
Forest fragmentation and predation on artificial nests in the Usambara Mountains, Tanzania

Thor R. Hanson^{1*}, William D. Newmark² and William T. Stanley³

¹Field Naturalist Program, Department of Botany, University of Vermont, Burlington, VT 05405, ²Utah Museum of Natural History, University of Utah, 1390 E. Presidents Circle, Salt Lake City, UT 84112 and ³Division of Mammals, Field Museum of Natural History, 1400 S Lake Shore Drive, Chicago, IL 60605, U.S.A.

Abstract

In the Usambara Mountains of Tanzania we compared nest predation rates in relation to forest fragment size and proximity to edge. To identify the most appropriate egg type to bait artificial nests, we first examined rates of nest predation among artificial nests baited with chicken, clay or a combination of chicken and clay eggs. Nests containing only chicken eggs experienced no predation events, while similar predation rates were recorded for the chicken/clay and clay-only treatments. Using nests baited with two clay eggs, we found no significant variation in predation rates related to fragment size or proximity to edge. Small-mouthed mammals comprised 87.7% of all predator types identified from tooth imprints left on clay eggs, and rodents were the most common small-mouthed mammals in our study area. An examination of museum specimens revealed that only one local small-mouthed mammal had an incisor gape greater than the width of a small chicken egg. Total rodent abundance did not vary significantly in relation to fragment size or proximity to edge. We believe the lack of an area or edge effect on patterns of nest predation is a result of the ubiquitous distribution of rodents in our study area.

Key words: area and edge effects, artificial nests, clay eggs, forest fragmentation, rodent distribution and abundance, Usambara Mountains.

Résumé

Dans les Usambara Mountains de Tanzanie, nous avons comparé les taux de prédatation des nids en fonction de la taille du morceau de forêt et de la proximité de la lisière. Pour identifier le type d'œuf le plus approprié pour appâter

des nids artificiels, nous avons d'abord examiné les taux de prédatation de nids garnis d'œufs de poules, d'argile ou d'un mélange des deux. Les nids qui ne contenaient que des œufs de poules ne faisaient l'objet d'aucune prédatation alors que les taux de prédatation étaient semblables pour les nids avec des œufs d'argile et de poules et ceux qui n'avaient que des œufs d'argile. En utilisant des nids garnis de deux œufs d'argile, nous n'avons trouvé aucune variation significative des taux de prédatation, ni selon la taille de la parcelle forestière ni selon la proximité de la lisière. Les mammifères à petite bouche composent 87.7% de tous les types de prédateurs identifiés à partir des marques de dents laissées sur les œufs d'argile, et les rongeurs étaient les mammifères à petite bouche les plus communs dans notre zone d'étude. Un examen des spécimens de musée a révélé que seul un petit mammifère local à petite bouche pouvait l'ouvrir plus que de la grosseur d'un petit œuf de poule. L'abondance totale des rongeurs ne variait pas significativement en fonction de la taille de la parcelle ou de la proximité de la lisière. Nous croyons que l'absence d'effet de la surface ou de la lisière sur les schémas de prédatation des nids est un résultat de la distribution ubiquiste des rongeurs dans notre zone d'étude.

Introduction

The degradation of forested habitats has been suggested as a leading cause of declines in many bird populations (Hagan & Johnston, 1992). Research in both temperate and tropical regions has revealed losses of avian diversity in fragmented forests (e.g. Lovejoy *et al.*, 1983; Lynch & Whigham, 1984; Newmark, 1991). Nest predation is recognized as a primary agent of nesting mortality in many bird populations (Major *et al.*, 1994) and an important factor in habitat selection and the organization of bird communities (Martin, 1995; Sieving & Willson, 1998). Many studies have found higher rates of nest predation in

*Correspondence: E-mail: thor@rockisland.com

Present address: Thor R. Hanson, Department of Forest Resources, University of Idaho, PO Box 441133, Moscow, ID 93943, U.S.A.

small forest fragments and along forest edges than in large forest fragments and in the forest interior (e.g. Gates & Gysel, 1978; Latta *et al.*, 1995; reviewed in Batarry & Baldi, 2004), and have pointed to these patterns as an important cause for local extinctions and population declines of birds. On the other hand, other studies have found no significant increase in rates of nest predation in relation to fragment size (e.g. Langen, Bolger & Case, 1991; Nour, Matthysen & Dhondt, 1993; Wong, Sodhi & Turner, 1998) or distance from forest edge (reviewed in Lahti, 2001).

A variety of explanations have been proposed for these inconsistencies among studies including problems of experimental design (Murcia, 1995), edge type (Angelstam, 1986; Andrén, 1995), degree of landscape fragmentation (e.g. Kurki & Lindén, 1995), and differences in predator communities (Nour *et al.*, 1993; Andrén, 1995).

Investigations of nest predation have traditionally used artificial nests in combination with chicken, quail, or clay eggs to assess predation rates (e.g. Loiselle & Hoppes, 1983; Wilcove, 1985; Sieving & Willson, 1998). Artificial nests do not duplicate natural ecological conditions (Major & Kendall, 1996; Sieving & Willson, 1998), and may experience different predation rates than natural nests (e.g. Burke *et al.*, 2004). Faaborg (2004) suggested that artificial nests are an unreliable predictor of actual predation activity and should be avoided, but others believe they provide a useful index of relative predation rates (Andrén, 1995; Willson *et al.*, 2001), and can play a role in an overall assessment of nest predator activity (Villard & Part, 2004) if used to document spatial patterns of relative predation risk.

An additional concern regarding the use of artificial nests is the potential influence of egg-type on predation rates. The common practice of baiting artificial nests with chicken or quail eggs may exclude many small-mouthed predators such as rodents that are documented egg predators, but cannot penetrate the larger, galliform eggs (e.g. Roper, 1992; Haskell, 1995). Largely in response to these shortcomings, clay eggs, or a combination of clay and natural eggs, are being increasingly used to document a wider range of predators (e.g. Møller, 1989; Nour *et al.*, 1993). An advantage of clay eggs is that they preserve tooth and beak marks and therefore can offer an insight into the composition of the predator community (Keyser, Hill & Soehren, 1998). Comparisons of predation rates of clay scented and nonclay scented quail eggs found no significant difference between the two egg-types indicating that the documented nest predators – rodents, small carnivores and corvids – were not influenced by the scent of

clay (Bayne & Hobson, 1999). On the other hand, recent findings suggest that artificial nests containing clay eggs may suffer higher rates of nest predation by rodents than do real nests (Pärt & Wretenberg, 2002).

Most studies of nest predation have been conducted in northern temperate regions. We are unaware of any studies in the tropics that have compared rates of nest predation between clay and galliform eggs or that have examined in either tropical or temperate regions the number of species in a potential mammalian nest predator community that can penetrate galliform eggs.

To date, only three studies (Carlson & Hartman, 2001; Maina & Jackson, 2003; Githiru, Lens & Cresswell, 2005) have examined nest predation in fragmented African forests. However, the results of several of these studies are contradictory. Carlson & Hartman (2001) found lower nest predation pressures along forest edges than the interior in the Udzungwa Mountains in Tanzania. In contrast, Maina & Jackson (2003) reported higher nest predation pressures along the forest edge relative to the forest interior in the Kakamega Forest in Kenya. Multiple factors may account for these differences. First, artificial nests in the Udzungwa Mountains were baited with only chicken eggs while in Kakamega nests were baited with plasticine eggs. Thus differences in findings may be a result of the relative ability of nest predators to penetrate galliform eggs. A second possible reason for variation in results may be difference in the predator communities. To date, there have not been any studies in any tropical region assessing the distribution and abundance of selected potential nest predators.

Here we report on the impact of forest fragmentation in the Usambara Mountains on avian nest predation. Specifically, we compare rates of nest predation between (i) clay and chicken eggs; (ii) small, medium and large forest fragments; (iii) forest edge and interior; (iv) categories of nest predators; (v) document maximum tooth-tip to tooth-tip incisor gape of all potential mammalian nest predator species occurring at our study sites relative to the width of small chicken eggs; and (vi) evaluate the distribution and abundance of rodents in relation to fragment size and proximity to edge.

Methods

Study site

This study was conducted in the east and west Usambara Mountains in north-east Tanzania. The study area in the

east Usambara Mountains was located in the Amani Nature Reserve and on the Monga and Bulwa Tea Estates ($38^{\circ}38'E$, $5^{\circ}05'S$) at an elevation of approximately 950 m. A network of nine forest fragments ranging in area from 0.1 to 7688 ha was surveyed. Across this network, approximately 18% of the landscape is natural forest. The study area in the west Usambara Mountains lies on the Ambangulu Tea Estate ($35^{\circ}25'E$, $5^{\circ}04'S$), 22 km northwest of the town of Korogwe, at an elevation of approximately 1200 m. Four forest fragments ranging in area from 1.9 to 886 ha were surveyed and within this network and approximately 11% of the landscape is natural forest. All of the forest fragments in Usambara Mountains have abrupt sharp edges. The study areas in the East and West Usambara Mountains are located 21 km apart and are separated by an arid valley 300 m in elevation.

Nest predation experiments

All experiments were conducted using artificial split bamboo nests (Hagen Corporation). Nests measured 10 cm in diameter and 6 cm deep and were lined with leaf litter gathered on site. Clay eggs, elliptical in shape, were fashioned from white modelling clay (Sculpey brand) and measured 24 mm by 18 mm, a size typical of many songbirds common in the study area (Mackworth-Praed & Grant, 1960). Small brown chicken eggs had an average dimension of 59 mm by 39 mm and were purchased at a local market. All eggs and nests were washed with stream water and aired outside for 3 days before commencing the study, and thereafter handled only by people wearing rubber gloves and rain boots to minimize human scent.

All nests were placed at a height between 0.25 and 1.50 m above the ground. Suitable locations included the forked branches of saplings and shrubs, as well as lianas and vines and stumps. A nest was considered preyed upon if one or more eggs were missing or bore the marks of a predation attempt. Nest predation studies were conducted between 23 July and 26 September 1999.

Egg-type experiments

We compared predation rates on nests baited with two chicken eggs, two clay eggs, and a combination of one chicken and one clay egg. In the largest fragment in the west Usambara Mountains, 30 nests were placed 30–50 m apart, along two transects (>1000 m apart) that ran perpendicular to the forest edge. Nests were checked after 5

and 7 days. We believe given the average home range size for small mammals in tropical forest habitat (Adler, Endreis & Piotter, 1997; Wells *et al.*, 2004) that nests were independent.

Fragment size and proximity to edge experiments

To examine the relationship between nest predation and fragment size, artificial nests were placed within thirteen forest fragments in the east and west Usambara networks. All nests were located 30–50 m apart and were baited with two clay eggs. Forest fragments were grouped into three size categories: small (<8 ha, $N = 8$), medium (30–40 ha, $N = 2$) and large (>500 ha, $N = 3$). The number of nests that were placed within a fragment ranged between 2 and 30. In the medium and large fragments, fifteen nests were placed 0–15 m interior from the forest edge and fifteen nests were placed >100 m interior from the forest edge. We defined forest interior habitat as >100 m from the forest edge because forest edge micro-climatic (air temperature, vapour pressure deficit and light intensity) gradients at these locations in the East and West Usambara Mountains extend on average <100 m from the forest edge (Newmark, 2001). In the small fragments, which lacked forest interior habitat (>100 m from forest edge), two to eighteen nests were placed 0–15 m interior from the forest edge. Small forest fragments were excluded in the proximity to edge experiment because of the absence of forest interior habitat. These experiments lasted five days.

Predator type classification

For each nest that was preyed upon, we examined the recorded imprints on the clay eggs with a 14 \times hand lens and classified the predator into five categories: small-mouthed mammal (width between outside edges of upper and lower incisors ≤ 5.0 mm), large-mouthed mammal (width between outside edges of upper and lower incisors > 5.0 mm), bird, reptile, or unidentified. We compared the width between the outside edges of the upper and lower incisors on clay eggs preyed on by mammals to the width of the base of the incisors of museum specimens of mammal species that occur in the Usambara Mountains. We classified a predator type as unidentified if we could not accurately identify the impressions on the clay egg, or if the clay egg had been removed from the nest and was missing ($N = 12$).

To examine whether mammalian nest predators found in the east and west Usambara Mountains could readily handle chicken-sized eggs (width = 39 mm), we measured following the general methodology of Haskell (1995) the maximum tooth-tip to tooth-tip incisor gape of museum specimens by placing the condyloid (rather than the coronoid as described by Haskell) processes of the mandible into the mandibular fossae and opened the jaw until the angular processes contacted the auditory bullae. These measurements were also compared to the width of a typical quail egg (23.5 mm), an egg-type commonly used in other artificial nest predation studies.

Rodent surveys

Rodents were sampled with trap lines that consisted of three types of traps: Museum Specials, Victor Rat Traps, and Sherman Traps. Traps totalling 29 to 100 per line were set in a generally straight line at locations deemed likely to be frequented by small mammals, on and above the ground. Traps were baited each evening with freshly fried coconut coated in peanut butter. A trap-night refers to one trap in operation for one 24-h period (07.00–07.00 hours). Traps were checked each morning and again each evening. Surveys were conducted between July and September in 1991, 1992 and 1993. The analysis of rodent abundance relative to proximity to edge was restricted to medium and large fragments because of the absence of forest interior habitat in small fragments.

Statistical analysis

Variation in rates of nest predation in relation to egg-type, fragment size, proximity to edge, and predator type were compared using one- and two-way χ^2 tests. Number of captures of rodents and in relation to fragment size and proximity to edge were compared with a nested ANOVA in which 125 trap-night samples were nested within study sites which in turn were nested within fragment size class or proximity to edge class.

Results

Egg-type experiment

Within the largest fragment in the west Usambara network where the egg-type experiment was conducted, predation rates of nests did not differ significantly ($\chi^2 = 0.09$;

Table 1 Comparison of nest loss in relation to egg-type and length of exposure along two transects in the largest forest fragment in the west Usambara Mountain network

Egg-type treatment	Percentage nests preyed on			
	Transect 1		Transect 2	
	5 days	7 days	5 days	7 days
2 Chicken	0	0	0	0
2 Clay	40	40	20	30
1 Chicken + 1 clay	30	40	20	40

$P > 0.10$) between transects (Table 1) indicating low spatial variation in nest loss. Therefore, we pooled the data from the two transects. Nest predation rates increased slightly between days 5 and 7 (Table 1). The rate of nest predation varied significantly ($\chi^2 = 10.13$; $P < 0.007$) by egg-type after 7 days (Table 1). Post-hoc 95% Bonferroni simultaneous confidence intervals indicated that the two chicken eggs-type nests experienced significantly less predation events than expected. There was no significant difference in predation rates between nests with two clay eggs and nests with one chicken plus one clay egg ($P > 0.10$). None of the chicken eggs were preyed on in any of the egg-type treatments.

The results of this experiment indicate (i) there were significant differences in rates of nest predation between egg types; (ii) nest predators on artificial nests were not using strictly olfactory or visual cues from chicken eggs to locate nests, and (iii) nest predators on artificial nests were as likely to prey on nests containing two clay eggs as they were nests containing one chicken egg and one clay egg. Remaining experiments were therefore conducted using only clay eggs to maximize the identification of predators from tooth imprints.

Fragment size and proximity to edge experiments

Nest predation rates did not vary significantly ($P > 0.10$) between small, medium and large fragments (Table 2). Nest predation rates also did not vary significantly ($P > 0.10$) between the forest edge and interior in the medium and large forest fragments (Table 3).

Comparison of predator type

The frequency of recorded predator type in the three experiments varied significantly ($\chi^2 = 128.0$,

Table 2 Comparison of predation events on artificial nests between small, medium and large forest fragments in the east and west Usambara Mountains

Percentage nests preyed on		
Small	Medium	Large
30	22	37

Table 3 Comparison of predation events on artificial nests between the forest edge and interior in medium and large fragments in the east and west Usambara Mountains

Percentage nests preyed on	
Edge	Interior
35	27

Table 4 Frequency of recorded predator types during egg-type, proximity to edge, and forest area experiments in the east and west Usambara Mountains, Tanzania

Predator type	Predation nest events
Small-mouthed mammal	57
Large-mouthed mammal	6
Bird	1
Reptile	1
Unidentified	24

$P < 0.0001$). Of the 65 identified nest predation events in the three experiments, small-mouthed mammals, large-mouth mammals, birds, and reptiles accounted for 87.7%, 9.2%, 1.5% and 1.5%, respectively (Table 4).

In the fragment size and proximity to edge experiments, we recorded only small-mouthed mammal, large-mouthed mammal and unidentified predator types. Two-way χ^2 tests indicate that predator type is independent of forest area ($P > 0.10$) and proximity to forest edge ($P > 0.10$). In this latter analysis, large-mouthed mammals and unidentified predators were combined for these tests because of small cell size. However, results are unchanged if large-mouthed mammals are excluded because of small cell size.

Incisor width and gape of mammalian nest predators

With the exceptions of the giant pouched rat (*Cricetomys gambianus* Waterhouse) and the lesser galago (*Galago*

senegalensis Geoffroy), all insectivore and rodent species that occur at our study sites in the Usambara Mountains have an incisor width ≤ 5.0 mm, while all carnivore, primate, and pig species have an incisor width > 5.0 mm (Table 5). Our small mammal trapping also reveals none of the shrew species with the exception of *Sylvisorex megalura* (Jentink), climb vines, stumps, shrubs or trees – the locations where we placed artificial nests. Thus with the exceptions of *S. megalura* and *G. senegalensis*, all potential small-mouthed mammalian nest predators at our study sites are rodents.

Nine of the ten large-mouthed mammal species found at our study sites have an incisor gape that exceeds the width of a small chicken-sized egg (39 mm). While none of the small-mouthed mammal species have an incisor gape greater than 39 mm, the lesser galago might still be able to handle chicken eggs because of its prehensile digits. Of particular relevance to our study is that only one of the seventeen resident rodent species has an incisor gape that exceeds the width of a chicken egg. Similarly, all the large-mouthed mammals but only three of the eighteen small-mouthed mammals have incisor gapes greater than the width of a quail egg.

Abundance and distribution of rodents

Based upon 7890 trap-nights, the most common rodent species at our study sites in the east and west Usambara Mountains, ranked by trap success, are *Praomys delectorum* (Thomas), *Hylomyscus arcimontensis* (Carleton & Stanley), *Lophuromys flavopunctatus* Thomas, *Grammomys ibeanus* (Osgood), *Grammomys macmillani* (Wroughton) *Graphiurus murinus* (Desmarest), *Rattus rattus* (Linnaeus), *Beamys hindei* Thomas, and *Aethomys kaiseri* (Noack) (Table 5). Of the species recorded, *R. rattus* is the only exotic species. *Graphiurus murinus* (Kingdon, 1974) and *R. rattus* (McLennan & MacMillan, 1985; Brown *et al.*, 1998) have previously been shown to prey on bird nests.

Total number of captures of rodents per 125 trap-night sample did not vary significantly by fragment size ($F = 0.53$, $P > 0.10$) or distance from edge in the medium and large forest fragments ($F = 0.31$, $P > 0.10$) (Fig. 1). In addition, number of captures of *Graphiurus murinus* and *R. rattus*, species known to eat bird eggs, did not vary significantly by fragment size ($F = 0.63$, $P > 0.10$; $F = 0.78$, $P > 0.10$, respectively) or for *Graphiurus* by proximity to edge ($F = 0.78$, $P > 0.10$) (Fig. 1). (*Rattus* was excluded from the latter analysis because of small sample size.)

Table 5 Number of captures of rodent species across all study sites in the east and west Usambara Mountains and mean (standard deviation) incisor width and maximum gape of potential mammalian nest predator species

Order/species	Number of captures	Width between base of upper incisors (mm)	Width between base of lower incisors (mm)	Maximum gape between lower and upper incisor tooth-tips (mm)	N	Classified predator type
Primates						
<i>Cercopethicus mitis</i>		17.1 (0.7)	12.2 (0.1)	77.6 (11.6)	4 ^a	Large-mouthed mamma
<i>Colobus angolensis</i> Sclater		17.1 (0.7)	12.9 (0.6)	77.7 (10.7)	3 ^a	Large-mouthed mamma
<i>Galago senegalensis</i>		4.6 (0.3)	3.2 (0.4)	23.7 (1.0)	5 ^a	Small-mouthed mamma
<i>Otolemur crassicaudatus</i> (Geoffroy)		8.6 (0.5)	4.7 (0.3)	45.6 (3.1)	3 ^a	Large-mouthed mamma
Insectivora						
<i>Sylvisorex megalura</i> (Jentink)		1.2 (0.2)	1.0 (0.03)	9.2 (1.0)	8 ^a	Small-mouthed mamma
Rodentia						
<i>Aethomys kaiseri</i>	1	3.2 (0.2)	2.7 (0.1)	12.7 (0.1)	3 ^a	Small-mouthed mamma
<i>Anomalurus derbianus</i> (Gray)		4.9 (0.5)	4.4 (0.3)	21.9 (1.4)	3 ^a	Small-mouthed mamma
<i>Beamys hindei</i>	1	3.0 (0.3)	2.6 (0.3)	20.5 (3.6)	8	Small-mouthed mamma
<i>Cricetomys gambianus</i> Waterhouse		6.9 (0.9)	5.1 (0.4)	40.0 (7.4)	4 ^a	Large-mouthed mamma
<i>Dendromus mesomelas</i> Brants		1.5 (0.03)	1.3 (0.04)	7.1 (0.6)	3 ^a	Small-mouthed mamma
<i>D. mystacalis</i> Heuglin		1.4 (0.1)	1.3 (0.1)	6.0 (0.8)	7	Small-mouthed mamma
<i>Grammomys ibeanus</i>	17	2.4 (0.2)	2.2 (0.1)	11.2 (0.9)	10	Small-mouthed mamma
<i>G. macmillani</i>	10	2.2 (0.2)	1.9 (0.2)	10.4 (1.1)	10	Small-mouthed mamma
<i>Graphiurus murinus</i>	9	2.3 (0.2)	2.0 (0.1)	9.5 (1.2)	10	Small-mouthed mamma
<i>Heliosciurus rufobrachium</i> (Waterhouse)		5.0 (0.2)	4.3 (0.4)	27.2 (3.2)	3	Small-mouthed mamma
<i>Hylomyscus arcimontensis</i>	103	1.8 (0.1)	1.3 (0.1)	9.3 (1.0)	10	Small-mouthed mamma
<i>Lophuromys flavopunctatus</i>	89	2.2 (0.2)	2.3 (0.2)	10.3 (1.8)	10	Small-mouthed mamma
<i>Mastomys natalensis</i> (Smith)		1.7 (0.1)	1.5 (0.03)	10.6 (0.5)	4	Small-mouthed mamma
<i>Mus musculoides</i> Temminck		1.2 (0.1)	1.0 (0.04)	6.6 (1.1)	6 ^a	Small-mouthed mamma
<i>Paraxerus vexillarius</i> (Kershaw)		4.2 (0.2)	3.8 (0.02)	25.1 (4.1)	10	Small-mouthed mamma
<i>Praomys delectorum</i>	245	1.7 (0.2)	1.5 (0.1)	10.0 (1.3)	4	Small-mouthed mamma
<i>Rattus rattus</i>	4	2.8 (0.3)	2.3 (0.02)	15.1 (2.5)	2	Small-mouthed mamma
Carnivora						
<i>Civettictis civetta</i> (Schreber)		19.0 (1.1)	14.6 (0.8)	100.7 (14.8)	3 ^a	Large-mouthed mamma
<i>Galerella sanguinea</i> (Rüppell)		6.3 (0.4)	5.3 (0.1)	41.3 (5.4)	3 ^a	Large-mouthed mamma
<i>Genetta maculata</i> (Gray)		7.6 (0.2)	6.2 (0.1)	61.8 (5.7)	3 ^a	Large-mouthed mamma
<i>Herpestes ichneumon</i> (Linnaeus)		10.5 (0.1)	9.0 (0.3)	70.1 (5.5)	3 ^a	Large-mouthed mamma
<i>Nandinia binotata</i> Gray		8.7 (0.4)	6.8 (0.2)	80.0 (9.1)	3 ^a	Large-mouthed mamma
Artiodactyla						
<i>Potamochoerus larvatus</i> (Cuvier)		47.8 (7.7)	45.7 (6.7)	233.3 (57.7)	3 ^a	Large-mouthed mamma

^aSample includes specimens from areas other than the east and west Usambara Mountains.

Discussion

In the Usambara Mountains in north-eastern Tanzania, rates of nest predation did not vary by fragment size or distance from forest edge. We believe the lack of an area or edge effect on rates of nest predation in the Usambara Mountains is a result of the ubiquitous distribution of rodents in our study area. Total rodent abundance as

measured by constant trap effort does not vary in relation to forest area or proximity to forest edge. However in Brazilian Atlantic and Amazonian forest fragments overall rodent abundance has been found to vary with distance from forest edge (Malcolm, 1997; Stevens & Husband, 1998); while in Venezuelan forested land-bridge islands, where predators were absent, overall rodent abundance varied inversely with fragment area (Lambert *et al.*, 2003).

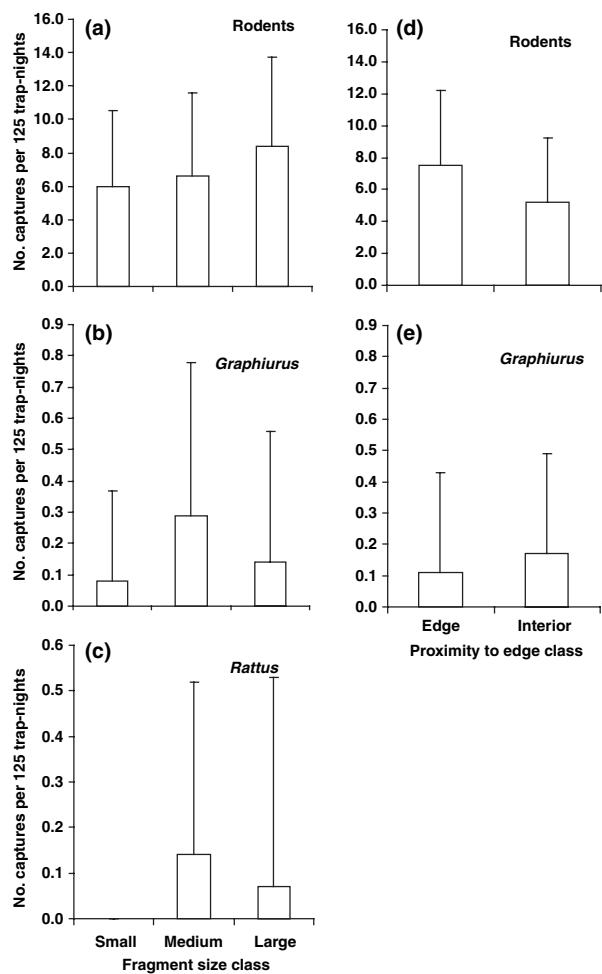


Fig 1 Comparison of mean (± 1 standard deviation) number of captures in the East and West Usambara Mountains of (a) rodents, (b) *Graphiurus*, (c) *Rattus* per 125 trap-nights among small, medium, and large fragments and (d) rodents and (e) *Graphiurus* between the forest edge and interior in medium and large fragments.

Thus, it is unclear how widespread rodent distributions such as those observed in the Usambara Mountains are in Africa as well as throughout the tropics in general although we suspect such a distribution may indeed be relatively common. In summary, our nest predation findings are consistent with the predator community hypothesis (Nour *et al.*, 1993; Andrén, 1995) that proposes that the composition and distribution of nest predators are an important determinant of patterns of nest predation.

In the Usambara Mountains, egg-type affected predation rates on artificial nests. Nests containing two chicken

eggs were preyed on significantly less frequently than nests containing two clay eggs or one chicken and one clay. Furthermore we did not record any predated chicken eggs in any of the egg-type treatments. The imprints on the clay eggs indicated the most commonly observed predator type on artificial nests in the Usambara Mountains were small-mouthed mammals. In our study, rodents were the predominant small-mouth mammal predator-type. Githiru *et al.* (2005) also found high levels of nest predation by rodents in the nearby Taita Hills, Kenya.

The appropriateness of an egg-type to detect predation events is almost certainly dependent upon the composition of the predator community. In the Usambara Mountains, the relative abundance of nest predators that can handle chicken eggs is low. A measurement of the tooth-tip to tooth-tip gape of all potential mammalian nest predators occurring at our study sites indicates that only one of the seventeen rodent species has an incisor gape larger than the width of a small chicken egg. Yet in other tropical and temperate regions comparatively high levels of nest predation have been documented using chicken eggs (Laurance, Garesche & Payne, 1993; Yahner & Mahan, 1997). Most notably, Carlson & Hartman (2001) reported average nest predation rates in the forest interior of 49% after 8 days using artificial ground nests containing one chicken egg in the Udzungwa Mountains, another of the Eastern Arc Mountains. This pattern thus suggests that the nest predator communities may vary considerably among even the Eastern Arc Mountains.

Finally, we end with a note of caution. Several recent studies have reported variation in patterns of nest predation between artificial and natural nests (Pärt & Wretenberg, 2002; Zanette, 2002; Burke *et al.*, 2004; Thompson & Burhans, 2004), while other studies have found no variation between artificial and natural nests (Voos, 2002). We believe that studies using artificial nests to assess predation risk need to be interpreted carefully. While we are confident that our results do reflect general spatial patterns of artificial nest predation by rodents in the Usambara Mountains, we would not want to extrapolate our findings to the predation of natural nests of particular species, nor to other potentially important nest predators such as snakes and birds that we rarely recorded. Further research examining patterns of nest predation on natural nests in the tropics is required.

Acknowledgements

We thank the MacArthur Foundation, Earthwatch Institute, Switzer Foundation, University of Vermont, National Geographic Society, and the Ellen Thorne Smith Fund for support, COSTECH and Amani Nature Reserve for permission to conduct research, D. Barrington, D. Capen and W. Poleman for their comments, and S. Goodman for assistance in collection of rodent data.

References

- ADLER, G.H., ENDREIS, M. & PIOTTER, S. (1997) Spacing patterns within populations of a tropical forest rodent, *Proechimys semispinosus*, on five Panamanian island. *J. Zool.* **241**, 43–53.
- ANDRÉN, H. (1995) Effects of landscape composition on predation rates of habitat edges. In: *Mosaic Landscapes and Ecological Processes* (Eds L. HANSSON, L. FAHRIG and G. MERRIAM), Chapman and Hall, London.
- ANGELSTAM, P. (1986) Predation on ground-nesting birds nests in relation to predator densities and habitat edge. *Oikos* **47**, 365–373.
- BATARY, P. & BALDI, A. (2004) Evidence of an edge effect on avian nest success. *Conserv. Biol.* **18**, 389–400.
- BAYNE, E.M. & HOBSON, K.A. (1999) Do clay eggs attract predators to artificial nests? *J. Field Ornithol.* **70**, 1–7.
- BROWN, K.P., MOLLER, H., INNES, J. & JANSEN, P. (1998) Identifying predators at nests of small birds in a New Zealand forest. *Ibis* **140**, 274–279.
- BURKE, D.W., ELLIOT, K., MOORE, L., DUNFORD, W., NOL, E., PHILLIPS, J., HOMES, S. & FREEMARK, K. (2004) Patterns of nest predation on artificial and natural nests in forests. *Conserv. Biol.* **18**, 381–388.
- CARLSON, A. & HARTMAN, G. (2001) Tropical forest fragmentation and nest predation – an experimental study in an Eastern Arc montane forest, Tanzania. *Biodivers. Conserv.* **10**, 1077–1085.
- FAABORG, J. (2004) Truly artificial nest studies. *Conserv. Biol.* **18**, 369–370.
- GATES, J.E. & GYSEL, L. (1978) Avian nest dispersion and fledging success in field-forests ecotones. *Ecology* **59**, 871–883.
- GITHIRU, M., LENS, L. & CRESSWELL, W. (2005) Nest predation in a fragmented Afrotropical forest: evidence from natural and artificial nests. *Biol. Conserv.* **123**, 189–196.
- HAGAN, J.M. & JOHNSTON, D.W. (Eds) (1992) *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington, DC.
- HASKELL, D.G. (1995) Forest fragmentation and nest predation: are experiments with Japanese quail eggs misleading? *Auk* **112**, 767–770.
- KEYSER, A.J., HILL, G.E. & SOEHNEN, E.C. (1998) Effects of forest fragment size, nest density, and proximity to edge on the risk of predation to ground-nesting passerine birds. *Conserv. Biol.* **12**, 986–994.
- KINGDON, J. (1974) *East African Mammals. Vol. II B. Hares and Rodents*. University of Chicago Press, Chicago, IL.
- KURKI, S. & LINDÉN, H. (1995) Forest fragmentation due to agriculture affects the reproductive success of the ground-nesting black grouse *Tetrao tetrix*. *Ecography* **18**, 109–113.
- LAHTI, D.C. (2001) The “edge effect on nest predation” hypothesis after twenty years. *Biol. Conserv.* **99**, 365–374.
- LAMBERT, T.D., ADLER, G.H., RIVEROS, C.M., LOPEZ, L., ASCANIO, R. & TERBORGH, J. (2003) Rodents on tropical land-bridge islands. *J. Zool. Lond.* **260**, 179–187.
- LANGEN, T.A., BOLGER, D.T. & CASE, T.J. (1991) Predation on artificial bird nests in chaparral fragments. *Oecologia* **86**, 395–401.
- LATTA, S.C., WUNDERLE, J.M., TERRANOVA, E. & PAGAN, M. (1995) An experimental study of nest predation in a subtropical wet forest following hurricane disturbance. *Wilson Bull.* **107**, 590–602.
- LAURANCE, W.F., GARESCHE, J. & PAYNE, C.W. (1993) Avian nest predation in modified and natural habitats in tropical Queensland: an experimental study. *Wildl. Res.* **20**, 711–723.
- LOISELLE, B.A. & HOPPES, W.G. (1983) Nest predation in insular and mainland lowland rainforest in Panama. *Condor* **85**, 93–95.
- LOVEJOY, T.E., BIERREGAARD, R.O., RANKIN, J.M. & SCHUBART, H.O.R. (1983) Ecological dynamics of tropical forest fragments. In: *Tropical Rain Forest: Ecology and Management* (Eds L. SUTTON, T. C. WHITMORE and A. C. CHADWICK). Blackwell, London.
- LYNCH, J.F. & WHIGHAM, D.F. (1984) Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biol. Conserv.* **28**, 287–324.
- MØLLER, A.P. (1989) Nest site selection across field-woodland ecotones: the effect of nest predation. *Oikos* **56**, 240–246.
- MACKWORTH-PRAED, C.W. & GRANT, C.H.B. (1960) *Birds of Eastern and Northeastern Africa*, 2nd edn. Longman, London.
- MAINAI, G.G. & JACKSON, W.M. (2003) Effects of fragmentation on artificial nest predation in a tropical forest in Kenya. *Biol. Conserv.* **111**, 161–169.
- MAJOR, R.E. & KENDAL, C.E. (1996) The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* **138**, 298–307.
- MAJOR, R.E., PYKE, G.H., CHRISTY, M.T., GOWING, G. & HILL, R.S. (1994) Can nest predation explain the timing of the breeding season and the pattern of nest dispersion of New Holland honeyeaters? *Oikos* **69**, 364–372.
- MALCOLM, J.R. (1997) Biomass and diversity of small mammals in Amazonian forest fragments. In: *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities* (Eds W. F. LAURANCE and R. O. BIERREGAARD). University of Chicago Press, Chicago, IL.
- MARTIN, T.E. (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* **65**, 101–127.
- MCLENNAN, J.A. & MACMILLAN, B.W.H. (1985) The predators of eggs and chicks of greenfinches in a mixed farming area in Hawke’s Bay. *Notornis* **32**, 95–100.
- MURCIA, C. (1995) Edge effects in fragmented forests: implications for conservation. *TREE* **10**, 58–62.

- NEWMARK, W.D. (1991) Tropical forest fragmentation and the local extinction of understory birds in the Eastern Usambara Mountains, Tanzania. *Conserv. Biol.* **5**, 67–78.
- NEWMARK, W.D. (2001) Tanzanian forest edge microclimatic gradients: dynamic patterns. *Biotropica* **33**, 2–11.
- NOUR, N., MATTHYSEN, E. & DHONDT, A.A. (1993) Artificial nest predation and habitat fragmentation: different trends in bird and mammal predators. *Ecography* **16**, 111–116.
- PÄRT, T. & WRETTENBERG, J. (2002) Do artificial nests reveal relative nest predation risk for real nests? *J. Avian Biol.* **33**, 39–46.
- ROPER, J.J. (1992) Nest predation experiments with quail eggs: too much to swallow? *Oikos* **65**, 528–530.
- SIEVING, K.E. & WILLSON, M.F. (1998) Nest predation and avian species diversity in northwestern forest understory. *Ecology* **79**, 2391–2402.
- STEVENS, S.M. & HUSBAND, T.P. (1998) The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. *Biol. Conserv.* **85**, 1–8.
- THOMPSON, F.R., III & BURHANS, D.E. (2004) Differences in predators of artificial and real songbird nests: evidence of bias in artificial nest studies. *Conserv. Biol.* **18**, 373–380.
- VILLARD, M. & PART, T. (2004) Don't put all your eggs in real nests: a sequel to Faaborg. *Conserv. Biol.* **18**, 371–372.
- VOOS, S. (2002) Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* **133**, 608–615.
- WELLS, K., PFEIFFER, M., BIN LAKIM, M. & LINSENMAIR, K.E. (2004) Arboreal spacing patterns of the large pencil-tailed tree mouse, *Chiropodomys major* (Muridae), in a rainforest in Sabah, Malaysia. *Ecotropica* **10**, 15–22.
- WILCOVE, D.S. (1985) Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**, 1211–1214.
- WILLSON, M.F., MORRISON, J.L., SIEVING, K.E., DE SANTO, T.L., SANTISTEBAN, L. & DÍAZ, I. (2001) Patterns of predation risk and survival of bird nests in a Chilean agricultural landscape. *Conserv. Biol.* **15**, 447–456.
- WONG, T.C.M., SODHI, N.S. & TURNER, I.M. (1998) Artificial nest and seed predation experiments in tropical lowland rainforest remnants of Singapore. *Biol. Conserv.* **85**, 97–104.
- YAHNER, R.H. & MAHAN, C.G. (1997) Effects of logging roads on depredation of artificial ground nests in a forested landscape. *Wildlife Soc. Bull.* **25**, 158–162.
- ZANETTE, L. (2002) What do artificial nests tell us about nest predation? *Biol. Conserv.* **103**, 323–329.

(Manuscript accepted 1 February 2007)

doi: 10.1111/j.1365-2028.2007.00760.x