Nest predation risk on ground and shrub nests in forest margin areas of Sulawesi, Indonesia

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Abstract. Forest loss and fragmentation in Indonesia may seriously affect the survivorship of forest birds and lead to local extinction of bird populations. We used 786 artificial nests baited with quail eggs to examine the effect of habitat alteration on nest predation in Lore Lindu National Park, Sulawesi. Natural forest and four habitats of forest margin areas: forest edge, forest gardens, coffee plantations, and secondary forest, were studied. Two types of artificial nests, ground and shrub nests were placed in these habitats at two different locations for a period of 8 days. In addition, we used automatic cameras and cage-traps to identify the predators. Nests in shrubs experienced significantly higher predation rates in forest margin areas than in natural forest. Predation on ground nests did not differ significantly between these habitat types, but was significantly higher than that on shrub nests in each habitat except forest edge. Rodents were the most common predators of both nests, but shrub nests were also susceptible to Dwarf cuscus (*Strigocuscus celebensis*), squirrels, and tree snakes. The nest predation rates we found were among the highest found in tropical rainforests, probably a consequence of the unique predator assemblages of Sulawesi. These results suggest that egg survival is negatively affected by human intervention and that human-induced habitats might have only limited importance for the conservation of Sulawesi's largely endemic understorey avifauna. These considerations might be important since forest margins comprise significant proportions of protected areas on Sulawesi and play an important role in future Park zoning concepts as well as in conservation-oriented land use management.

Introduction

Deforestation for agricultural development and new settlements are currently threatening protected areas in North and Central Sulawesi (O'Brien and Kinnaird 1996; Bynum 1999; Waltert et al. 2004a). Conversion of forest for agriculture might generate forest margin areas and increase the amount of forest edges. These changes might affect native biota since generalised predators that are adapted to edge habitats can more easily penetrate the remaining forest (Whitcomb et al. 1981; Wilcove 1985) and may cause decline in bird populations (Yahner 1988). Several studies in temperate forests have shown that edge habitats experience a higher predation rate than forest interior

habitats (Gates and Gysel 1978; Wilcove 1985; Andrén and Angelstam 1988; Marini et al. 1995), whereas other studies have reported the opposite (Storch 1991), or no edge effect at all (Yahner and Wright 1985; Angelstam 1986; Keyser et al. 1998). The presence of increased nest predation due to edge creation was also documented in neotropical, Singapore and Javan forests (Loiselle and Hoppes 1983; Gibbs 1991; Burkey 1993; Cooper and Francis 1998; Sodhi et al. 2003). High predation rates may occur in forest margin areas due to more diverse predator assemblages and their numerical responses to habitat alteration.

Sulawesi is an island with exceptionally high vertebrate endemism (e.g. Whitten et al. 1988). Due its numerous endemic bird species (88 species and 11 endemic genera), this island is ranked among the most important Endemic Bird Areas of the world (Stattersfield et al. 1998). Also the predator assemblages of Sulawesi's forests are unique, characterised in particular by the absence of large mammal predators, and a high diversity of rodents, mainly from the genus *Rattus*, *Taeromys*, *Margaretamys*, and *Bunomys* which has its distribution centre in Central Sulawesi (Musser 1987; Nowak 1991; Amori and Gippoliti 2001).

Understorey birds are regarded being sensitive to forest alteration and habitat disturbance (Wong 1985; Waltert 2000; Waltert et al. 2005a) and ground-nesting birds are often the first to disappear after fragmentation of tropical forests (Thiollay 1992; Stouffer and Bierregaard 1995). Many forest understorey birds in Central Sulawesi can also be found in secondary forest (Coates et al. 1997; Waltert et al. 2004b; Sodhi et al. 2005; Waltert et al. 2005b), but so far no information exists on the influence of habitat alteration on their population survival in such habitats. Especially nest predation could seriously reduce egg and nestling survival which is a primary determinant of reproductive success in bird communities (Ricklefs 1969; Loiselle and Hoppes 1983; Martin 1988; Laurance et al. 1993). Little is known about reproductive success of tropical forest birds either in disturbed or undisturbed habitats.

We studied nest predation in natural forest and forest margin areas in Central Sulawesi. This paper aims to assess whether predation rates vary between habitat types (natural forest and forest margins) and nest placement (ground vs. shrub nests), to identify the potential nest predators, and to allow comparisons of predation rates from Sulawesi with other tropical regions. The results might have important conservation implications because forest margin habitats in buffer zones might constitute large areas of protected areas, and future conservation management might have to focus also on the existence of secondary habitats within the agricultural landscape matrix.

Methods

Lore Lindu National Park is located in Central Sulawesi, Indonesia (1°8′–1°3′ S; 119°90′–120°16′ E). The park covers 217,000 ha, which consists of 20%

montane forest, 70% hill and lower montane forest with most of the rest being lowland forest (±10%). It has been declared as a Man and the Biosphere Reserve (MAB) by UNESCO. The annual rainfall ranges from 2000 to 3000 mm in the north to 3000–4000 mm in the south. Significant areas of land within the Park are claimed as traditional homelands of local people resulting in several land use systems and marginal forests.

Study sites were located in Palolo valley (700–1100 m a.s.l.) and Napu valley (1100–1200 m a.s.l.) where natural forest as reference habitat still exists. Natural forest and four habitats of forest margin areas: forest edge, forest gardens, coffee plantations, and secondary forest, were selected in Palolo and three in Napu valley; forest edge, secondary forest and natural forest (Figure 1). Those habitats were also chosen by the STORMA (Stability of Rainforest Margin) project as forest margin habitats and natural forest, see http://www.storma.de.

Natural forest is an area where the original forest cover is still present. Vegetation composition comprises Euphorbiaceae, *Artocarpus* spp., Meliaceae, Gnetaceae, *Cananga odorata*, Ulmaceae, *Ficus* spp. and *Calamus* spp. (Gradstein et al. 2003). Secondary forest is defined as re-growth from disturbed natural forest where the break in continuity is still observable in the structure as well as in floristic composition of the vegetation (Corlett 1994; Wong et al. 1998). In our study sites, secondary growth forest was selectively logged in the past and is now frequently entered by local people gathering non-timber forest products. Forest garden is defined as a traditional land-use form of the forest margin containing
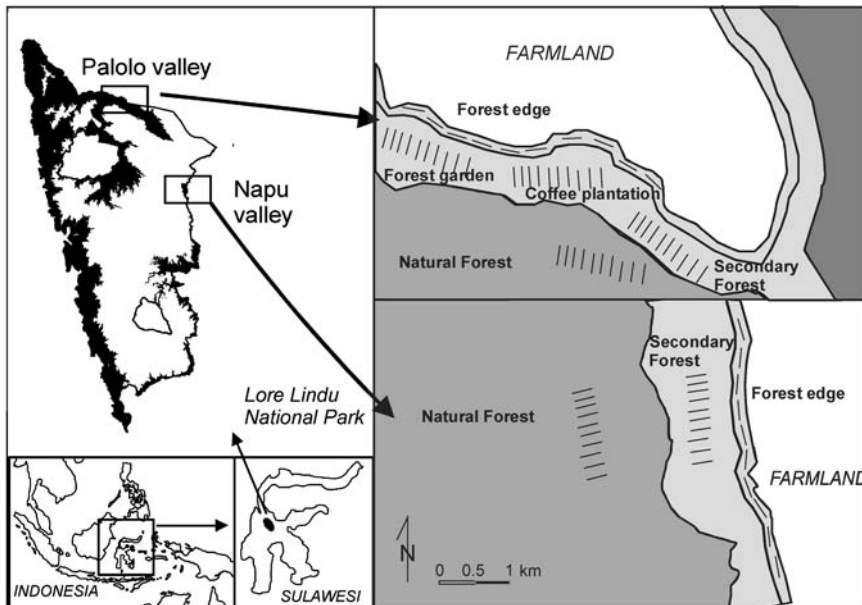

Figure 1. Study sites in Lore Lindu National Park, Central Sulawesi, Indonesia.

cultivated plant species, their wild relatives as well as forest vegetation. This is a typical system of many Indonesian forest margins (Weidelt 1996). Coffee plantation is a habitat type in forest margin areas where the coffee plants are interspersed by several forest shade trees. In this study, forest edge is a linear intersection between forest landscape and agricultural fields (maize and beans).

Experimental design of artificial nests

Ten parallel line transects, 100–200 m apart, were established in each habitat, except the forest edge at which the transects were located in one row approximately 10 m inside the forest from its edge (Figure 1). The forest edge was defined as the first line of tree trunks inside the forest. Each transect was approximately 120 m long and 30 m width, and contained five plots (0, 30, 60, 90, and 120 m). A plot consisted of one ground nest and one shrub nest, that were 15 m apart. The position of both nests are parallel across the width of the transect. To facilitate relocation, ground nests were usually placed near buttresses of trees or the base of larger saplings (as done by Wong et al. 1998) to simulate the nest sites of ground-nesting forest birds such as quails, rails, doves and pittas (Coates et al. 1997). Shrub nests were placed 1–2 m above the ground in shrubs or in the forked branches of plants to resemble nests of understorey shrub-nesting birds (e.g. Black-naped Monarch, *Hypothymis azurea* and Sulawesi Babbler, *Trichastoma celebense*) occurring in this region.

All nests were made of wire baskets, 10 ($\pm$2) cm (diameter)$\times$5 cm (in depth). They were lined on the inside and outside with dry vegetation such as grass, leaves and lichen found in the study area, so that their contents could not be seen from below and sides. A total of 786 (393 ground and 393 shrub) nests was placed along the transects in Palolo and Napu valley. Nests were not placed in the same location in consecutive trials, nor were they placed on the vegetation with the plot markers. Domesticated Japanese Quail (*Coturnix japonicus*) eggs (33×27 mm) were purchased from local markets and two eggs were placed in each nest. The eggs and nests were aired outdoors for at least 1 week prior to use in order to reduce any artificial odours.

Experimental trials were conducted during two periods; from 8 January to 24 March 2001 in Palolo valley and from 2 January to 27 March 2002 in Napu valley. These periods coincided with the wet season in Sulawesi and the breeding season for many undestorey bird species in the study area. During the setting up of the experiments, nests and eggs were handled with gloves and boots were worn to minimise human scent cues to predators (Laurance et al. 1993). Predation rates were calculated 8 days after eggs had been introduced. Eggs were considered predated if one or both eggs were missing, cracked or eaten. All sightings of potential predators during experimental trials were recorded.

Identification of predators with automatic cameras

Ten identical camera Fuji B36 units were assembled in Göttingen, Germany, following the prototype camera design from the Institute for Bird Research 'Vogelwarte Helgoland', 21 Vogelwarte, 26386. Only eight camera units could be used during the fieldwork, as two cameras were damaged prior to installation. Those units were installed simultaneously in each habitat of both valleys. The camera installation was carried out after nest predation trials; in Palolo valley from 28 March to 24 June 2001 and in Napu valley from 30 March to 27 June 2002.

Artificial nests of the same type used in the experiments, were baited with one quail egg. A triggering mechanism was inserted into the nest with a microswitch connected to an electrical plate and the camera. The trigger held the quail egg and the micro-switch functioned when the nest and egg were attacked. The cameras had an automatic flash and were always loaded with 12-exposure rolls of colour print film (AGFA, film speed 200 ASA). A rechargeable battery TR 6–4 (6 V 4 Ah) was used to provide power for each camera and its electrical connection with cable to the nest.

Camera nests were placed on both the ground and in shrubs at random locations at least 30 m apart along nest transects (Bayne and Hobson 1997). Each camera was mounted on a wooden tripod and was installed about 100 cm from an artificial nest. The height of the camera was about 100 cm for shrub nest, and 40 cm for ground nests.

All cameras were checked every day for 20 consecutive days or until the nest was destroyed. If nest predation did not occur within 10 days of the installation of the nest, the camera and nest were moved to a new location. We counted the total number of photographs taken of each species of nest visitor at each habitat. It is implicitly assumed that the most common nest predators would be photographed most frequently.

Small mammal trapping

To estimate relative abundance of small mammals in each habitat, baited cage-traps (28×12×12 cm) were set for four consecutive nights at each habitat. Small mammal trapping was not conducted simultaneously with the artificial nest experiments (Bayne and Hobson 1997). The traps were baited with ripe banana, mature coconut and dried fish and 30 traps were placed 20 m apart within two experimental transects. All traps were installed in the morning and checked each subsequent morning between 0700 and 1100 hrs. The bait was replenished as required. Animals were then identified to putative species, photographed and weighed. The capture rate was expressed as the number of captures per trap. Most of the animals were released unharmed after they had been examined. Trapping was undertaken in April 2001 (Palolo valley) and in March–April 2002 (Napu valley) after nest predation trials were completed.

Statistical analyses

Predation events were counted for each nest, rather than each egg, because two eggs in the same nest were probably not preyed independently. The percentage of nests lost in each transect of experiment were analyse using analysis of variance (ANOVA) after arc-sine transformation. The proportion of nest loss in the three habitats; forest edge, secondary forest and natural forest in Palolo valley and the replicates in Napu valley, were analysed with a three-way repeated measure analysis of variance (ANOVA). The three factors were; (1) sites (Palolo valley and Napu valley) (2) habitats (forest edge, secondary forest and natural forest) and (3) nest locations (ground vs. shrub). One-way ANOVA was used to assess the nest predation rate among five different habitats in Palolo valley following the edge–interior gradients. To compare predation rates on artificial ground and shrub nests in Palolo valley, a *t*-test was used. Non-parametric analysis of variance (Mann–Whitney *U*-test and Kruskal–Wallis ANOVA) was used to determine if the frequency of predator visits and the abundance of potential predators differed among habitats. The significance level for all statistical tests was set at 0.05 value. All statistical tests were done using STATISTICA 5.1. (Statsoft 1995).

Results

The predation rate on ground and shrub nests combined in Palolo valley was 61.7% which means that 300 out of 486 artificial nests were preyed upon during the 8 day interval. Of the 300 predated, 191 (63.7%) were from ground nests and 109 (36.3%) were from shrub nests. In Napu valley, 187 of 300 nests (62.3%) were preyed in an eight day period, 115 nests (61.5%) were ground nests and 72 nests (38.5%) were shrub nests.

The effects of site, habitat and nest type

There was no significant difference in the overall rate of nest predation between sites, Palolo valley and Napu valley (three-way ANOVA; $F_{1,118} = 0.008$, $p = 0.928$). However, predation rates differed significantly in the three habitat types ($F_{2,117} = 10.098$, $p < 0.01$) and between ground and shrub nests ($F_{1,118} = 47.309$, $p < 0.01$). Nest pedation was significantly higher on ground nests (62.8%) than on shrub nests (37.2%). All interactions among the factors have significant effect on nest predation rates. Those are interaction between site and habitat ($F_{5,114} = 3.946$, $p = 0.002$), between site and nest type ($F_{3,116} = 16.217$, $p < 0.01$), habitat and nest type ($F_{5,114} = 24.251$, $p < 0.01$) and the interaction between site, habitat and nest type ($F_{11,108} = 10.682$, $p < 0.01$).

Table 1. Differences in predation rates between artificial ground nests and shrub nests in various habitats of Palolo valley, n = predated nests, df = 9.

Habitat	Ground (n)	Shrub (n)	t-test	p-level
Forest edge	42	36	1.351	0.209
Forest garden	36	23	3.330	0.001
Coffee plantation	37	22	2.281	0.048
Secondary forest	43	21	4.494	0.002
Natural forest	33	7	6.074	0.0002

The effect of habitat gradient on nest predation in Palolo valley

A one-way ANOVA test was used to assess the nest predation rate among five different habitats in Palolo valley following the edge–interior gradients. There was no significant difference in ground nest predation among the five habitats studied along the gradient from forest edge to natural forest ($F_{4,45}$ = 0.831, p = 0.513; Figure 2a). However, the predation rates on shrub nests in these habitats were significantly different ($F_{4,45}$ = 7.254, $p < 0.01$). Comparing the means of predated nests per transect, natural forest experienced the lowest shrub nest predation rate (0.8) followed by secondary forest (2.1), coffee plantation (2.2) and forest garden (2.4) at intermediate level and the highest rate occurred in forest edge (3.6) (Figure 2b).

Using a *t*-test to compare means, it was found that ground nests suffered generally higher predation rates than shrub nests in all habitats studied. All the differences were significant, except those occurring along forest edge (t = 1.35, df = 9, p = 0.209) (Table 1).

In order to compare our results with other reports on predation rates in other tropical forests, the daily predation rates occurred in Palolo valley was calculated to percentage of total nests predated. Daily nest predation rates varied between 9.0% in natural forest and 10.6% at forest edge for ground nests and between 2.0% and 9.0% for shrub nests (Figure 3).

Identification of nest predators

Automatic cameras recorded 62 photos of animals visiting ground and shrub nests in Palolo valley and 22 pictures in Napu valley. All identifiable predators on ground nests in both valleys were rats, the most common species being Wild Sulawesian rat (*Rattus hoffmanni*) and Sulawesian giant rat (*Paruromys dominator*). Predators on shrub nest included Dwarf cuscus (*Strigocuscus celebensis*), Sulawesian giant rat (*Paruromys dominator*) and Sciruidae (unidentifiable to species level). Out of 24 pictures, the arboreal rat *P. dominator* was the most common visitor on shrub nests in Palolo valley (71%), 12.5% were *Strigocuscus celebensis* and 8.3% squirrels. A comparison across habitats in Palolo valley
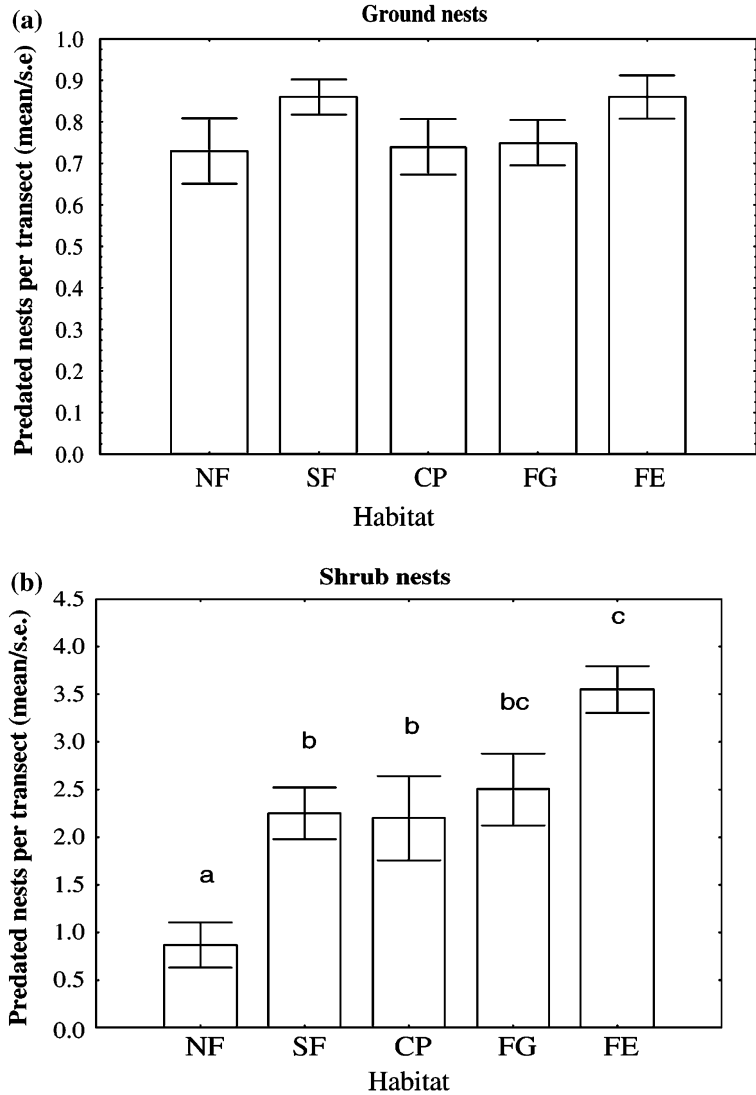
(a)

Ground nests

(b)

Shrub nests

Figure 2. (a, b). A comparison of mean predation rates after 8 days (±1 SE) on shrub and ground nests (N = 243) in Palolo valley, NF = Natural Forest, SF = Secondary forest, CP = Coffee plantation, FG = Forest garden and FE = Forest Edge, each habitat consisted of 10 transects. Different letters (a, b, c) show the significant difference (one-way ANOVA-test, $p < 0.05$).

revealed that rats were found more frequently along forest edge (46%) than other habitats: only 24%, 12%, and 18%, were found in forest gardens, cocoa plantations, and secondary forest, respectively, and none were recorded in natural forest. The differences were significant (Kruskal–Wallis test, $H = 12.349$, df = 4, $p < 0.05$). All documented visitors on shrub nests in Napu
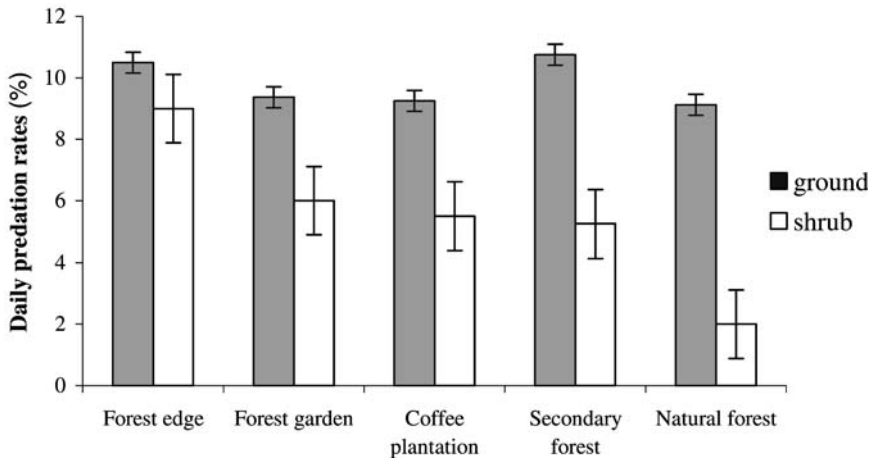
Figure 3. Daily predation rates (±1 SE) of artificial ground and shrub nests in Palolo valley.

valley were arboreal rats, whose frequencies were significantly different across habitat types (Kruskal–Wallis, $H = 8.286$, df $= 4$, $p < 0.05$). Around 70% were documented in forest edge, 30% in secondary forest and no picture taken from shrub nests in natural forest. The frequency of predator visits on ground nests did not significantly differ among habitat types in either Palolo valley (Kruskal–Wallis, $H = 7.816$, $p > 0.05$) or Napu valley ($H = 4,986$, $p > 0.05$).

Additional sightings of potential predators on shrub nests included Brown tree snake (*Boiga irregularis*) which was seen approaching a real nest and nestlings of Black-naped Monarch (*Hypothymis azurea*), whereas the Monitor lizard (*Varanus salvator*), dogs (*Canis familiaris*) and feral cats (*Felis catus*) were seen visiting the artificial ground nests. Black macaques (*Macaca tonkeana*) were reported to prey on bird nest and damage the shrub nests in Napu valley (Pombo, personal communication).

With the help of traps, five rodent species were captured in Palolo valley: Sulawesian giant rat (*Paruromys dominator*),Wild Sulawesian rat (*Rattus hoffmanni*), Black rat (*Rattus rattus*), *Bunomys chrysocomus* and *Taeromys celebensis*, and six species in Napu valley: *Bunomys chrysocomus*, *B. penitus*, *Paruromys dominator*, *Rattus hoffmanni*, *R. rattus*, and *R. xanturus*. Three species *Bunomys chrysocomus*, *B. penitus* and *Rattus xanturus* were not identified by cameras. There were no significant differences among transects in any habitat types in the abundance of small mammals captured in Palolo valley (Mann–whitney *U*-test, $p > 0.05$) nor in Napu valley (Mann–whitney *U*-test, $p > 0.05$) in all cases.

Discussion

The results of experimental trials in this study indicated that the pattern of predation rates on both nest types with spatial replicates (Palolo and Napu valley) was similar. Our findings on ground nests do not support the edge effect hypothesis, because the predation rates along forest edge (84% and 86% in two sites, respectively) were not significantly different from those in natural forest (73% and 66%). Several studies in neotropical and Southeast Asian rainforest reported edge effects on ground nest predation at various edges, including transitions between a minor road and forest, between logged and unlogged forest as well as forest–pasture edges (Burkey 1993; Cooper and Francis 1998; Estrada et al. 2002). Gibbs (1991) documented an increased predation risk on ground nests at edges between indigenous and second growth forest in Costa Rica, but not at edges between forest and pasture. Other experiments on ground nest predation in tropical forest have failed to detect a generally occurring edge effect (Arango-Vélez and Kattan 1997; Wong et al. 1998, Carlson and Hartman 2001).

The absence of an edge effect in our forest margin habitats may probably be caused by the edge type which was the transition between two structurally different landscapes (forest–agricultural field edges). Gibbs (1991) suggested that the lack of an edge effect on predation rates in the forest–field transition could be related to the extremely different landscape surroundings of the forest habitat that do not support the activity of several potential nest predators. It is, however, questionable why predation rates were as high in natural forest as they were in forest margin habitats. We suggest three possible explanations for this. First, forest dwelling species were the main predators responsible for nest predation in natural forest as well in forest margin areas. Second, abundance and species richness of ground nest predators might have been similar in all habitat types including natural forest. This was indicated by the small mammal trapping and photographic identification of nest predators. Results from automatic cameras showed that small mammals are the possible major predators in this region. Third, high intensity of human activities along forest margin areas probably deter forest dwelling species from approaching the edges, but attract other potential predators like house rats, feral cats from settlements and dogs accompanying farmers. This assumption supports the pattern occurring in tropical forests of Tanzania, that potential forest-dwelling predators are restricted to certain habitats and not attracted to sharp habitat edges (Carlson and Hartman 2001).

Although we found no habitat effects on ground predation rates, the high level of predation occurring in these areas should be put into context. A comparison of our predation rates with those obtained at other tropical forest sites (Söderström 1999) indeed suggests that Sulawesi's ground mammal fauna has an important impact on ground nests. Daily ground nest predation rates in this study varied between 9.0% in natural forest and 10.6% at forest edge (73% and 86% within 8 days) and were higher than results from other tropical forest,

except the highest daily predation rates found in an area after hurricane disturbance (Latta et al. 1995; Söderström 1999).

In contrast to ground nests, predation rates on shrub nests were highest in forest margin areas compared to the natural forest in both sites. This result corroborate the presence of edge effect on nest predation. The possible reasons of this fact could be: (1) the occurrence of different nest predators and high number of arboreal rats in forest margin habitats as recorded from the automatic cameras. Different species of shrub nest predators may be present in each habitat type. Edge effects on predation rates at forest margin areas vs. forest interior were usually attributed to the greater number of nest predator species in edge habitat (Andrén and Angelstam 1988). (2) Less vegetation cover along forest margin habitats may be allowing predator species to find nests easily. In this study, the forest edge transects were only situated 10 m away from the outer forest edge and the other forest margin habitats have relatively sparse shrub vegetation cover. This condition could not support the concealment of shrub nests from the outlook of potential predators such as avian predators and may cause an edge effect at the edges (Söderström et al. 1998) and other forest margin habitats. However, the camera-traps revealed birds did not seem to play a major role at our sites. (3) Forest margin areas might be used by some nest predators as a travel corridor for foraging, thereby increasing the variety of shrub nest predators operating along the edges and probably in other marginal habitats. One of the reasons why forest margins may support relatively diverse and abundant predator assemblages is the use of edges as travel lanes by potential predators (Andrén 1995; Marini et al. 1995). Thus, increased predator diversity at forest margin areas may reduce the nest success of understorey birds. (4) The presence of top predators in natural forest may control the density of small nest predators. We encountered foot prints and faeces of the Malay palm civet (*Viverra tangalunga*) in natural forest of both sites. This could be the reason why no small mammals were recorded from there. In contrary, we documented a large number of rodents operating on shrub nests in forest margin habitats. A 'mesopredator release hypothesis' (Terborg 1974; Crook and Soulé 1999; Södestrom 1999) may occur in forest margin habitats because the absence of top predators in such habitats may cause the increased abundance of small nest predators than in natural forest.

Studies in temperate region showed the similar predation rates on ground and shrub nests (Rudnicky and Hunter 1993; Söderström 1999). However, several studies conducted in tropical forest (Loiselle and Hoppes 1983; Wilcove 1985; Martin 1987) reported higher predation rates on ground nests than shrub nests, our study showed the same results. The high number of rodent species and their abundance in the study sites might be responsible for these facts. Sulawesi rainforest supports a high diversity of small mammals: 46 species of Muridae, eight species of Sciuridae and nine species of Soricidae (Whitten et al. 1988), all of which are considered to be forest dwelling, 38 species of rats and five species of squirrels have been reported in Lore Lindu National Park (Maryanto and Yani 2001). Our results showed a number of murid species as

potential predators on ground nests and only one arboreal rat documented preying on shrub nests.

Predator assemblages of nest predators for ground and shrub nests in our study sites are different. Whilst murids, lizards, dogs and feral cats mostly preyed on ground nests, the nest predators on shrub nests included small scansorial (climbing) mammals like Dwarf cuscus (*Strigocusus celebensis*), Sciuridae, and some arboreal rats such as Sulawesian giant rat (*Paruromys dominator*); tree snakes (e.g. *Boiga irregularis*) and black macaques. We can also expect avian species to prey on shrub nests (Telleria and Díaz 1995; Cooper and Francis 1998), although there were few of these predators evident at our study sites. It is assumed that differences in the predator assemblage may account for the differences in predation rates we noted. Some of the shrub nest predators are probably only opportunistic egg predators, for instance the *Strigocusus celebensis* which is mainly frugivorous.

Small mammals are the main predators on ground nests in tropical forest in Costa Rica, Australian, Singapore and Mexico (Gibbs 1991; Laurance et al. 1993; Wong et al. 1998; Estrada et al. 2002). In this study, small mammals appeared to be the major predators on both ground and shrub nests. Compared to studies in temperate regions, avian species accounted for most of the predation events on shrub nests whereas mammals mainly preyed upon ground nests (Andrén et al. 1985; Angelstam 1986; Söderström et al. 1998).

Artificial nests have been used frequently in many studies on nest predation to understand patterns of predation on bird nests and also to investigate different nest predator fauna. This is possible because they provide sample sizes rarely available with real nests and the treatments can be readily standardised (Major and Kendal 1996). It is assumed that nest predators seek, encounter and respond to artificial nests in the same manner as to natural nests (Martin 1987; Carlson and Hartman 2001).

Predation risk on artificial nests could be used to predict the possible pattern of predation pressure on real nests. If predation on real nests in tropical forest exhibit the same pattern as that we observed on artificial nests and if nest predation affects avian life histories, this would affect ground nesting birds who would be expected to have shorter nestling periods, more broods and a smaller clutch size compared to shrub nesters (Martin 1993, 1995). In addition, if nest predation rates differ between ground and shrub nests, selection should also favour nest sites associated with a low probability of nest predation (Collias and Collias 1984).

Limitations and implications

Our experimental set up did not replicate nature. Shrub nests in the wild are not located in linear transects. Therefore, predators using the linear habitats for foraging may have been more easily able to find the nests (Estrada et al. 2002). Nevertheless, if we assume that the main predators use similar foraging

strategies in all habitats studied, the differences between primary forest and forest margin habitats we found might be attributed to existing differences in predation levels. In some cases, the hardness eggshell of quail eggs may restrict predation by some small mammals (Major and Kendall 1996). However, this would not bias our results as we are comparing among habitat types using the same methods. The fact that nest predation was greater in forest margin habitats should be considered when managing protected areas.

While in our study sites, the observed higher predation levels within the first 10 m of forest edge might not have important implications for bird population persistence, since these edges cover only a very small proportion of the available habitat. However, the elevated predation rates in other marginal habitats: forest garden, coffee plantation and secondary forest might be more crucial. The remaining lowland and hill forest habitats in our study area are situated along the borders of the National Park and at great risk to disturbance or even deforestation. Since those forest margins already cover significant portions of these forest types, disturbance and deforestation along the Park's borders might be a serious threat for many endemic forest bird species.

Most understorey bird species are still found in both natural and secondary forest areas (Waltert et al. 2004b). However, their long-term persistence will largely depend on retaining forest habitat at adequate quantities. Our results suggest it could be essential to retain undisturbed forest for conservation. Knowledge about the effect of habitat alteration on nest predation may hopefully influence decisions for reserve management.

Acknowledgements

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