to the edge as well as those at greater distances into the forest interior (0, 2.5, 6.3, 15.6, 39.1, 97.7, 244.1 and 1525.9 m). This range of distances encompassed, if not exceeded, the range of distances over which edge effects on nest predation have been studied internationally. The interior distance (1525.9 m) was located in an adjacent area to the main study site, approximately 1 km to the east, where a public track allowed easy access to relatively

undisturbed continuous forest. The forest was continuous and undisturbed between these two locations. The 'edge' was defined as the point of edge creation (where the tree trunks occur), rather than the point of edge maintenance (the limit of the undergrowth) (Ranney *et al.* 1981).

The main site consisted of a section of continuous forest, with a forest edge of 500 m in length. Coordinates for each nest were established by allocating one of the seven distances and then generating a random number between 0 and 500 (the horizontal coordinate parallel to the edge). This spatial separation of replicates within 500 m parallel to the edge should go some way towards minimizing the potential for overlapping home range sizes of individual animals at sampling distances located close to the edge itself. To increase the accuracy of locating nest coordinates, five measuring lines were established at 100 m intervals along the edge of continuous forest. These measuring lines extended perpendicular from the edge into the interior, to the maximum distance of 244.1 m. Measuring lines should not be confused with transect lines, as nests were not placed directly along these lines. At the additional site where the eighth distance was located, a 500 m measuring line was established parallel to the forest edge, which was equivalent to the length of forest edge sampled at the main study site, and nests were placed along this line at random locations.

To test predation rates in relation to nest height, predation of arboreal versus ground nests were measured at each coordinate. Nests were not placed on the ground and arboreally at the same time, so as to avoid nest interference. Instead, only one nest was placed at a particular location at one time, and the order in which the first nest were placed either on the ground or arboreally was decided at

random. Arboreal nests were placed in trees that could hold the weight of the largest predator and were accessible via branches. These trees were within 2 m of the nest coordinate. Ground nests were placed directly below the location of the arboreal nest. No attempt was made to conceal nests in either instance.

Nest predation was measured at each distance from the forest edge using 18 arboreal nests and 18 ground nests, resulting in 36 replicate nests at each distance. Each nest location was marked using flagging tape, which was placed in the surrounding area. Throughout the experiment, rubber gloves and boots were used to prevent human scent interfering with the results (Brand & George 2000). Field work was conducted during February 2002 and each nest was left for four nights. Predation was defined as the alteration (such as bite marks or scratches) or removal of at least one egg.

Once a nest was placed, six environmental parameters were recorded to allow for potentially confounding site variables. These parameters were nest type (blackbird or song thrush), height of arboreal nests, age of trees in the surrounding area (mature or juvenile), age of the tree in which the nest was placed (mature or juvenile), and average air temperature and rainfall of the area during nest exposure.

To investigate habitat use by birds and the relationship between bird density and nest predation intensity, bird abundance was also measured in relation to distance from the forest edge. The local abundance of birds may vary as a result of variation in predation intensity, or it may be that greater bird abundance provides an increased food source for predators, resulting in increased predator densities. Consequently, bird abundance is an important variable to measure to further understand predator-prey dynamics. Bird counts were carried out along each measuring line during August 2002, between 0730 – 1015 h. Recording bird calls at the same distances as the nest experiment would have resulted in considerable overlap in calling individuals recorded near the forest edge. Therefore, bird counts were only conducted at 0, 39.1, 97.7, 244.1 and 1525.9 m. At each of these distances, all individuals seen or heard were recorded for five minutes (Freeman 1999). Each measuring line was sampled twice, resulting in each of the five distances being sampled 10 times. The order in which each measuring line was sampled and the starting point of each (edge or interior) was randomized to prevent any potential biases of start time. After arriving at the site, counting did not begin for five minutes to allow startled birds to return and inquisitive birds to lose interest (Earl 2000).

Lowland kanuka/broadleaf forest fragment (Kaikoura)

Seventy-five nests of introduced and native birds were monitored in the lowland Kaikoura forest fragment from November – December 2001. Flagging tape was used to mark the nest location, but was placed in the near vicinity and not next to the nests, so as not to attract predators. To prevent observer effects on nest predation, all nest checks were brief (Flaspohler *et al.* 2001) and rubber boots were worn at all times (Brand & George 2000). Nests were revisited approximately every four days to monitor their status. Nests were recorded as successful when at least one chick fledged and fledging was determined by the observation of fledglings near the nest within two days of the last visit (Flaspohler *et al.* 2001).

Nests were recorded as preyed on if egg or chick remains were found, or if nest contents disappeared before chicks were expected to fledge. If nestlings fledged or a nest was preyed on between monitoring visits, the outcome was recorded as the day half way between visits (Mayfield 1975). All nests were then analysed with respect to their distance from the nearest forest edge. Nests were grouped into four distance categories (0 – 6.3 m, 6.4 – 39.1 m, 39.2 – 97.7 m and 97.8 – 244.4 m), which were similar to the mountain beech study, and allowed statistical analyses of the data. Nest predation rates were calculated for song thrush separately (the species with the largest sample size) and for all species combined.

Statistical analyses

The Mayfield (1975) method was used to calculate daily predation rates at both sites, where the number of nests preyed on is divided by the total number of 'exposure days' of all nests. However, the Mayfield (1975) method does not account for partial losses, meaning that nests that fledge one young are equivalent to those that fledge more than one young. Therefore, if partial nest losses were common, this method may be inappropriate for calculating nest success (Donovan *et al.* 1995). Subsequently, partial losses in the lowland forest fragment were not included in analyses. Predation levels in the mountain beech study with respect to distance from the forest edge, and in conjunction with nest height (ground versus arboreal) and other measured environmental parameters, were analysed using logistic regressions and logistic ANCOVAs (Generalized Linear Models) using R (Ihaka & Gentleman 1996). The correlation between bird abundance and predation at this site was tested using MINITAB (both variables were square root transformed prior to analysis to normalise residuals). Predation levels at the lowland forest fragment site were analysed using a logistic ANOVA (Generalized Linear Model) in the statistical package R (Ihaka & Gentleman 1996). A significance level of $P < 0.05$ was used in all tests.

Results

Mountain beech forest

At Cass there was a significant relationship between predation rate and distance from the forest edge (χ^2_{286} = 206.39, $P < 0.001$). A significant relationship between predation rate and nest height was also recorded (χ^2_{285} = 197.45, $P < 0.001$), with predation rates significantly greater for ground nests ($\bar{x} = 0.50$) than arboreal nests ($\bar{x} = 0.12$) (Table 1 & 2). When analysed separately, the relationship between predation rate and distance from the forest edge was significant for ground nests (χ^2_{142} = 79.63, $P < 0.001$), but not for arboreal nests (χ^2_{143} = 143.65, $P = 0.531$). There was a marginally significant interaction effect between distance and nest height (χ^2_{284} = 245.97, $P = 0.05$), and this is likely due to the higher predation rates recorded in ground nests, which ultimately resulted in the significant relationship between overall predation rates in relation to distance from the forest edge. The highest predation rate was recorded at 244.1 m, but there was no simple linear relationship between predation rate and distance from the forest edge, with peaks and depressions exhibited across the eight distances (Figure 2). None of the measured environmental variables had a significant effect on predation rates (all $P > 0.05$).

Nests were preyed on by mice (*Mus musculus*), hedgehogs (*Erinaceus europaeus*), rats (*Rattus* spp.) and possums. The brushtail possum was the only species for which predation rates could be statistically analysed. Predation by possums varied significantly with distance from the forest edge for ground nests (χ^2_{142} = 88.64, P < 0.001), but not for arboreal nests (χ^2_{142} = 129.74, P = 0.239). Again, there was no simple linear relationship with increasing distance from the forest edge for arboreal or ground nests (Tables 1 & 2; Figure 2).

The abundances of all bird species (which were all passerines) were combined to give a single measure of bird abundance. Mean bird abundance was greatest at the forest edge and decreased into the interior (Figure 3). There was no correlation between predation rates and bird abundance (r = 0.269, P = 0.662).

Table 1. Percentage of ground nests attacked by predators, their Daily Predation Rates (DPR) and the number preyed on by each predator species in relation to distance from the forest edge, Cass, Arthur's Pass, New Zealand. 'Unknown' nest predator refers to situations when the eggs were removed from the nest and could not be relocated. Eighteen nests were sampled at each distance.

| Distance (m)	% Nests Attacked	DPR	Mouse	Hedgehog	Rat	Possum	Unknown	Total
0.0	83.3	0.21	1	1	3	10	0	15
2.5	44.4	0.11	0	1	0	6	1	8
6.3	55.5	0.14	0	0	0	10	0	10
15.6	61.1	0.15	0	0	0	10	1	11
39.1	38.9	0.10	0	0	0	7	0	7
97.7	22.2	0.06	0	0	0	4	0	4
244.1	94.4	0.24	0	0	0	17	0	17
1525.8	0.0	0.00	0	0	0	0	0	0
Total	50.0	0.13	1	2	3	64	2	72

Table 2. Percentage of arboreal nests attacked by predators, their Daily Predation Rates (DPR) and the number preyed on by each predator species in relation to distance from the forest edge, Cass, Arthur's Pass, New Zealand. 'Unknown' nest predator refers to situations when the eggs were removed from the nest and could not be relocated. Eighteen nests were sampled at each distance.

| Distance (m)	% Nests Attacked	DPR	Mouse	Hedgehog	Rat	Possum	Unknown	Total
0.0	16.7	0.04	0	0	0	3	0	3
2.5	0.0	0.00	0	0	0	0	0	0
6.3	0.0	0.00	0	0	0	0	0	0
15.6	27.8	0.07	1	0	0	3	1	5
39.1	11.1	0.03	0	0	1	1	0	2
97.7	0.0	0.00	0	0	0	0	0	0
244.1	33.3	0.08	0	0	1	4	1	6
1525.8	5.6	0.01	1	0	0	0	0	1
Total	12.5	0.03	2	0	2	11	2	17
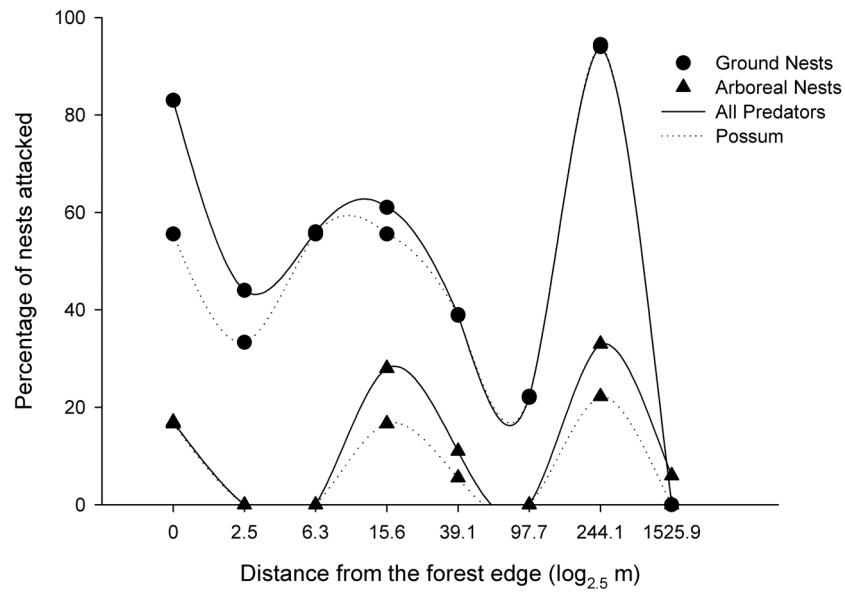
Figure 2. Percentage of ground and arboreal nests preyed on by all predators, and possums separately, with increasing distance from the forest edge into the forest interior, Cass, Arthur's Pass, New Zealand.
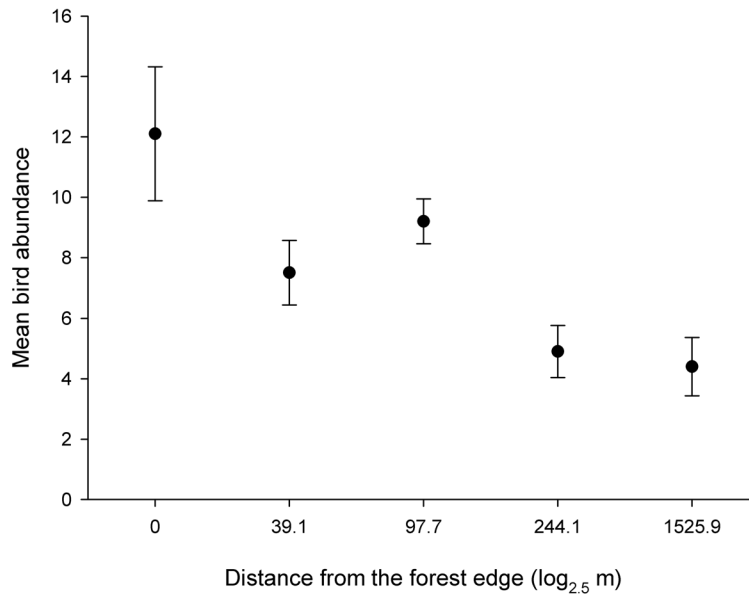
Figure 3. Mean bird abundance recorded during five minute bird counts at increasing distance from the forest edge, Cass, Arthur's Pass, New Zealand. The species recorded were bellbird (*Anthornis melanura*), blackbird, brown creeper (*Mohoua novaseelandiae*), chaffinch (*Fringilla coelebs*), dunnock (*Prunella modularis*), goldfinch (*Carduelis carduelis*), greenfinch (*Carduelis chloris*), grey warbler (*Gerygone igata*), New Zealand robin (*Petroica australis*), redpoll (*Carduelis flammea*), silvereye (*Zosterops lateralis*), song thrush and yellowhammer (*Emberiza citrinella*).
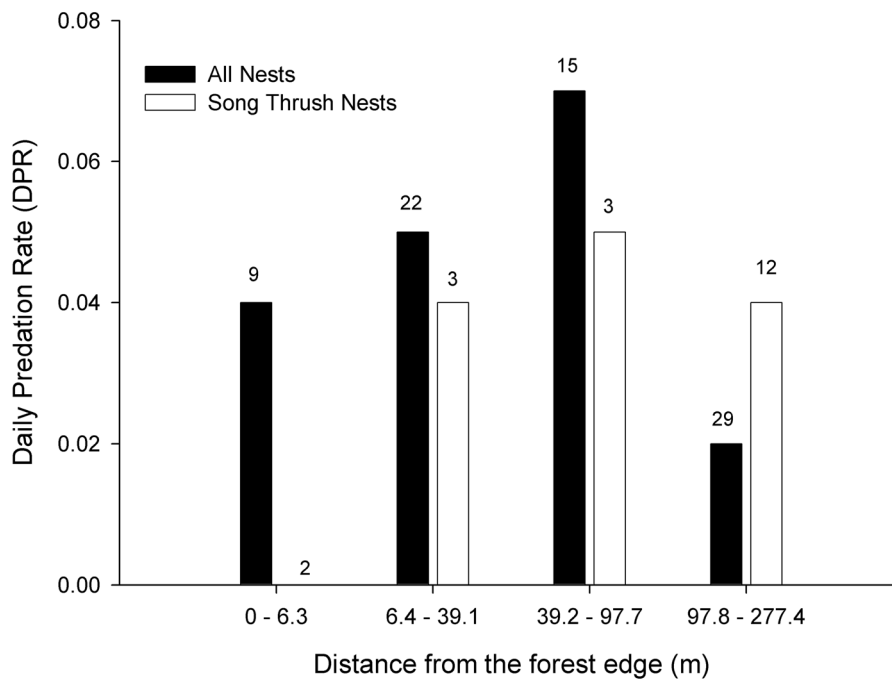
Figure 4. Daily predation rates of nests of all bird species combined and song thrush separately, with increasing distance from the forest edge into the interior, Kowhai Bush, Kaikoura, New Zealand. Numbers above the bars indicate nest sample sizes. Nests were recorded for bellbird, blackbird, brown creeper, chaffinch, dunnock, fantail (*Rhipidura fuliginosa*), goldfinch, grey warbler, New Zealand robin, rifleman (*Acanthisitta chloris*), redpoll, silvereye, song thrush and yellowhammer.

Lowland kanuka/broadleaf forest fragment

At Kaikoura, predation rates on pooled nests of all bird species varied significantly with distance from the forest edge (χ^2_{71} = 48.72, P = 0.02). The relationship between predation rate of nests and distance from the forest edge was not linear, with predation highest at the distance category of 39.2 - 97.7 m and lowest at 97.8 - 244.4 m (Figure 4).

Predation rates on song thrush nests analysed separately did not differ significantly with distance from the forest edge (χ^2_{13} = 9.93, P = 0.30), although predation rates were highest at intermediate distance categories and lowest at the forest edge (Figure 4).

Discussion

Edge effects on nest predation in two habitats

In the two habitats in this study, predation in relation to distance from the forest edge was patchy and idiosyncratic, with highest predation rates recorded at intermediate distances from the forest edge. Therefore, our hypothesis that nest predation rates would be greater at the edge and decrease into the forest interior was not supported.

Other studies on edge effects have also shown sequential peaks and depressions in the recorded variable at intermediate distances from the forest edge (Palik & Murphy 1990, Hester & Hobbs 1992), although none that we know of have been

recorded for nest predation specifically. Murcia (1995) suggested that edge effects are unlikely to be simplistic and monotonic. Instead, edge effects from multiple causal factors may interact with each other, potentially creating the peaks and depressions observed here. In this study, higher predation rates at intermediate distances from the forest edge are most likely due to species-specific variation in predator behaviour in response to habitat boundaries.

The main predator in the experimental nest study was the possum and the behaviour of this species may be the main driver of the predation pattern observed with increasing distance from the forest edge. Possums are not strictly territorial, as the home ranges of males and females overlap extensively (Cowan & Clout 2000). Thus, the peaks and depressions in predation are unlikely to be territory boundaries of individual possums, especially as the distances close to the forest edge were very small. Possums are commonly found at high densities at the forest edge (Efford 2000) and den at the edge of their foraging range (Viggers & Lindenmayer 2000), with maximum home range lengths of between 245 m (females) and 295 m (males) (cited in Cowan & Clout 2000). In addition, mammalian predators have been suggested to use forest edges as 'travel lanes' (Söderström 1999, Chalfoun *et al.* 2002), which may be the case with possums. In contrast, Byrom (2000) recorded possum density to be highest 200 metres into the forest interior during a study of different forest types in New Zealand, including beech forest. These results contradict the common belief in New Zealand that possum density is greatest at the forest edge (Byrom 2000). Predation of nests by possums is assumed to be

opportunistic. Localities where possums spend the majority of their time are predicted to have higher rates of nest predation. As a consequence, there is likely to be high spatial and temporal variation in nest predation rates within forests. In particular, predation by possums may be higher at the location of dens and at intermediate distances into the forest interior, perhaps explaining the peaks in predation observed in the present study. These locations may also have better resources in the form of larger or more abundant trees.

Interestingly, peaks and depressions in vegetation biomass have frequently been observed with increasing distance from forest edges, driven by 'competition-induced waves of biomass' (Reichman *et al.* 1993). This phenomenon occurs when some plants at the forest edge receive more resources (such as light) than others, allowing them to outcompete adjacent individuals toward the forest interior. These smaller plants have reduced growth or biomass and are subsequently outcompeted by adjacent individuals even further into the forest interior, resulting in standing wave-like patterns in the height or biomass of plants with distance from the forest edge (Reichman *et al.* 1993). Possums are predicted to be more abundant in these areas where vegetation is more plentiful or of a higher quality and this may result in higher predation rates through opportunistic predation. Future studies would benefit from measuring vegetation characteristics around the vicinity of each nest, predator densities and movement rates, in conjunction with predation rates. Although some studies have previously looked at possum movement and behaviour, radiotracking of possums in relation to distance to the forest edge to

determine where they spend the majority of their time would also be instructive, and particularly useful in conjunction with a study such as this, allowing links between possum foraging activity and nest predation rates to be deduced.

Pest control at the edge of the lowland forest fragment in Kaikoura occurred for five years prior to the study, with the most recent poisoning operation occurring three months before the study. Pest control may have influenced predation rates at this site, making it difficult to interpret trends in nest predation as a function of distance from the forest edge. It is presumed that pest control would also affect predator distribution in the second category distance (6.4 - 39.1 m), but to a lesser degree than at the forest edge. Therefore, pest control may explain why daily nest predation rates increased from the forest edge to the third distance category (39.2 - 97.7 m). It is possible that if pest control had not occurred predation rate would be higher at the edge, decreasing linearly into the forest interior. However, although pest control is often successful, some control operations do not manage to completely eliminate predators, with different predator species replacing target predators or controlled areas being reinvaded by the target species (Côté & Sutherland 1997). It would only be possible to deduce whether pest control is a contributing factor to the predation rates seen in this study if predation rates on birds, and the relative densities of predators before and after poisoning, were known.

There was no relationship between bird abundance and nest predation rates in the mountain beech forest site. Instead, bird abundance was highest at the forest edge and varied unpredictably with increasing distance from the forest edge.

In contrast, although predation rate also varied unpredictably with increasing distance from the forest edge, predation was highest at an intermediate distance from the edge. This may indicate that predation has no direct impact on spatial variation in bird abundance. Predation of adults, eggs and nestlings of birds by possums has been observed in the natural environment (Brown *et al.* 1993, McLennan *et al.* 1996, Innes *et al.* 2003). Possum predation has also been implicated in the decline of some native species (Nugent *et al.* 2000), such as the kaka (*Nestor meridionalis*; Powlesland *et al.* 2003). Nest predation, however, is not always a strong determinant of bird abundance, as some species may compensate for losses from nest predation by making compensatory changes in other mortality risk factors or by improving reproductive output (Newton 1998). In addition, birds may still prefer to forage at forest edges (as shown in this study), but may not nest at the edge because of a higher predation risk. A more effective method of correlating bird abundance to predation intensity would be to measure the abundance of nests, as well as the abundance of birds.

The most parsimonious explanation for the predation rates shown in the two habitats with increasing distance from the forest edge is simply that predation is patchy within beech forests and lowland forest fragments in New Zealand. There was no consistency in the distances at which peaks and depressions in predation rates occurred at the two sites. This patchy predation may be due to the behaviour and opportunistic feeding on nests by wide-ranging generalist predators, and not correlated with distance from the forest edge.

Predation intensity on arboreal versus ground nests

Predation was significantly higher for ground nests than arboreal nests in the experimental nest study, which supports some previous studies (Piper & Catterall 2004, Shochat *et al.* 2005), but contrasts with others, which found that predation was greater in arboreal nests (Yahner & Scott 1998, Brand & George 2000). In a review of predation rates on artificial nests in tropical and temperate forests, avian predators typically preyed on arboreal nests, most likely because they visually detect nests by scanning from perches and flying within a forest (Söderström 1999), whereas mammals typically preyed on ground nests, as they search for prey primarily via olfactory means (Söderström 1999). Thus, ground nests will have greater rates of predation in locations where mammals are the dominant predators (Ratti & Reese 1988). Whether this relationship holds, in a general sense, for New Zealand avian versus mammal predators is unknown. Both the major predators (possums) and minor predators (rats, mice and hedgehogs) at the Cass site were mammals, and no predators were avian. Avian predators, such as the Australasian harrier (*Circus approximans*), the long-tailed cuckoo (*Eudynamys taitensis*) and the kingfisher (*Halcyon sancta*), may prey on nests in New Zealand (McLean & Jenkins 1980).

There are many potential reasons for the decline of ground nesting birds in New Zealand, such as predation by introduced species, human hunting and deforestation, and these may act in a synergistic fashion (Didham *et al.* 2005). However, it is assumed that the greater extinction rate of native terrestrial ground nesting birds (up to 23 species) compared to arboreal nesters (up to 11 species) is primarily due to the introduction of mammalian predators (Holdaway 2001). This study is the first in New Zealand to find experimental evidence that predation intensity by introduced mammals is significantly higher on ground nests, thus accounting to some degree for the greater proportional decline of ground nesters compared to arboreal nesters.

Implications for bird conservation and pest control in New Zealand

Knowledge of predator behaviour and movement determines vulnerability of these species to control, allowing effective placement of traps and bait stations (Cowan & Clout 2000). In particular, measuring and monitoring variation in possum density is important to understand this species as a pest (Byrom 2000). The fact that predation at these two sites was shown to be high not only at the forest edge, but also at irregular intermediate distances into the forest interior, may mean that pest control should extend further into the forest to control introduced mammals. However, these patterns in nest predation may simply represent localised results, and not general trends within beech forests and lowland forest fragments in New Zealand. It is especially important to understand predator and prey dynamics in forest fragments, as fragments play an increasingly important role in preserving New Zealand biodiversity. Moreover, it is important to understand the direct and indirect effects that pest control focused on the forest edge has on the nest success of birds. The use of wax eggs to identify predators is a useful and effective method, providing that the bite 'prototypes' used as the reference source are of a good quality and represent a range of 'partial' bite

imprints and species.

Although there are many factors resulting in the lack of ground nesting birds in New Zealand, the higher rates of predation found for experimental ground nests in this study supports the suggestion that ground-nesting may have been one of the life history traits that increased the vulnerability of native species to predation (Holdaway 1999).

Acknowledgements

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