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Running head: Nest-site selection in degraded cloud-forest

Flexible nest-site selection under anthropogenic habitat change in an Afrotropical understorey insectivore

DRIES VAN DE LOOCK,^{1,2,3} * DIEDERIK STRUBBE,¹ KOEN W. THIJS,⁴ THOMAS VAN DE PEER,⁴ LIESBETH DE NEVE,¹ MWANGI GITHIRU,^{3,5} ERIK MATTHYSEN² & LUC LENS¹

¹ *Terrestrial Ecology Unit, Ghent University, K. L. Ledeganckstraat 35, 9000 Ghent, Belgium*

² *Evolutionary Ecology Group, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Wilrijk, Belgium*

³ *Department of Zoology, National Museums of Kenya, P.O. Box 40658-00100, Nairobi, Kenya*

⁴ *Division of Forest, Nature and Landscape, University of Leuven, Celestijnenlaan 200 E, Box 2411, 3001 Leuven, Belgium*

⁵ *Wildlife Works, P.O. Box 310-80300, Voi, Kenya*

* Corresponding author: dries.vandelooock@ugent.be

Human activities impact upon natural habitats used by birds for breeding and foraging, and lead to changes in the composition and spatial distribution of predator communities, mainly through loss, fragmentation and disturbance of formerly pristine habitat. Yet possible fitness consequences of such

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changes through impacts on bird nest-site selection remain poorly known. Here we study nest-site selection and reproductive success of Placid Greenbuls *Phyllastrephus placidus* in the Taita Hills, SE Kenya. We show that habitat features associated with nest-site selection by this insectivorous, open-cup nesting bird species vary among forest fragments that are exposed to different levels of habitat disturbance. Such differences in sites selected for breeding result from a plastic response to fragment-specific conditions, or may be driven by fragment-specific variation in the distribution and availability of certain habitat features. Given the overall high nest predation rates in our study area, we expected variation in nest-site selection to correlate with reproductive success and nestling condition, but detected no such relationships. Because predator density and nest predation rates may vary strongly in space and time, a better understanding of spatio-temporal variation in predator communities is needed to assess the possible adaptive value of nest-site selection strategies for reducing the high predation rates that are typical for this, and many other open-cup nesting tropical passerines.

Keywords : Cabanis's Greenbul, habitat disturbance, forest degradation, cooperative breeding, nest predation, cloud-forest

The fitness of an individual strongly depends on its reproductive strategy (Morris 1989, DeCesare *et al.* 2014, Losier *et al.* 2015), and factors affecting nest site selection are therefore likely to be under selective pressure (Martin 1998, Chalfoun & Schmidt 2012). Predation on eggs and nestlings is a major cause of reproductive failure in birds (Wilcove 1985), particularly in open-cup nesting passerines, where up to 80% of nest-losses can be attributed to predation (Ricklefs 1969, Martin 1993, Ibáñez-Álamo *et al.* 2015). Open-cup breeders are hence expected to select 'safe' nest sites that are less likely to be detected by - or accessible to - predators (Martin & Roper 1988, Eggers *et al.* 2006, Chalfoun & Martin 2009, Latif *et al.* 2012). For example, dense tree foliage may hinder the transfer of auditory, olfactory and visual cues, and hence reduce the likelihood of nest detection (Martin & Roper 1988, Liebezeit & George 2002, Borgmann & Conway 2015).

Because birds are known to trade off current reproductive success against their potential for future reproduction (Stearns 1992, Roff 2002), factors other than nest predation risk may drive adaptive nest site selection. For instance, incubating birds may increase their survival by selecting nest sites that allow early visual detection of approaching predators (Miller *et al.* 2007, Magaña *et al.* 2010), or they may require a nesting site allowing them to fulfil their energetic needs under harsh climatological conditions (Conway & Martin 2000, Hart *et al.* 2016). Furthermore, chick development may be improved by nesting in resource-rich areas that may not necessarily coincide with areas of high nest concealment (Chalfoun & Martin 2007, Crampton & Sedinger 2011). Ultimately, avian nest-site selection reflects the interaction between several factors that optimize the trade-off between costs (e.g. nest predation, interspecific competition) and benefits (e.g. access to resources, female survival) of a specific site (Chalfoun & Schmidt 2012).

Natural fluctuations of these factors in space and time (e.g. spatial variation in predation communities or inter-annual variation in food resources) may result in adaptive plasticity in nest-site selection, whereby breeders select different nest sites under different circumstances (Schaefer 1976, Forstmeier & Weiss 2004, Janiga & Višňovská 2004). For instance, under experimentally raised predation pressure, Siberian Jays *Perisoreus infaustus* chose nest sites with greater protective cover (Eggers *et al.* 2006). However, due to anthropogenic activities such as logging and agriculture, natural landscapes may change dramatically through large-scale loss, fragmentation and disturbance of formerly continuous, pristine habitat (Fischer & Lindenmayer 2007, Lindenmayer & Fischer 2007). Such large-scale habitat modification may affect the composition or spatial distribution of predator communities, for example due to changes in core-edge ratios of remnant habitat patches (Saunders *et al.* 1991, Chalfoun *et al.* 2002), while selective tree logging, cattle grazing or the invasion of exotic species may cause further small-scale changes in vegetation structure and micro-climate (Lahti 2001, Chalfoun *et al.* 2002, Robinson & Sherry 2012, Vetter *et al.* 2013). Because such anthropogenic changes in land-use and habitat structure occur much more rapidly than under natural regimes, they may result in non-adaptive nest site selection (Robertson & Hutto 2006) as breeders may experience unfamiliar habitat (e.g. Bowman & Woolfenden 2002) or be faced with novel predators (e.g. Crooks

& Soulé 1999). Due to their high level of habitat specificity, low mobility and confinement to the forest interior, tropical forest understory insectivores are particularly sensitive to these habitat changes (Sekercioglu *et al.* 2002). Yet studies on nest site selection have been biased to the temperate region (Chalfoun & Schmidt 2012), with a marked lack of studies from the Afrotropical region (Deikumah *et al.* 2014, Di Marco *et al.* 2017).

To bridge this knowledge gap, we studied nest-site selection and reproductive success in two populations of a typical understory insectivore, the Placid Greenbul *Phyllastrephus placidus*, that are exposed to different levels of past and current habitat disturbance. Both populations suffer high nest predation rates (up to 70% of nests fail due to predation, Spanhove *et al.* 2014) and nest-site selection may constitute an important mechanism through which individuals reduce predation probability. One population inhabits a moderately disturbed forest fragment of ca. 120 ha characterized by late-succession tree species and limited contemporary human disturbance (forest fragment Ngangao, NG).

The second population is in a heavily disturbed forest fragment of ca. 80 ha that is exposed to ongoing firewood collection and cattle grazing, and characterized by few late-successional trees, but many pioneer species (forest fragment Chawia, CH), Fig. 1; Pellikka *et al.* 2009; Aerts *et al.* 2011). On a larger, landscape scale, this species prefers indigenous forest over exotic plantations, agricultural land and other landscape types (Aben *et al.* 2012), and can hence be classified as a forest specialist which depends on the forest interior for breeding and survival (*sensu* Bennun *et al.* 1996). However, within the sharply defined boundaries of remnant cloud-forest fragments, little is known about how micro-habitat characteristics influence greenbul breeding success. As a forest specialist sensitive to habitat fragmentation and degradation (Bregman *et al.* 2014), such information is especially relevant for guiding conservation actions, particularly where improving habitat quality of extant, remnant patches is more realistic than the establishment of new, sufficiently large and natural forests (Aben *et al.* 2016). Therefore, we first compare nest-site selection within and between populations by comparing environmental variables between nesting sites and randomly chosen sites without evidence of nesting. We focus on habitat variables considered relevant for predator avoidance or resource availability. Second, we use a multi-model inference strategy to assign a probability score to each measured site,

reflecting the likelihood that a certain site will be used as a nesting site based on its environmental characteristics (Nest Site Probability Score: NSPS). We then (1) assess whether reproductive success (i.e. hatching and fledging success) is positively related to NSPS to test our expectation that predation avoidance drives nest-site selection, and (2) assess whether nestling condition is positively related to NSPS to test whether resource access, rather than predation pressure, serves as a prime driver of greenbul nest-site selection.

METHODS

Study species and area

The indigenous cloud-forests of the Taita Hills of SE Kenya (03°20'S, 38°15'E) are part of the Eastern Arc biodiversity hotspot and characterized by exceptionally high levels of both endemism and anthropogenic habitat disturbance (Lovett & Wasser 1993, Myers *et al.* 2000, Burgess *et al.* 2007). These forests have been under pressure since pre-colonial times (Lovett & Wasser 1993), which has resulted in ca. 95% indigenous forest loss across the region (Pellikka *et al.* 2009). At present, 13 indigenous forest patches remain, interspersed by small-scale agro-forestry and exotic plantations (Pellikka *et al.* 2009). These patches all differ in size, level of disturbance and isolation, and nine of them host differently-sized populations of the Placid Greenbul (formerly considered a subspecies of the Cabanis's Greenbul *Phyllastrephus cabanisi*). In the Taita Hills, this medium-sized insectivore either breeds in pairs or in small cooperative groups consisting of the breeding pair and one to five subordinates, of which up to three subordinates may also feed the nestlings (Van de Loock, unpubl. data). As forest specialists (*sensu* Bennun *et al.* 1996), they depend on the forest interior where they nest and forage in the understorey on invertebrate prey (Fry & Keith 2000). The onset of short rains in November dictates the start of the breeding season, which extends until March. Usually two eggs (range: 1-3) are laid in an open, cup-shaped nest, built in the branch fork of a seedling or climber and resembling trapped leaf debris. Eggs are incubated by the female for about 15 days and nestlings fledge 11 (10-13) days later. Natural predation pressure is high, with up to 70% nest failure (Spanhove *et al.* 2014), and fewer than 50% of the fledged young surviving until nutritional independence at about 55 days post-fledging (Van de Loock *et al.* 2017). While the species is

currently not considered at risk in its global distribution range (Least Concern, IUCN 2014), structural body size measurements of the remaining Taita Hills populations suggest the species is stress-sensitive to forest disturbance (Lens *et al.* 1999). In addition, mark-recapture analysis, as well as homing experiments, have revealed low to moderate rates of mobility and among-fragment dispersal (Lens *et al.* 2002, Aben *et al.* 2012, 2014).

Survey and sampling design

We mapped Placid Greenbul nests in two populations (forest fragments CH and NG) from 2006 and monitored these intensively during the 2009/10 and 2010/11 breeding seasons. Upon detection, each nest was visited every fourth day to monitor egg or nestling stages while minimizing disturbance, and tarsus length and body mass were measured when nestlings were nine days old. We randomly selected 113 of 264 discovered nests for environmental measurements (CH: 46 nests; NG: 67 nests), using a stratified approach with respect to the position of each nest relative to the fragment edge or interior.

Next, we selected 99 random sites that had never contained a nest within a 25m radius since 2006 (CH: 38 sites; NG 61 sites; Fig. 1). During 2012, we measured 17 habitat characteristics (Table 1) that we considered relevant for predator avoidance or resource availability within a 10m radius of both nest and non-nest sites, by centring a circular plot ($\pm 314\text{m}^2$) around each nest or the nearest tree for non-nesting sites (nest-patch scale *sensu* Benson *et al.* 2009; Crampton & Sedinger 2011). In addition, we identified the vegetation composition in each plot. To do this, we summed the basal area of all mature tree specimens ($> 5\text{m}$ high) for each individual species within each plot. Next, we conducted a regional (i.e. both fragments combined) Principal Components Analysis on the basal area of a subset of 20 tree species that are forest community indicators within our study area (Thijs 2015). We retained the first three axes (Eigenvalue > 1), cumulatively explaining over 50% of the variation, and calculated the plot scores on each of these axes. Each axis represents a gradient between contrasting forest communities, for instance between pioneer and late-successional forest (Table 1; see supplementary material and Table S1). Detailed descriptions and average values (\pm SD) of each habitat variable are given in Table 1. The average values express the availability of a specific habitat variable to the population in the respective fragment. We calculated F-test statistic for each variable in

function of fragment identity to detect significant differences in availability. From these 20 habitat variables we selected a set of 14 uncorrelated predictor variables to assess if, and to what extent, nest site selection differed between both populations (Overview in Table 1; all Pearson's $r < 0.5$ in either population; Table S2 ; Zuur *et al.* 2010).

Nest site selection

Prior to statistical analysis, all 14 predictors were standardized to a mean of zero and standard deviation of one to make model coefficients directly comparable. Because testing for differences in nest site selection strategies between the two populations would require modelling of 14 two-way interactions with variable 'fragment', we instead opted to create separate statistical models for each fragment. We then compared parameter estimates for each of our predictors in each fragment. We built a full multiple logistic regression model with binomial distribution and logit-link (GLM; nest: 1 vs. non-nest: 0), including all 14 scaled predictors, and adopted an AIC-based multi-model inference approach to quantify the relative importance of each specific habitat feature for nest-site selection. We weighted and ranked all possible models based on a small-sample information criterion (AICc; Burnham & Anderson 2002), and derived 'full' average parameter estimates and 95% confidence intervals ('zero-method' *sensu* Grueber *et al.* 2011) based on a reduced set of models with good empirical support ($\Delta AICc \leq 4$; Burnham & Anderson 2002). Models were run using the MuMIn package in R (Barton 2016). We used Nagelkerke's pseudo R^2 to quantify model explanatory power (Nagelkerke 1991).

Reproductive correlates of nest-site selection

We used the averaged models obtained earlier to predict site-scores in each fragment. This score is the likelihood that, given its habitat characteristics, a site would be selected for nesting and is henceforth referred to as the Nest Site Probability Score (NSPS). We then quantified relationships between NSPS and reproductive success for 60 nests with known breeding outcome (CH: 19 nests; NG: 41 nests). Reproductive success was both measured as 'hatching success' and 'fledging success', which is the probability that at least one egg of a clutch hatches, or fledges, respectively. We do this because the

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effects of nest site selection may vary between stages of the breeding cycle depending on parental behaviour. For example, parents largely remain cryptic during incubation, but visit the nest frequently during nestling provisioning (Roper & Goldstein 1997, Martin *et al.* 2000). We used GLMs with logit link functions and binomial error distributions to model both hatching success and fledging success as a function of NSPS. In both analyses, reproductive success was modelled as a binary variable whereby nests either failed (i.e. no egg hatched or no nestling fledged) or succeeded (i.e. ≥ 1 egg hatched or ≥ 1 nestling fledged). Due to logistical difficulties, we only obtained information on nest-exposure (i.e. the timespan a nest is monitored) of a subset of nests. The outcome of an analysis on this subset, which account for the fact that survival probability depends on the interval length between two nest checks (daily survival rates *sensu* Shaffer 2004), was similar to the results based on simple binary nest fate and are given in the supplementary material (Table S3). This suggests that our models are unbiased with respect to nest-exposure. Finally, we applied a linear mixed model (LMM) to assess relationships between NSPS and nestling Scaled Mass Index (SMI). This index corrects body mass for variation in body size using a linear regression of log-body mass on log-tarsus length estimated by type-2 (standardized major axis) regression, and is a reliable proxy of organismal health and fitness (Peig & Green 2010). Tarsus length was strongly correlated with body mass on a log-log scale ($r = 0.88$, $p < 0.001$), and we obtained a regression slope of 1.59 and average tarsus length of 24.01 mm for SMI calculation after excluding one outlier (i.e. $|\text{standardized residual}| > 3$). We thus calculated the SMI as $\text{body mass} \times (24.01/\text{tarsus length})^{1.59}$ (Peig & Green 2009, 2010). Because only a minority of nests successfully fledged, sample sizes for this model were reduced (CH: 7 nests, 12 nestlings; NG: 17, 30).

For each analysis on hatching success, fledging success, and nestling condition, we weighted and ranked three a priori models based on AICc. We defined the following models with success or SMI as dependent variable and (i) fragment, (ii) fragment + NSPS, and (iii) fragment \times NSPS (i.e. the interaction between both variables) and its main effects as predictor variables. We added year as a categorical variable in all models to control for any factor that may affect reproductive success or SMI between years, and brood size in the SMI-models only, to control for the effect of brood size on SMI.

We also added nest identity as random factor in the SMI-models, to account for non-independence of siblings. We used Nagelkerke's pseudo R^2 (GLM) and marginal R^2 (LMM) to quantify model explanatory power (Nagelkerke 1991, Nakagawa & Schielzeth 2013). LMM models are fitted by maximum likelihood (ML) with Satterthwaite approximated denominator degrees of freedom using the 'lme4' package in R (Bates *et al.* 2015). Plots of fitted values against residuals indicated that normality or homoscedasticity assumptions were not violated. All analysis were performed in R 3.3.3 (R Core Team 2017). Data are available from the Dryad Digital Repository: <http://dx.doi.org/xxxx>.

RESULTS

The two forest fragments (CH and NG) differed significantly for most of the 14 habitat variables (Table 1, Fig. 2; only concealment opportunities, tree height, the amount of dead wood, the sapling Shannon diversity and Vegetation Composition PC2 did not differ). In both forests, Placid Greenbul nest sites were significantly better concealed than randomly selected sites, and there was a non-significant tendency for nests to occur in areas with lower amounts of dead wood (strongest in CH, where zero was only marginally included in the 95% CI; Fig. 2, Table S4). In NG, individuals nested at sites with significantly taller trees and showed a non-significant tendency to nest further from the indigenous forest edge and selected sites (Fig. 2, Table S4). In CH, there was a non-significant tendency to nest in areas characterized by a higher abundance of plants typically used as nest substrates (Fig. 2, Table S4). Our models explained jointly up to 50% (CH) and 35% (NG) of the variation in nest-site use (Nagelkerke's pseudo R^2 of the most explanatory model in the $\Delta AICc \leq 4$ model subset; Table S5).

Overall, 58% (35 out of 60 nests) of our randomly selected Placid Greenbul nests failed before fledging, of which 74% (26 out of 35 nests) failed before hatching. Predation was the main cause of nest failure (88%), while the remaining brood failures were due to nest abandonment (i.e. containing cold eggs or dead nestlings) for unknown reason. Variation in NSPS (Nest Site Probability Score) did not explain variation in hatching or fledging success, also not in interaction with forest fragment (low AICc support and zero included in the 95% CI of the parameter estimates; Table 2). Nest success did

not differ between both populations, but varied among years (Table 2). Our models explained up to 7% and 18% of variation in hatching or fledging success, respectively (Nagelkerke's pseudo R^2 of the most explanatory model; Table 2). Likewise, variation in nestling condition (SMI) was not explained by variation in NSPS, nor did we detect an interaction between NSPS and forest fragment (Table 3). SMI only varied with brood size, but not among years or populations (Table 3) and our models explained up to 19% of the variation (marginal R^2 values of the most explanatory model; Table 3).

DISCUSSION

Nest site selection constitutes a central life-history event in tropical birds and may strongly affect individual fitness. Yet, compared to temperate species, few studies so far have assessed how and to what extent tropical birds cope with anthropogenic habitat disturbance through nest-site selection strategies. Here, based on two years of breeding monitoring of the Placid Greenbul, a typical understory insectivorous species of the East-African Taita Hills, we found that Placid Greenbuls from two populations inhabiting fragments differing in their degree of anthropogenic disturbance use nest sites that differ in habitat characteristics. Given the generally high predation pressure in the study area, we expected nest-site selection to be primarily driven by anti-predation strategies. However, we found no evidence that nests at sites more likely to be used for breeding experienced lower predation rates, and nor did these nests produce nestlings in better condition.

As open-cup nesters generally benefit from greater nest concealment (Liebezeit & George 2002, Remeš 2005), Placid Greenbuls may be expected to prefer to nest at sites offering well vegetated and leafy cover, as in dense, shrubby areas. Such areas are typically patchily distributed in forests with an intact canopy layer, whereas (selective) logging that causes thinning of the canopy layer often results in a more uniform, dense understory scrub layer due to increased light penetration (Fredericksen & Mostacedo 2000, Marsden *et al.* 2002). These structural changes are often accompanied by shifts in the species community, whereby some species increase in abundance at the cost of others (e.g. Sagar *et al.* 2003). In the most disturbed fragment (CH), species of understorey plant previously found to be typical nest substrates for the Placid Greenbul (notably *Dracaena steudneri*, Table 1, Table S6) may

attain high local densities under these disturbed conditions (represented by high average value in CH only; Table 1, Fig 2). Apart from offering a concealed nesting site, the high local density of these nest-substrate plants creates an area with many potential nest sites. Because many potential nest sites might reduce the search efficiency of predators, nesting at such sites may help reduce predation risk in this heavily disturbed fragment. Predation risk can also be reduced by avoiding areas with abundant dead wood, as woody debris is used by predatory small reptiles and mammals for denning and nesting (Harmon *et al.* 2004). Indeed, camera-trap recordings of rodents near nests and encounters of egg-predating snakes in our study area (Van de Loock & Bates 2016) indicate that woody debris can act as shelter for greenbul nest predators. Together, the fact that in both study areas, the nest sites of this species are characterized by a greater concealment and a lower prevalence of dead wood is in line with our expectation that Placid Greenbuls may nest at sites likely to reduce predation risk, irrespective of the overall degree of habitat degradation of the forest fragment they inhabit.

The main difference in nest site selection between our study populations is that greenbuls only favoured nesting at sites with taller trees and further away from the indigenous forest edge in the least disturbed fragment (NG; Fig. 2). Traditional silvicultural practices involve harvesting tall, valuable and easily exploitable trees and (re-)planting fast- and often tall-growing exotic species (Lamprecht 1989). In heavily disturbed habitat such as fragment CH, tall trees might therefore represent both (for foresters invaluable) indigenous left-over trees as relicts from past, more pristine conditions (e.g. Schlawin & Zahawi 2008), as well as long-established exotic species. Indeed, tall stands of exotic *Eucalyptus* are more prevalent in fragment CH (Pellikka *et al.* 2009, Omoro *et al.* 2010). This suggests that tall trees might not be indicative of favourable greenbul nesting or foraging habitat in such heavily disturbed habitats (Gray *et al.* 2007, Johnson 2007). In addition, another consequence of severe habitat modification is its effect on the spatial distribution of predator communities (Saunders *et al.* 1991, Chalfoun *et al.* 2002). For instance, forest-dependent nest predators of greenbuls may prefer the forest interior of small patches because of a higher habitat quality, lower human impact, or both (Carlson & Hartman 2001, Spanhove *et al.* 2009). Under these conditions, greenbuls nesting in the centre of a remnant forest fragment might become prone to more nest failure because of predation

(‘inverse edge effect’ Lahti 2001, Vetter *et al.* 2013), a pattern which has indeed been reported earlier for our study areas (Spanhove *et al.* 2014). This inverse edge effect implies that in fragment NG, where greenbul nests were more likely to be found further from the edge, breeding birds may potentially be exposed to a higher, not lower, predation risk. In contrast, because the vegetation structure of fragment CH is severely altered and resembles edge habitat throughout the fragment, greenbuls from fragment CH may no longer rely on such structural habitat variables. However, given that in our study area only two larger fragments can be compared, we cannot definitively rule out that observed differences in nest-site selection between both study populations are a consequence of a differing availability of certain habitat features between the forest fragments (Sih *et al.* 2011, Tuomainen & Candolin 2011), rather than resulting from a plastic response to fragment-specific conditions.

Although we found clear evidence that in both forest fragments, greenbul nests are not placed randomly with respect to available habitat variables, we did not find evidence for any relationship with our fitness indicators (i.e. reproductive success and nestling condition). While we cannot dismiss the possibility that we failed to include potentially important habitat variables that might be used by Placid Greenbuls to select nesting sites (pseudo R^2 of the nest-site selection models only ranged from 0.35 (NG) to 0.50 (CH)), we suggest two specific possible causes that may obscure the relationships we hypothesized. First, nest predation is a highly stochastic event (e.g. Wilson & Cooper 1998, Githiru *et al.* 2005, Vigallon & Marzluff 2005), and larger sample sizes may be required to uncover more subtle relationships between nests selected and predation rates experienced. Second, it is likely that individuals may detect, and respond to, variation in perceived predation pressure (e.g. Eggers *et al.* 2006). This may be a contributing factor in the Taita Hills as well, as Spanhove *et al.* (2014) found that greenbul nest predation rates can vary in space and time. Hence, we require more detailed information on predator presence and phenological factors such as timing of nest initiation, for a more robust test on the adaptive value, if any, of greenbul nest-site selection.

More generally, a failure to detect strong relationships between nest-site selection and reproductive success is commonly reported in literature (see Chalfoun & Schmidt 2012). Therefore, we here propose four mechanisms that should be taken into consideration by future studies of the breeding ecology of Placid Greenbuls and other tropical open-cup nesting passerines. First, parents may actively deter predators and thereby compensate for poor nest concealment, allowing successful breeding in predator-rich environments (Andersson *et al.* 1980, Weidinger 2002, Remeš 2005, Merrill *et al.* 2016). This may, in particular, be the case for cooperative breeders, where subordinates assist in protecting offspring against predators before and after fledging (Mumme 1992, Innes & Johnston 1996, Riehl & Jara 2009). In the Taita Hills, Placid Greenbuls display a facultative cooperative breeding strategy with up to five subordinates, and fledglings raised in larger groups have previously been shown to have a higher probability of post-fledging survival (Van de Loock *et al.* 2017). Second, as nest predation is highly stochastic, a higher reproductive success might not be achieved by selecting nest sites that reduce predation risk, but rather by reducing re-nesting intervals (Roper *et al.* 2010). This can be a particularly rewarding strategy in long-lived, tropical species with extended breeding seasons, as in our study system, and may hence explain why we observe up to four nesting attempts within one breeding season (Van de Loock, pers. obs.). Third, optimal nest site selection may be constrained by the fact that territories or home ranges are primarily selected to fulfil year-round nutritional needs and survival probability of the parents (or cooperative flocks) at larger spatial and temporal scales (hierarchical process *sensu* Wiens, Rotenberry & Horne 1987; Chalfoun & Martin 2007 ; Orians & Wittenberger 1991; Cornell & Donovan 2010). Fourth, variation in hunting strategies among different predator guilds can mask relationships between nest success and nest-site characteristics. For instance, nest sites may be optimized to match the hunting strategies of the predominant predator in one area, but be optimized differently to match different predators in another (Santisteban *et al.* 2002, Schmidt *et al.* 2006, Benson *et al.* 2010). In addition, high local densities of nests at preferred sites may facilitate nest predation as predators may learn cues and develop targeted hunting strategies (Pelech *et al.* 2010, Weidinger & Kočvara 2010).

In conclusion, while anthropogenic habitat change and disturbance can influence reproductive success of bird populations through several mechanisms, possible consequences of such changes through impacts on nest-site selection are not yet fully understood (Robinson & Sherry 2012, Ibáñez-Álamo *et al.* 2015). Here, we report differences in nest-site selection between populations inhabiting forest fragments differing in the degree of anthropogenic disturbance, but conclude that more research is needed to disentangle possible underlying drivers, as discussed above. In particular, we propose a better understanding of the spatio-temporal variation in predator communities would be a first important step to identify the underpinnings of nest-site selection strategies of this, and other tropical passerines (Lima 2002).

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Tables and Figure

Figure 1. Map of the Taita Hills (SE Kenya), indicating the location of the indigenous forest fragments (black), the largest town (Wundanyi) and the 1500m a.s.l altitudinal zone (grey contour line). Nest sites (●) and random, non-nest sites (○) are indicated for both studied populations from Ngangao forest fragment (NG, moderately disturbed) and Chawia (CH, heavily disturbed).

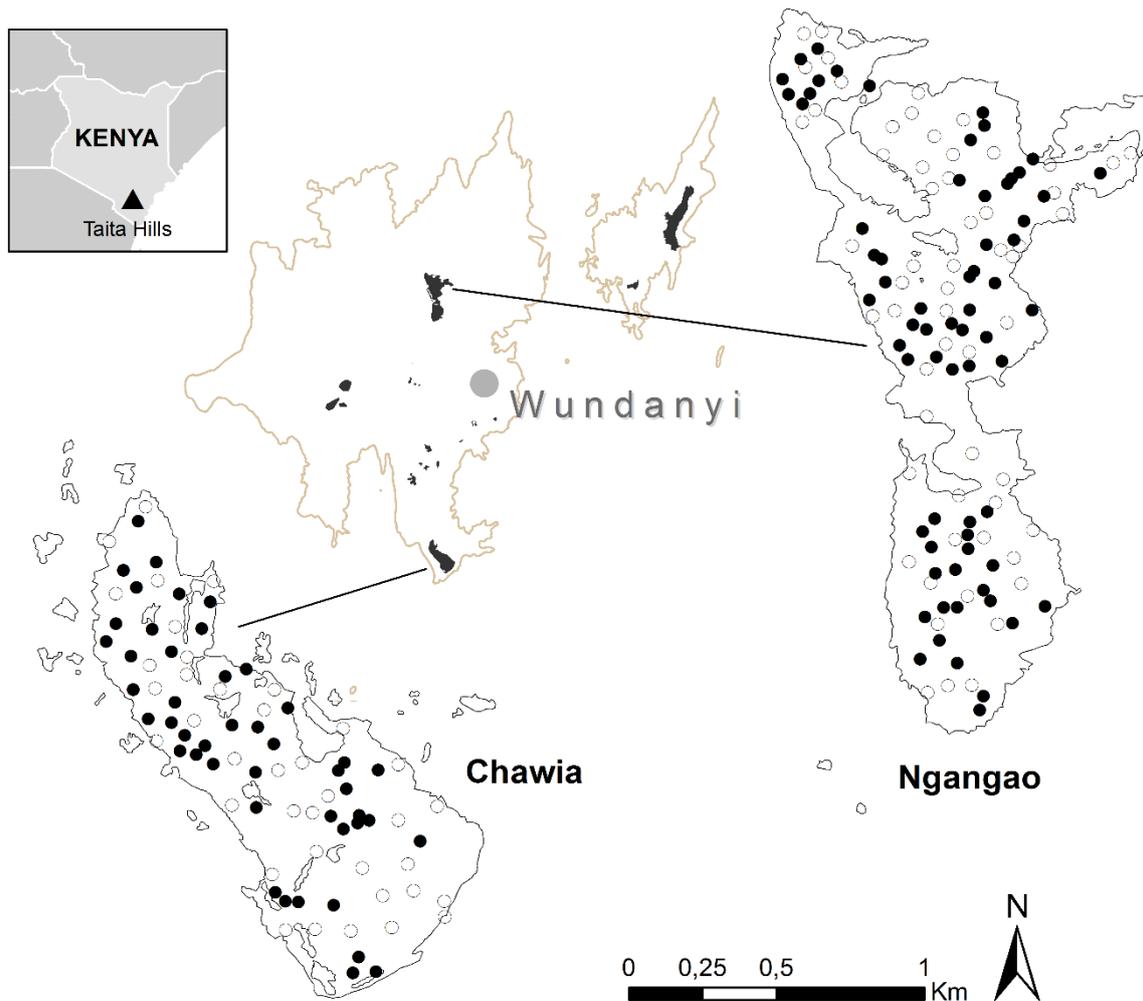


Figure 2. Nest-site Selection (left panel). Placid Greenbul nests were more (+, right from dotted line), or less (-), likely to be found at specific habitat features in both a heavily disturbed (CH) and moderately disturbed (NG) forest fragment. Values (symbols) represent model-averaged parameter estimates and 95% CI (lines). **Habitat values** (right panel). Relative availability of all habitat in both fragments. Boxplots visualize the median, the first and third quartile; the whiskers extend to 1.5 * Inter-quartile range and values beyond this range are considered outliers and not plotted to improve visibility. Values standardized and centred ($x - \text{mean} / \text{SD}$), and differences ($p \leq 0.05$; F-test) in availability (average value) between both forest fragments are denoted by *.

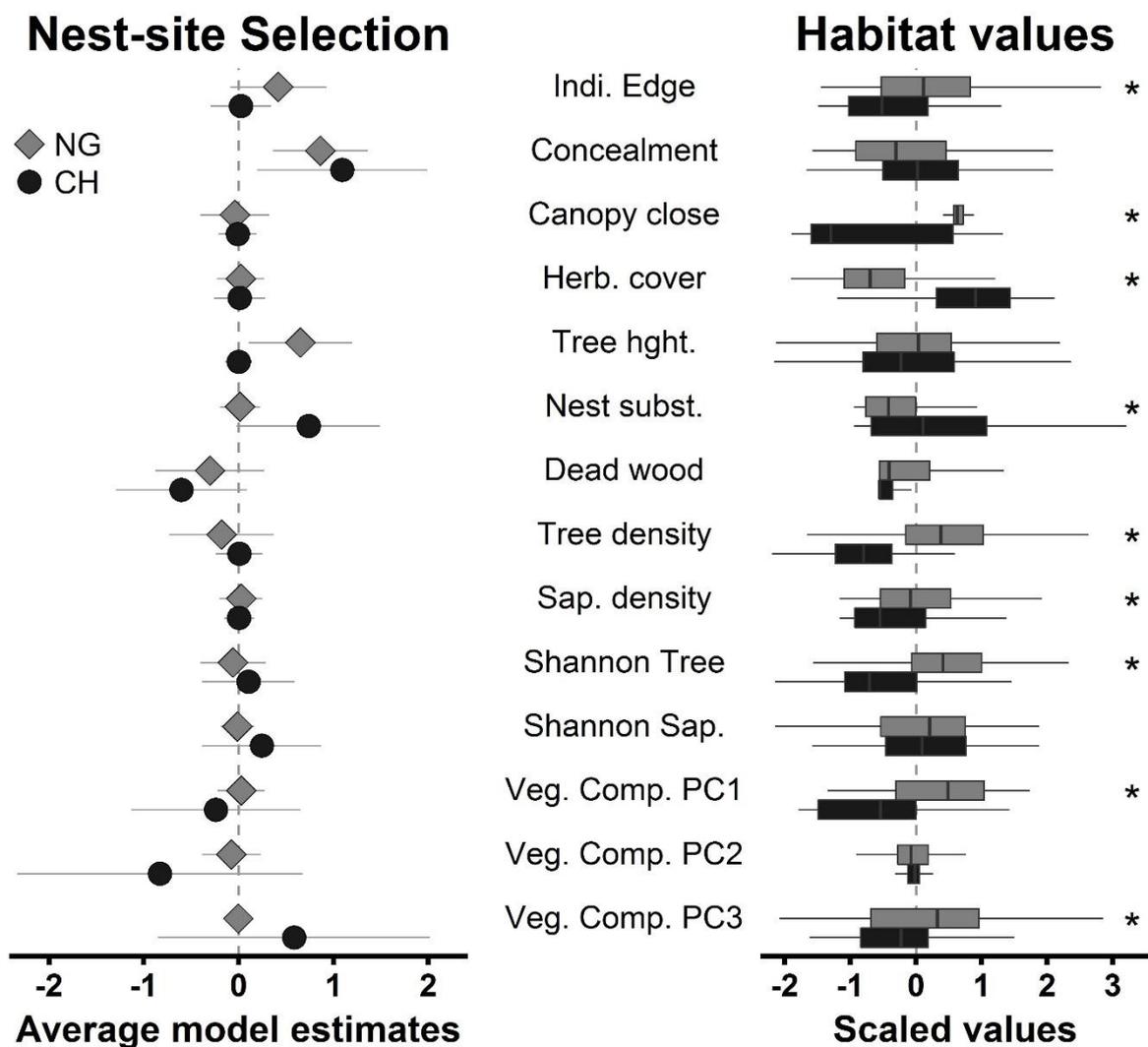


Table 1. Habitat variables measured at (113) nest-sites and at (99) randomly selected non-nest sites of two Placid Greenbul populations from a heavily disturbed (CH) and moderately disturbed (NG) forest fragment. Out of 20 habitat variables, 14 uncorrelated variables are retained as nest-site predictors (marked by a filled circle; ●). Average values \pm SD over all nest and non-nest sites combined indicate the availability and distribution of each habitat feature. Differences ($p \leq 0.05$; F-test) in average between both forest fragments are noted in **bold**. When applicable, abbreviated names used in Fig. 1 are noted in brackets.

Variable	Unit	Description	Values \pm SD		
			CH	NG	
<i>Variables quantified at the center of the plot</i>					
1	Distance edge	m	Distance from plot centre to the nearest forest edge (measured using ArcGIS 9.2, ESRI, Redlands, CA)	123.35 \pm 74.77	136.74 \pm 73.92
2	● Distance indigenous edge [Indi. Edge]	m	Distance from plot centre to the nearest indigenous forest edge (measured using ArcGIS 9.2)	63.02 \pm 43.58	89.69 \pm 54.44
3	● Concealment	%	Determined by placing the middle of a 0.5 \times 0.5 m ² cover board consisting of 25 squares in front of the nest or between 1 and 1.5 m above the ground for non-nest sites ^a . At 5 m distance, the percentage of the board obscured by vegetation was recorded in four cardinal directions and averaged	38.42 \pm 18.97	33.66 \pm 22.60
<i>Variables quantified at plot level</i>					
4	● Canopy closure	%	Average % closed canopy measured with a spherical densitometer in the four cardinal directions	40.09 \pm 27.75	78.10 \pm 14.66
5	● Herbaceous cover [Herb. Cover]	%	Percentage of the forest floor covered based on 40 systematic presence/absence reading at 1 m intervals from plot centre in each cardinal direction by using an ocular tube ($\varnothing = 9$ mm)	68.27 \pm 19.20	33.69 \pm 17.70
6	Litter cover	%	As above	30.06 \pm 18.41	64.36 \pm 16.78
7	Shrub cover	%	Percentage of the forest floor covered by the vertical projection of shrub crowns	66.44 \pm 14.05	58.70 \pm 17.22
8	● Tree height [Tree hght.]	m	Average height of the three tallest trees, measured with a Suunto inclinometer	25.09 \pm 10.20	25.74 \pm 8.04
9	● Nest substrates [Nest subst.]	#	Number of <i>Dracaena steudneri</i> , <i>Chassalia</i> sp., <i>Uvaria lucida</i> , <i>Landolphia buchananii</i> (Dominant nest substrates during 2007 – 2008 – see Table S6)	22.15 \pm 20.33	12.19 \pm 13.27
10	● Dead wood	m ³ /plot	Total volume of fallen and standing dead wood $V = \pi (DBH)^2 / 4$ with DBH the diameter at breast height for all fallen and standing, respectively, trees	0.60 \pm 1.34	0.70 \pm 1.05

			with a diameter ≥ 12 cm.		
11	Basal area	m ² /ha	Total basal area calculated from DBH of all the mature trees (height ≥ 5 m) in the plot	163.45 \pm 132.93	149.86 \pm 135.40
12	● Tree density	#/ha	Number of mature tree stems	632.64 \pm 325.53	1113.35 \pm 363.94
13	● Sapling density [Sap. density]	#/ha	Number of sapling stems (height < 5 m)	568.31 \pm 614.48	759.32 \pm 559.05
14	Tree species	#	Number of mature tree species	5.70 \pm 2.22	9.61 \pm 2.88
15	Sapling species	#	Number of sapling species	4.68 \pm 2.46	5.36 \pm 2.35
16	● Shannon Tree spec.		Shannon diversity index (H') for mature trees species (≥ 5 m).	0.83 \pm 0.45	1.29 \pm 0.40
17	● Shannon Sapling spec. [Shannon sap.]		Idem for sapling species (< 5 m)	1.19 \pm 0.53	1.31 \pm 0.46
18	● Vegetation composition PC1 [Veg. Comp. PC1]		First axis of a PCA (Principal Component Analysis) on species basal area data to assess gradients in vegetation composition. This axis represents a gradient from typical pioneer species (-) to late successional species (+)	-0.070 \pm 0.11	0.047 \pm 0.10
19	● Vegetation composition PC2 [Veg. Comp. PC2]		Second axis of the PCA. Gradient from interior (-) to edge and gap species (+)	0.010 \pm 0.051	-0.0060 \pm 0.093
20	● Vegetation composition PC3 [Veg. Comp. PC3]		Third axis of the PCA. Gradient from late-successional species found at higher altitudes (-) to species typical for late successional, but lower altitudinal patches (+)	-0.015 \pm 0.043	0.011 \pm 0.075

^a Averaging nesting height : 1.33 \pm 0.59 m (n = 326).

Table 2. Summary of model selection on a set of three a priori Generalized Linear models investigating effect of Nest Site Probability Score (NSPS) on hatching and fledging success (≥ 1 egg hatched or ≥ 1 nestling fledged) of Placid Greenbul nests showing the coefficients with 95% CI on the logit scale.

Model	Intercept	Year ^a	Fragment ^b	NSPS	NSPS \times Fragment	df	R^2 ^c	AICc	Δ AICc
<i>Fledging success</i>									
1	0.40 (-0.71, 1.54)	-1.43 (-2.60, -0.35)	-0.10 (-1.29, 1.09)	--	--	3	0.15	80.1	0.00
2	0.84 (-0.94, 2.72)	-1.35 (-2.54, -0.23)	-0.047 (-1.25, 1.17)	-0.81 (-3.41, 1.76)	--	4	0.15	82.0	1.92
3	-0.36 (-3.33, 2.48)	-1.48 (-2.74, -0.32)	-1.84 (-1.71, 5.61)	1.29 (-3.27, 6.07)	-3.06 (-8.80, 2.37)	5	0.18	83.2	3.09
<i>Hatching success</i>									
1	0.45 (-0.61, 1.57)	-0.66 (-1.72, 0.37)	0.20 (-0.92, 1.32)	--	--	3	0.04	86.8	0.00
2	-0.10 (-1.84, 1.66)	-0.77 (-1.89, 0.30)	0.16 (-0.97, 1.28)	1.00 (-1.45, 3.55)	--	4	0.05	88.4	1.66
3	-1.13 (-4.26, 1.63)	-0.87 (-2.02, 0.23)	1.73 (-1.70, 5.48)	2.78 (-1.61, 7.86)	-2.52 (-8.25, 2.66)	5	0.07	89.9	3.15

^a reference category is breeding season 2009 – 2010, estimated category 2010 – 2011

^b reference category fragment CH, estimated category fragment NG

^c Nagelkerke's pseudo R^2

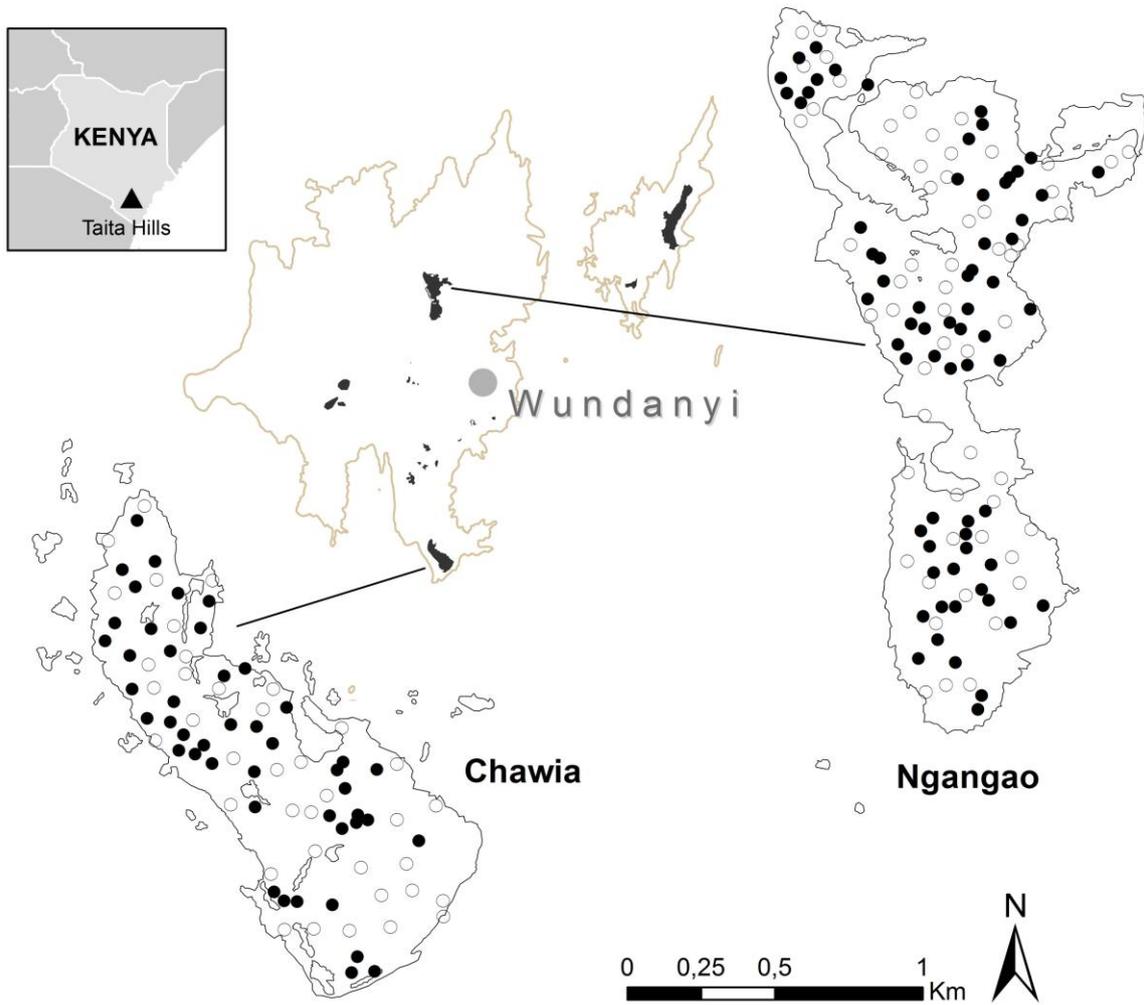
Table 3. Summary of model selection on a set of three a priori Linear Mixed Effect models investigating effect of Nest Site Probability Score (NSPS) on Placid Greenbul nestling scaled mass index (Nestling SMI) showing the coefficients with 95% CI.

Model	Intercept	Brood size	Year ^a	Fragment ^b	NSPS	NSPS \times Fragment	df	R^2 ^c	AICc	Δ AICc
<i>Nestling SMI</i>										
1	20.57 (19.22, 21.92)	-0.77 (-1.42, -0.11)	-0.36 (-1.12, 0.39)	0.48 (-0.23, 1.20)	--	--	6	0.18	122.6	0.00
2	20.53 (19.03, 22.07)	-0.77 (-1.42, -0.11)	-0.36 (-1.12, 0.39)	0.48 (-0.24, 1.20)	0.073 (-1.29, 1.36)	--	7	0.18	125.5	2.88
3	20.45 (18.40, 22.56)	-0.76 (-1.43, -0.09)	-0.37 (-1.16, 0.41)	0.58 (-1.35, 2.49)	0.20 (-2.42, 2.70)	-0.17 (-3.22, 2.91)	8	0.19	128.6	5.94

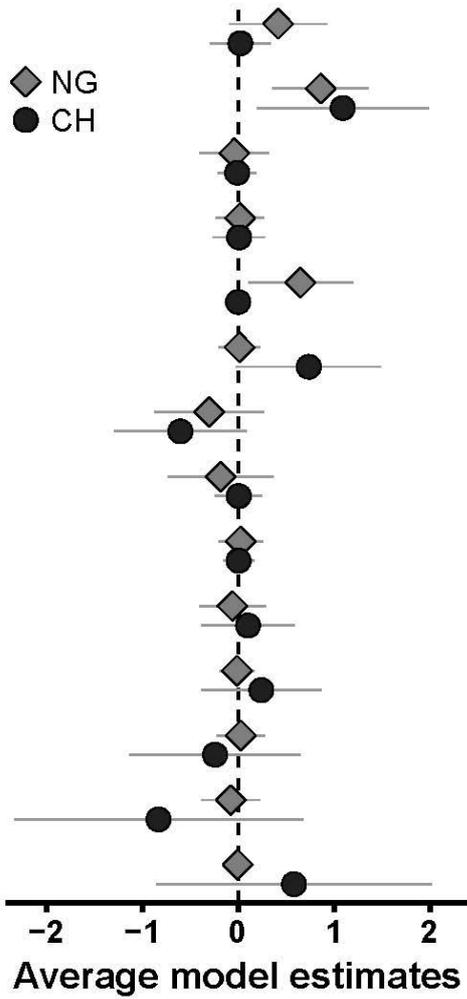
^a reference category is breeding season 2009 – 2010, estimated category 2010 – 2011

^b reference category fragment CH, estimated category fragment NG

^c Marginal R^2



Nest-site Selection



Habitat values

