Nest predation in Afrotropical forest fragments shaped by inverse edge effects, timing of nest initiation and vegetation structure

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ABSTRACT

High levels of nest predation influence the population dynamics of many tropical birds, especially when deforestation alters nest predator communities. Consequences of tropical forest fragmentation on nest predation, however, remain poorly understood, as natural predation patterns are only well documented in a handful of tropical forests. Here, we show the results of an extensive study of predation on natural nests of Cabanis's Greenbul during three years in a highly fragmented cloud forest in SE Kenya. Overall predation rates derived from 228 scrub nests averaged 69%, matching the typical high predation level on tropical bird species. However, predation rates strongly varied in space and time, and a model that combined fragment-, edge-, concealment-, year- and nest timing effects was best supported by our data. Nest predation rates consistently increased from forest edge to interior, opposing the classic edge effect on nest predation, and supporting the idea that classic edge effects are much rarer in Afrotropical forests than elsewhere. Nest concealment also affected predation rates, but the strength and direction of the relationship varied across breeding seasons and fragments. Apart from spatial variation, predation rates declined during the breeding season, although the strength of this pattern varied among breeding seasons. Complex and variable relationships with nest predation, such as demonstrated here, suggest that several underlying mechanisms interact and imply that fixed nesting strategies may have variable - even opposing - fitness effects between years, sites and habitats.

KEYWORDS: tropical birds; habitat fragmentation; nest success; Taita Hills; *Phyllastrephus cabanisi placidus*

RUNNING HEADLINE: Variation in nest predation within Afrotropical forest fragments

INTRODUCTION

Predation on eggs and nestlings constitutes a major cause of reproductive failure in birds (Wilcove 1985, Martin and Roper 1988), and high predation rates may contribute to the decline in avian populations (Martin and Clobert 1996, Stratford and Robinson 2005, Robinson and Sherry 2012). Understanding spatial and temporal variation in nest predation therefore is a prerequisite to predict avian population dynamics and viability under landscape or climate change (Robinson et al. 1995, Chalfoun et al. 2002, Grant et al. 2005). This particularly applies to species from tropical rainforests that currently suffer from severe anthropogenic effects such as habitat loss and biological invasions, without similar episodes in the recent past. Yet, data on natural nest predation from the tropics remain scarce and are strongly biased towards Neotropical forests (Robinson et al. 2000, Kvarnbäck et al. 2008, Ryder et al. 2008, Brawn et al. 2011; but see Thompson 2004, Spanhove et al. 2009a, Newmark and Stanley 2011 for some examples on Afrotropical forest birds). Nest predation studies from the tropics therefore remain invaluable, as they may document unusual patterns which can lead to new insights in processes that are even relevant for bird communities well outside the original study area.

Reproductive failure due to nest predation is generally high in small, isolated and degraded forest fragments (Small and Hunter 1988, Tewksbury et al. 2006), in particular near forest-matrix ecotones (edge effect on nest predation *sensu* Gates and Gysel 1978, Andrén and Angelstam 1988),). However, a vast amount of studies do not support a general negative impact of fragmentation on breeding success, and a few studies even support the opposite patterns (Lahti 2001, Batáry and Báldi 2004, Vetter et al. 2013). In Afrotropical forests in particular, nest predation rates are often lower near forest edges or in small forest remnants with high edge-to-interior ratios. For instance, in the forest remnants of the Taita Hills (SE Kenya), Spanhove et al. (2009a) revealed relaxed predation rates on nests of the forest-dependent White-starred Robin (*Pogonocichla stellata*) in the smallest fragments with the highest edge-to-interior ratio. Experiments with artificial ground nests in the same area revealed highly similar results (Githiru et al. 2005, Spanhove et al. 2009c). In the nearby Usambara mountains of NE Tanzania, inverse edge effects were shown in six out of eleven forest species (Newmark and Stanley 2011), and predation rates on artificial shrub nests did not vary significantly with fragment size or distance from the forest edge (Hanson et al. 2007). Carlson and Hartman (2001) recorded higher predation rates on artificial eggs inside intact forests compared to fragment edges in the Udzungwa Mountains, another Eastern Arc mountain in central Tanzania, while in the lowland Kakamega forest of Western Kenya, a weak classic edge effect was found. However, the largest and least disturbed forest remnants of Kakamega showed the highest (not lowest) predation rates (Maina and Jackson 2003). In conclusion, Afrotropical studies on natural or artificial nests hardly support the classic effects of forest fragmentation on nest predation.

Apart from fragmentation effects, nest predation rates have also been shown to heterogeneously vary with nest concealment, nest height, canopy structure (Martin 1992, 1993, Lambert and Kleindorfer 2006, Colombelli-Négrel and Kleindorfer 2009) and timing of breeding (Mezquida and Marone 2001, Peak 2007). Furthermore, they tend to differ among successive stages of the breeding cycle, i.e. egg laying, incubation, and nestling feeding (Peak et al. 2004, Grant et al. 2005, Brawn et al. 2011). While some studies revealed higher predation rates during egg laying (Mezquida and Marone 2001), others held increased parental and nestling activity responsible for the higher rates recorded during the nestling stage (Redondo and Castro 1992, Ibáñez-Álmano et al. 2012). Some studies yet found even more complex temporal relationships, such as decreased predation rates during egg-laying, increased rates during incubation, and decreased rates after hatching (e.g. cubic or saw-tooth relationships; Grant et al. 2005, Low and Pärt 2009). These variable patterns not only reflect underlying variation in the abundance, activity patterns or prey selection of predators, but may also relate to shifts in predators response due to parental behaviour. Such variation hence pleads for the study of predation rates on natural – rather than artificial – nests to comprehend patterns in nest predation.

In this study, we analysed predation rates on natural nests of Cabanis's Greenbul (*Phyllastrephus cabanisi*) during three consecutive breeding seasons in two isolated cloud forest fragments in south-east Kenya. Like most other tropical species, Cabanis's Greenbul tend to lay smaller clutches, incubate their eggs longer, provide longer post-fledgling care, and show higher adult survival rates compared to temperate forest birds of comparable size and ecology (Martin 1996, Stutchbury and Morton 2001; data on Cabanis's Greenbul from Keith et al. 1992, and Callens 2012). Using models that can accommodate spatial and temporal variation in predation risk, we analysed to what extent predation rates vary with distance to the forest edge, concealment, vegetation structure, timing of breeding and breeding stage. Given the strong heterogeneity in strength and direction of the relationships with nest predation emerging from the literature (see higher), we here apply an information-theoretic approach to rank a set of eighteen logistic-exposure models (*sensu* Shaffer 2004), without making *a priori* predictions on single factor effects.

METHODS

Study area

########### Approximate position of figure 1############

The Taita Hills (maximum altitude 2220 m) are located in south-east Kenya (03°20'S, 38°15'E), on the dry Tsavo plains that isolate these hills from other highland blocks by over 80 km in either direction (Lovett 1985, Pellikka et al. 2009, Figure 1). While long (Mar-May) and short (Nov-Dec) rainy seasons alternate within the Intertropical Convergence Zone, mist and cloud precipitation is a year-round phenomenon in the Taita forests (mean annual precipitation ca. 1200 mm; Pfeifer et al. 2011). The verdant Taita Hills constitute the northernmost extension of the Eastern Arc Mountains, and with less than 2% of the original montane forest cover remaining and a loss of over 50% indigenous forest since 1955 (Pellikka et al. 2009), this archipelago is ranked among the most threatened sites in this globally important biodiversity hotspot (Lovett and Wasser 1993, Myers et al. 2000). At present, the Taita Hills cover around 430 ha of indigenous forest, fragmented into three larger forest patches (86-185 ha) and nine tiny remnants (2-8 ha), embedded in a densely populated mosaic of small-scale subsistence agriculture, bushes and exotic plantations (Pellikka et al. 2009). The remaining indigenous forest patches are mostly of a degraded Afromontane type, characterized by *Albizia gummifera*, *Macaranga conglomerata, Newtonia buchananii*, *Phoenix reclinata*, *Strombosia scheffleri*, *Tabernaemontana stapfiana*, and *Xymalos monospora* in the tree layer (Chege and Bytebier 2005, Aerts et al. 2011).

Nest data for this study were collected in two of the larger forest remnants, i.e. Chawia forest (CH, 86 ha) and Ngangao forest (NG, 120 ha), which are the only two reasonably accessible forest fragments where the study species occurs in sufficient large numbers. CH is located at the top of a gently sloping cliff (1470-1600 m), while NG is located ca. 10 km north of CH, on an eastern slope (1700-1952 m) of a north-south oriented mountain ridge. The former forest is considered to be more intensively disturbed compared to NG, due to its long history of forest clearing and strong human-induced disturbance (Beentje 1987, Wilder et al. 1998, Chege and Bytebier 2005, Callens 2012).

Study species

Cabanis's Greenbul (*Phyllastrephus cabanisi s.l.*) is a forest specialist from central- to east-African (sub)tropical lowland to montane moist forest (Keith et al. 1992, Bennun et al. 1996). Within the Taita forest archipelago, the subspecies *P. c. placidus* (sometimes considered as a full species, Placid Greenbul) has been recorded in twelve indigenous forest fragments, The species builds cup-shaped nests at an average height of 1.3 m in shrub, climbers or small tree species such as *Chassalia discolor, Culcasia scandens, Dracaena steudneri* and *Uvaria sp.* The onset of breeding coincides with the start of the short rain season and the breeding season generally runs from mid-October till the end of March (Keith et al. 1992). Most clutches contain two eggs (22 x 15 mm), which are incubated during 17 days and most nestlings fledge after 11-13 days. Based on occasional visual observations and video-recordings at Cabanis's Greenbul nests during 2007-2010 in the Taita Hills (Callens 2012), the following nest predators were encountered: African Goshawk (*Accipiter tachiro*), Black Goshawk *(A. melanoleucus*), Sykes's Monkey *(Cercopithecus mitis albogularis)* and Yellow Baboon *(Papio cyanocephalus*). We refer to Spanhove et al. (2009a) for a more comprehensive list of putative nest predators in the Taita Hills, comprising mammals (rodents, shrews, civets and mongooses), reptiles (snakes) and birds.

Nest monitoring

During three breeding seasons (2007- 2010), six experienced observers searched all suitable habitat and used behavioural clues to locate as many Cabanis's Greenbul nests as possible in both forest fragments. Once detected, nest fate was recorded every third day on average (95% confidence interval: 1-6 days), allowing analysis based on 'daily predation rates' *sensu* Mayfield (1961). Nests observed during the building phase only, or initially detected with fully-grown fledglings expected to fledge the same day were omitted from further analysis. To avoid biases in the calculation of daily predation rates, we censored the final monitoring intervals for five nests that failed due to reasons other than nest predation (mainly abandoned nests).

For each nest, the distance to the nearest indigenous forest boundary was calculated in Arcmap 9.2 (Environmental Systems Research Institute, 1999-2006), using a combination of GPS coordinates (Garmin GPSMAP60CSx, root mean square error of 6m under canopy) and a forest boundary vector layer based on aerial photographs (25.01.2004, Pellikka et al. 2009) and land cover data derived from a SPOT 4 image (15.10.2003, Clark and Pellikka 2009). As deforestation has almost halted in the Taita Hills, these forest boundary data were still sufficiently accurate to calculate distance-to-edges for all nests. Exotic plantations and large open areas within the forest were not considered as indigenous forest. Nest concealment (i.e. percentage covered by foliage at a distance of 1 m) was visually estimated from the four cardinal directions and the average was used in subsequent analysis. Canopy cover was derived from standardised canopy pictures, but this variable was omitted in further analysis as it was confounded with nest concealment (significant higher concealment under an open canopy), because concealment was considered to be the ecological most relevant parameter.

To study temporal variation in nest predation, we used the onset of egg laying in each nest instead of the actual date of the nest monitoring, as the latter was strongly correlated with nest age. The clutch initiation date was inferred as follows (in order of priority): (i) the observation date minus the age of the nestlings when first observed minus the average incubation time (i.e. 17 days) (124 nests; maximum expected error of 2 days); or (ii) the midpoint between the last observation of a nest under construction and the first observation of a nest with eggs; or (48 nests, max. error 4 days) (iii) the midpoint of all observation days of a nest with eggs (assumed to reflect the mid of incubation) minus half of the average incubation time (i.e. 8.5 days) (56 nests, max. error 8.5 days). Clutch initiation dates allowed us to estimate nest ages and were used to assess relationships between the timing of breeding and nest predation.

Statistical analysis

Relationships with nest predation were analysed with logistic-exposure models, which are generalized linear models with binomial distribution and a link function designed for flexible nest predation analysis based on daily predation rates. More specifically, these models account for the fact that survival probability depends on the interval length by defining the logistic-exposure link function as $\ln[\theta^{1/t} / (1-\theta^{1/t})]$, with θ the daily survival rate and t the interval length (in days) between two nest checks (Shaffer 2004). Eighteen *a priori* defined models were constructed in which the explanatory variables were logically grouped according to putative sources of variation (see Table 1 of the results). As such, distance to the forest edge, fragment and their interaction were mostly entered simultaneously, which corresponds with the most likely scenario of fragment-specific edge effects. Similarly, clutch initiation date was grouped with year and their interaction, reflecting different temporal patterns in nest predation between the three successive annual breeding seasons. For the nest age, the inclusion of a quadratic term allowed us to model more complex age- and stage-related patterns in predation as described in the introduction. This limited number of candidate models avoids substantial data dredging which would be a major risk when testing all possible combinations of mean terms and interactions (see Burnham and Anderson 2002). Models were ranked and weighted based on a small-sample information criterion (AICc, Burnham and Anderson 2002), and inference was made from an "unconditional" model derived from the weighted averaging of candidate models (Burnham and Anderson 2002, using the MuMIn package in R (Bartón 2012)). Parameter averaging was based on all 18 *a priori* models ('full method'), which produces unbiased parameter estimates but no variance estimates, or restricted to the models that contain the parameters ('subset method'), where the parameter estimates are typically biased away from zero, but where variances are estimable (Barton 2012). For comparison reasons, we also provide the results of two alternative model selection methods (Online Reference 1).

RESULTS

A total of 228 active nests were monitored (56 nests in 2007-08, 86 nests in 2008-09, 86 nests in 2009-10), of which the majority was discovered at an early stage of nest development (91 in the building stage, 113 in the egg stage and 24 in the nestling stage). Overall, 126 of the clutches were predated prior to fledging. Frequent nest checks resulted in 1134 time interval checks in which the nest fate was recorded. Daily predation rates estimated from logistic-exposure models averaged at 0.038, corresponding with an overall predation rate of 69% (95% confidence interval: 63-75%) over a 30 day interval.

Predation rates strongly varied among nests. The best fitting models comprised both temporal and spatial effects in the fixed part (Table 1), indicating that predation on Cabanis's Greenbul nests differed between both fragments and varied with the combined effect of clutch initiation date and distance to the edge. At a finer spatial scale, concealment also affected nest predation rates, however, only in models that accounted for variation at larger scales (Table

1). Models that contained fewer parameters were less strongly supported by our data, suggesting that nest predation cannot be explained by a few key characteristics. An age-related shift in predation rates was not clearly supported by our data (Table 1). Both a classic p-value based stepwise backward model selection procedure and an automated AICc-based model selection procedure resulted in a comparable selection (Online Resource 1), i.e. models that combined temporal and spatial parameters in similar ways.

########### Approximate position of Table 1############

The averaged model supported an increase in nest predation toward the interior of both forest fragments. In fragment NG, daily predation rates nearly doubled from the edge toward the interior (Figure 2a), while a five-fold increase was detected in fragment CH (Figure 2b). Nest concealment also affected nest predation rates, however, relationships were not consistent in both fragments. In NG, nest predation decreased with increasing concealment (Figure 2c), while in CH, an opposite pattern was found (Figure 2d). In NG, nest predation rates tended to be equally affected by vegetation structure as by edge effects (both showed approx. a twofold change). In CH, predation rates increased only three times from least to the best concealed nests, compared to five times due to inverse edge effects. In both fragments, timing of breeding had the strongest effect on nest predation: nests initiated early in the breeding season had a higher probability to become depredated compared to later ones (Figures 2e and 2f). However, this pattern strongly varied between years as shown by a tenfold decrease in the first year compared to a very weak trend in the last one.

########### Approximate position of Figure 2############

DISCUSSION

Results from this study show that on average 69% of all initiated clutches of Cabanis's Greenbul were depredated at the egg or nestling stages. This rate corresponds well with the average predation rate on tropical birds (Robinson et al. 2000, Stutchbury and Morton 2001). Within the Taita Hills, nest predation rates were highly variable in space and time. Rates consistently increased from the forest edge toward the interior, a finding that strongly opposes the predictions from 'classic' edge effects on nest predation (*sensu* Gates and Gysel 1978, Lahti 2001). Higher predation in the forest interior rather supports the notion of an 'inverse' edge effect, as earlier observed on nests of the White-starred Robin (*Pogonocichla stellata)* in the Taita Hills (Spanhove et al. 2009a), and of a small number of other species elsewhere (Lahti 2001, Newmark and Stanley 2011).

Inverse edge effects on nest predation can be caused by (at least) two different mechanisms. First, relaxed predation rates near forest edges may reflect low local abundances of native (ground-dwelling) nest predators, possibly due to competition from, or predation by, domestic or feral predators (Maina and Jackson 2003). At the same time, meso-predator release (*sensu* Crooks and Soulé, 1999) due to the loss of primary predators from small or degraded forest fragments may cause high predation rates in the forest interior, the combined effect of which may result in inward (rather than outward) gradients in predation risk. While domestic dogs were abundant near forest edges in our study area, their impact on predator populations of Cabanis's Greenbul (presumed to be mainly arboreal) remains unknown.

Alternatively, inverse edge effects may result from a preference for interior forest habitat by nest predators, either because of higher habitat quality, lower human impact, or both (Carlson and Hartman 2001, Spanhove et al. 2009b). We assume that for Cabanis's Greenbul, such mechanism is more likely to explain the observed pattern in nest predation, as the only predators confirmed from visual observations and video-taping (two raptors, African and Black Goshawk, and two monkeys, Syke's Monkey and Yellow Baboon) were mostly recorded in the interior of indigenous forest fragments, and monkeys are frequently chased by farmers surrounding the fragments. While forest-restricted predators may cause inverse edge effects on nest predation, such patterns can be expected to be masked due to predation by matrix and edge-associated predators, especially by corvids (Nour et al.1993). The lack of significant numbers of corvids in and around Afrotropical forests may hence be responsible for the lack of support for classic edge- and fragmentation effects on nest predation. Formal discrimination between these alternative mechanisms, however, requires targeted population studies on a wider suite of nest predators.

Irrespective of these (or other) underlying mechanisms, strongly reduced levels of nest predation in more degraded forest patches or closer to forest edges may ultimately result in increased (rather than decreased) breeding success of small forest passerines in severely fragmented landscapes (Spanhove et al. 2009a). Such counter-intuitive process may (partly) explain the observed increase in the effective size (N_e) of Cabanis's Greenbul populations in forest CH over the last decade, while no such increase was inferred in the more pristine forest NG (analyses based on microsatellite genotypes sampled between 1996-2010; Callens 2012). Similarly, such processes may also explain why predation rates in the Taita Hills were two times lower than those recorded in continuous Usambara forest, and nearly six times lower than in Usambara's forest fragments (Newmark and Stanley 2011). Although the overall forest type is comparable between both areas, the Taita Hills forest suffered from stronger fragmentation, resulting in much smaller forest remnants. Such differences at the landscape-scale may thus trigger avian communities within forest patches (see also Lee et al. 2002).

Apart from edge-related variation, predation rates in fragment NG were also lower in more concealed nests, most likely because visual, chemical or auditory cues that attract nest predators were more strongly masked (Martin 1993, Caro 2005, Colombelli-Négrel and Kleindorfer 2009). Surprisingly, however, an opposite trend was observed in fragment CH, where more strongly concealed nests suffered from higher predation levels. Such unexpected effect may result from the fact that high levels of nest concealment are often indicative of dense understory habitat, where nest predators such as rodents and shrews can thrive. Abundances of these species have been shown to be higher in CH compared to NG (Odhiambo 2000, Oguge et al. 2004), although evidence for nest predation by either of them is currently lacking, nor do we have accurate density estimates to directly test this hypothesis.

Beside spatial variation, predation rates on Cabanis's Greenbul nests also showed strong temporal variation, both within and between breeding seasons. The most striking finding was a steep decrease in predation rates during the course of the first two breeding seasons, while no obvious differences were detected between predation in the nestling stage compared to egg stage. Temporal shifts in predation are widely documented in the literature, both with increasing (e.g. Mezquida and Marone 2001, Grant et al. 2005, Peak 2007) and decreasing (e.g. Peak 2003, Shustack and Rodewald 2011) predation rates in the course of a breeding season, revealing a plethora of possible differences between egg and various nestling stages (e.g. Martin 1992, Peak et al. 2004, Grant et al. 2005, Brawn et al. 2011, Ibáñez-Álmano et al. 2012). Without in-depth insights into the predator community dynamics, however, attempts to explain these patterns typically involve post-hoc reasoning and would remain highly speculative in this case study. Characteristics of the landscape structure (e.g. the extreme levels of habitat fragmentation) and behaviour of the Cabanis's Greenbul (e.g. the cooperative breeding behaviour or the lack of begging behaviour of nestlings) may further have shaped to the observed patterns of nest predation. Even without a full understanding of the underlying processes, detailed predation studies based on natural nests such as this one remain highly needed to document the worldwide variability in nest predation patterns, and combining multiple studies in meta-analysis may allow us to draw conclusions on the role of behaviour, landscape and nest characters (e.g. Batáry and Báldi 2004, Vetter et al. 2013).

Spatial and temporal variation in the strength or direction of relationships with nest predation suggests that predator communities, predator densities, or predator strategies may vary in space and time. As an example, for generalist (omnivorous) predators that also feed on fruits and seeds, phenological differences in fruit setting between fragments and years, a well-known phenomenon in tropical fragmented landscapes (see Lehouck et al. 2009 for a study in the Taita archipelago), may affect their dependency on eggs or nestlings. Complex and variable relationships with nest predation, such as demonstrated here, suggest that several underlying mechanisms may interact and imply that fixed nesting strategies may have variable (and even opposing) fitness effects between years and habitats. In particular, the opposite influence of concealment on nest predation between the two fragments prevents us from defining general guidelines on forest management to safeguard the reproduction of forest birds. Yet, our results consistently identified forest edges as low-predation zones for a shrub-nesting bird species, and this finding should be considered when drawing conservation plans for fragmented Afrotropical forest.

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TABLES

Table 1. Fit statistics of eighteen *a priori* defined statistical models that explain spatial and temporal variation in daily predation rates on Cabanis's Greenbul nests in two cloud forest fragments. Models are compared based on the number of parameters (k), an information criterion corrected for sample size (AICc), difference in AICc from the most parsimonious model (ΔAICc), and model weight (W_j) indicating the relative support for each model.

Model	*k*	*AICc*	*ΔAICc*	W_j
Landscape [a] + Timing [b] + Concealment [c]	11	740.30	0.00	0.40
Landscape [a] + Timing [b]	9	740.73	0.43	0.32
Landscape [a] + Timing [b] + Concealment [c] + Stage [d]	13	741.65	1.35	0.20
Fragment	2	746.53	6.23	0.02
Landscape [a]	4	746.61	6.31	0.02
Landscape [a] + Concealment [c]	6	746.73	6.43	0.02
Landscape [a] + Stage [d]	6	747.54	7.24	0.01
Landscape [a] + Concealment [c] + Stage [d]	8	747.73	7.43	0.01
Distance_to_Edge	2	752.02	11.72	0.00
Nest_Age	2	756.75	16.45	0.00
Clutch Initiation Day	2	757.54	17.24	0.00
Null Model	1	757.68	17.38	0.00
Stage [d]	3	757.94	17.64	0.00
Concealment	2	759.58	19.28	0.00
Concealment + Stage [d]	4	759.92	19.62	0.00
Year	3	760.48	20.18	0.00
Timing [b]	6	762.55	22.25	0.00
Timing [b] + Concealment	7	764.34	24.04	0.00

[a] comprises FRAGMENT, DISTANCE_TO_EDGE, and the two factor interaction

[b] comprises CLUTCH_INITIATION_DATE, YEAR and the two factor interaction

[c] models with LANDSCAPE and Concealment effects include the FRAGMENT x Concealment interaction

[d] comprises NEST_AGE and its quadratic factor

FIGURE CAPTIONS

Fig. 1 Land cover map of the Taita Hills study area above 1300m asl, SE Kenya (b), showing indigenous forest, plantation, bushland (inclusive small tree patches) and the matrix of urban and agricultural land. Failed and successful nests are indicated on the detailed maps of Ngangao (a) and Chawia (c) forest fragment

Fig. 2 Daily predation rates on Cabanis's Greenbul nests in relation to (i) distance to forest edge in fragment Ngangao (a) and Chawia (b); (ii) nest concealment in fragment Ngangao (c) and Chawia (d); and (iii) clutch initiation date in fragment Ngangao (e) and Chawia (f). Estimates (and 95% confidence interval) are based on partial effects of the 'subset'-averaged model and restricted to the observed range of the explanatory variable

FIGURES

Figure1

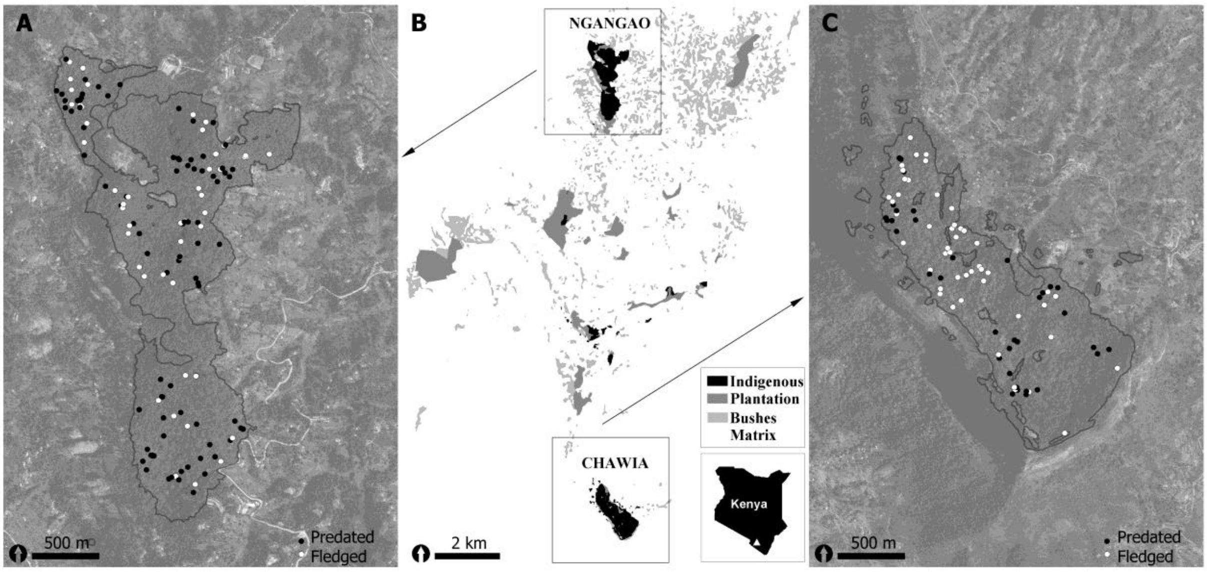
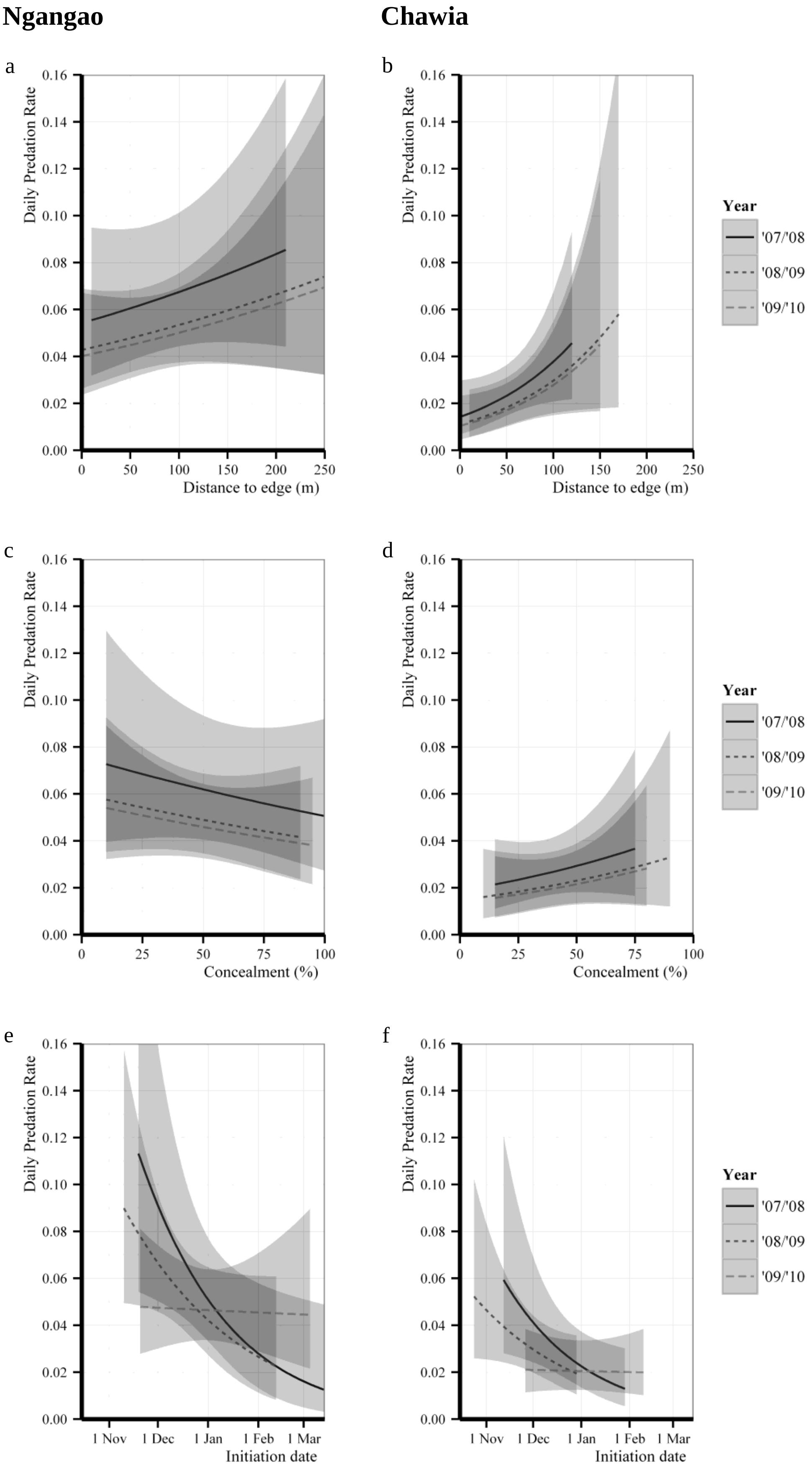


Figure 2.


Ngangao
Chawia
a
b
c
d
e
f
Daily Predation Rate
0.00
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Distance to edge (m)
0
50
100
150
200
250
Concealment (%)
0
25
50
75
100
Initiation date
1 Nov
1 Dec
1 Jan
1 Feb
1 Mar
Year
'07/'08
'08/'09
'09/'10

Figure

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