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The importance of protected and unprotected areas for colony occupancy and colony size in White-necked Picathartes *Picathartes gymnocephalus* in and around Gola Rainforest National Park, Sierra Leone

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Summary

Most attention on tropical biodiversity conservation has focussed on protected areas. Recognising and enhancing the value of biodiversity outside, as well as inside, protected areas is increasingly important given recognition that biodiversity targets will not be met through protected areas alone. We investigated the extent to which protection influences colony occupancy and colony size of a species of conservation concern, the rock-nesting White-necked Picathartes *Picathartes gymnocephalus*. We used mixed models to compare long term trends at 42 colonies located both inside and outside a protected area of forest, Gola Rainforest National Park, and considered colonies further inside the boundary as being better protected. Colony occupation was primarily predicted by the level of protection, with occupation highest within protected areas, but was not different between colonies situated close to or far from the boundary. Mean colony occupation was consistently high in protected areas, and lower in unprotected areas. The surface area of colony rocks was also an important predictor with larger rock faces having a higher probability of occupancy. Our best models also included distance to forested habitat, presence of cleared forest and evidence of hunting as less important predictors. Over the eight-year study, after controlling for rock surface area, active colony size declined significantly. However, declines were only significant in colonies in unprotected forest, whilst colonies located within protected areas were buffered from significant decline. Together this suggests colony occupancy and the number of active nests are influenced by protection and human disturbance. Although a lack of demographic and population dynamic work on picathartes prevents identifying mechanisms, we show that despite unprotected colonies having lower occupancy and fewer active nests they can persist in human altered and disturbed areas, partly because larger traditionally used rocks remain important nesting sites.

Introduction

Protected areas retain a key role for conservation in the tropics (Jenkins and Joppa 2009, Laurance *et al.* 2012) but there is increasing recognition that they will not be sufficient on their own to prevent significant loss of biodiversity. Not only are current targets unlikely to be met through existing protected areas (Tittensor *et al.* 2014, Butchart *et al.* 2015), but it is clear that very many species are not adequately reflected in the protected area network (De Klerk *et al.* 2004, Rodrigues *et al.* 2004). Even for well protected species, substantial parts of their population may still occur in unprotected areas (Swanepoel *et al.* 2013).

The designation of protected areas may lead to increased protection from habitat loss and degradation (Andam *et al.* 2008) but protection from other forms of human disturbance can be much harder to achieve, especially in areas close to the boundary where communities continue to make use of protected forest for subsistence activities such as hunting. Effective protection is often greatest deeper within protected areas compared to their edge (Harrison 2011) although for most species little is known about resilience and persistence in unprotected compared to protected areas, and how this varies in relation to distance from the edge.

Human presence and disturbance is a well recognised threat to many birds of conservation concern across the world, and its impact on populations is well studied (Beale and Monaghan 2004). Human presence can impact birds at the scale of the nest or home range. Impacts can be indirect, altering birds' ability to exploit vital resources by restricting access to resources such as food and nest sites, or direct, altering the quality of resources such as habitat. Colonial nesting birds can be particularly vulnerable to disturbance as nesting sites are typically large and suitable sites are often rare in the landscape leading to colony abandonment if alternative nest sites are not locally available (Carney and Sydeman 1999). This may be exacerbated in habitat specialist species that require connecting habitat and habitat patches of a sufficient size at the territory scale.

Both protected and non-protected areas of rainforest in Western and Central Africa support important populations of both species of Picathartes, White-necked *Picathartes gymnocephalus* and Grey-necked *Picathartes oreas*. Picathartes are ground-dwelling forest birds endemic to the rainforests of Western and Central Africa, which nest on bare rock faces in small colonies (Fry *et al.* 2000). Both species are classified as 'Vulnerable' by the IUCN (BirdLife International 2012) due to having small and highly fragmented populations, and because of the continued loss of their forest habitat. Previous studies of picathartes identify several factors related to human presence and disturbance that have negative effects on colony occupancy and active colony size. These include hunting (Atuo *et al.* 2014), clearance for agriculture (Thompson and Fotso 2000, Asamoah 2011), mining (Asamoah 2011), habitat loss (Awa II *et al.* 2009b), lowered colony activity in unprotected forest (Asamoah 2011, Monticelli *et al.* 2011) and habitat degradation associated with human activity (Thompson 1997). Low breeding success in some studies has also been linked with direct human disturbance (Thompson 1998, Awa II *et al.* 2009b). Despite these negative associations with human disturbance, picathartes are found at unprotected sites heavily modified and used by humans, including sites adjacent to farms (Awa II *et al.* 2009a) and urban areas (Salewski *et al.* 2000, Thompson and Fotso 2000), and have been recorded nesting on human made structures (Christy and Maisels 2007).

Here we investigate the extent to which protection influences colony occupancy and temporal trends in colony size of White-necked Picathartes by comparing long term trends at colonies both inside and outside a protected area. White-necked Picathartes have been monitored at colonies in and around the Gola Rainforest National Park, Sierra Leone, over an area encompassing 700 km^2 of protected forest and a similar area of unprotected forest since 1988. Protection within the national park consists of ranger patrols preventing illegal activities such as logging, farming and hunting. Previous analysis from three years of more comprehensive monitoring of this population between 2006 and 2009 showed that colonies in unprotected forest experienced lower levels of colony activity and were more likely to be unoccupied, although colony activity did not differ between protected and unprotected forest (Monticelli *et al.* 2011). Here we use the same data complemented by a further five years of monitoring data to investigate in more detail factors influencing colony occupancy and longer term change in the size of colonies. We were especially interested to know if colony occupation and temporal trends in active colony size differed across the landscape in relation to the level of protection afforded by the relatively well protected areas of Gola Rainforest National Park compared to unprotected forest. In doing so we gain insights into the value of non protected area landscapes for this species, a first step in assessing the need for other conservation approaches.

Methods

Study area and colonies

Colonies were located within the Gola Rainforest National Park and in surrounding unprotected community forest, Sierra Leone (located between 7°18′ and 7°51′N and 10°37′ and 11°21′W, Figure 1). Gola consists of lowland moist evergreen high forest, which in community forest is fragmented by agriculture, and has an altitudinal range of 70–410 m. Rainfall is mainly seasonal, with the wet season extending from May to October, with annual rainfall of 2,500–3,000 mm. Most colonies were also visited and monitored in earlier work (Allport *et al.* 1989, Thompson 1997, Monticelli *et al.* 2011) with five more recently found colonies additionally included in the present study. A further seven historically used colonies, all located outside the national park, were visited annually but had no active nests found in any year of the study and were omitted from all analyses. Colonies with several different colony nesting rocks < 100 m apart containing nests were considered the same colony.

Colony and disturbance monitoring

Because of the shy behaviour of picathartes and their dense forest habitat, monitoring is most accurately achieved at breeding colonies, which are believed to be used traditionally over many

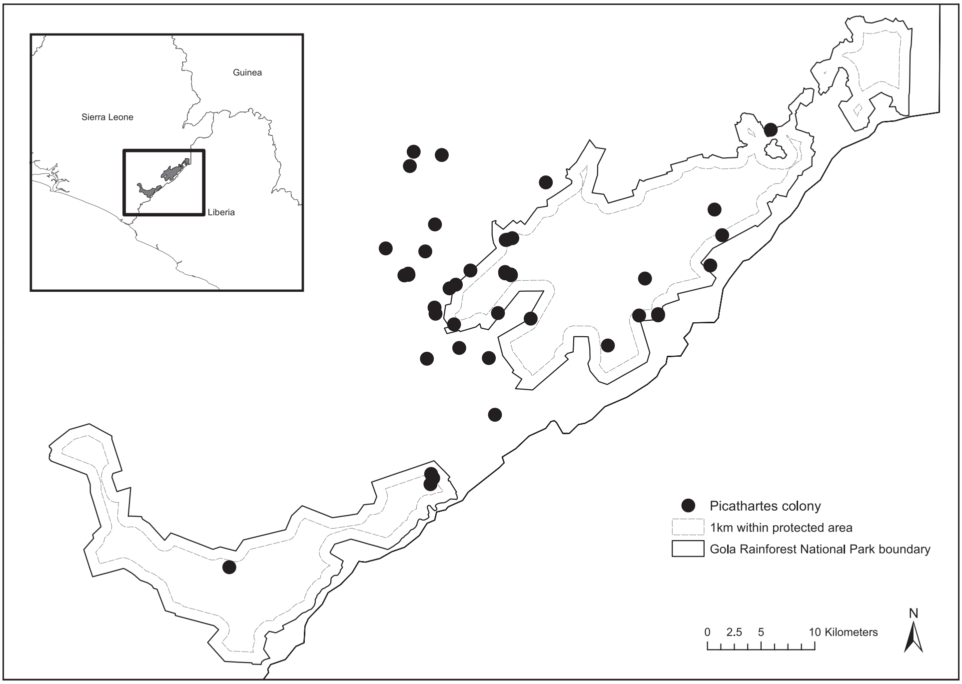

Figure 1. Locations of White-necked Picathartes colonies ($n = 42$) in relation to the boundary of the Gola Rainforest National Park, with the 1-km demarcation used in analyses between colonies categorised as WITHIN > 1 km (inside the national park and > 1 km from the boundary) or WITHIN < 1 km (inside the national park and < 1 km of the boundary).

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decades and probably much longer. Monitoring numbers of pairs using breeding colonies is the approach taken by most other studies of picathartes (Awa II *et al.* 2009b, Monticelli *et al.* 2011, Atuo *et al.* 2014). In the present study, colonies were visited once during the peak period of breeding activity between October and February. Picathartes make mud nests fixed to the under-hang of a rock or small cave, and typically nest in small colonies (2–5 pairs, but up to 40). Colonies were visited once per breeding season in seasons spanning 2006–2007 to 2013–2014, except for 2007–2008 when no visits were made. In some years not all colonies were relocated, or access was prevented by village communities, and so some colonies had incomplete data but were included where data were collected. During each survey, counts were made of nests and any signs of nest occupancy or breeding activity. To improve the accuracy of direct counts from a single visit the number of nests showing recent signs of activity was included as well as obviously active nests. At the time of survey each nest found was categorised as being either broken (old inactive nests, which disintegrate over a period of years), under construction (old nests being repaired with fresh material or new nests under construction), or active showing current evidence of activity (completed lined nests and nests containing eggs, young or droppings, or with feathers or eggshell present in or directly below the nest). Our colony occupancy metric was binary, with at least one under construction or active nest present representing an occupied colony and where no active or under construction nest was found the colony was considered unoccupied. Our colony size metric was the total of all nests categorised as being under construction or active which were combined for this analysis, as all these nests were likely to be used by a pair during the survey season. Each colony rock width and height were measured once by two or more people using tape measures, and rock surface area calculated from these measurements. Where several rocks made up a colony surface area from rocks were summed to give a single value.

Evidence of human activities within 100m of colony rocks was recorded each season at all visited colonies. Six categories of activity were recorded; tracks, logging, farming, mining, hunting and camping. Only logging, farming and hunting activity were found frequently enough to be included in analysis, and we combined logging and farming because forest clearance was a precursor to farming. Recent signs of tree felling, and in some cases power saws heard operating, constituted evidence of forest clearance for farms, the presence of fields evidence of farming and the presence of snares or gun cartridges evidence of hunting. The geographical distance from each colony to the nearest village, stream, forest edge and boundary of the Gola Rainforest National Park was calculated in a geographical information system (ArcGIS version 10.3, ESRI, Redlands, CA).

Statistical analyses

The statistical approach used to examine factors influencing colony occupancy was based on multi-model inference and model selection using Akaike's Information Criterion adjusted for small sample size (AICc). Models were compared by ranking each model according to AICc with the most parsimonious model (ΔAIC < 2) selected from a set of candidate models and Akaike weights used to assess the relative likelihood of each model (Burnham and Anderson 2002). Models with a ΔAICc of < 2 were averaged using MuMIn (Barton 2011) in the statistical package R (R Development Core Team 2014). As recommended by Burnham and Anderson (2002), for model averaging, a 95% confidence set ($\sum\omega = 0.95$) of models were averaged and unconditional confidence intervals calculated. MuMIn was also used to calculate variable weights from models.

Models investigating colony occupation were compared using AIC and were all generalized linear mixed models (glms) fitted in R using the lme4 library (Crawley 2007), specifying a binomial error distribution and logit link function. A binary response variable was used that stated whether a colony was actively occupied in a season or not. The global model included variables likely to influence colony occupation. At the colony scale we included binary variables that indicated whether evidence of hunting and forest clearance was found. Proximity of colonies to watercourses has previously been identified to be of some importance to breeding picathartes and

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colony location (Awa II 2008, Monticelli *et al.* 2011) so we included a co-variable describing distance to the nearest stream. As picathartes are forest-dependent for foraging, the proximity of nesting colonies to forest habitat could also be important, especially as colonies are located at traditionally used rock sites and so may persist even when forest habitat is reduced and the forest edge becomes close or adjacent to colonies (Awa II *et al.* 2009a). A variable describing distance between colonies to the nearest forest edge was included, and to the nearest village as colonies situated nearer to villages may be subject to greater levels of disturbance. Our main variable of interest was the location of colonies in relation to the Gola Rainforest National Park boundary which should provide protection from human related disturbance, both direct and indirect. We allocated each colony into one of three colony location categories; inside the national park and > 1 km from the boundary (WITHIN > 1 km), these sites should be afforded the greatest level of protection; inside the national park and < 1 km of the boundary (WITHIN < 1 km), these colonies should be protected but due to their proximity to the boundary maybe more vulnerable to disturbance; and outside the park in unprotected forest (OUTSIDE), colonies not afforded any protection. Finally we included a co-variable that described the colony rock surface area, as larger rock surface areas were expected to support a larger number of nests and therefore have a higher probability of being occupied. An interaction term between colony location and nearest village was also included. All models specified both colony identity and breeding season as random effects.

We were also interested in whether colony size changed temporally over the study period, and whether this varied with the level of colony protection (colony location). Temporal changes in colony size in relation to the most important factors identified in the colony occupancy modelling were further examined using generalised linear models (glms). These simpler models used the count of active nests each breeding season as the response variable rather than a binary variable. Models only included the variable of interest and season as explanatory variables, along with rock surface area to control for the effect of rock area on nest density. Temporal differences in colony size between the three categories of colony location were then compared by adding a colony location interaction term with the variable of interest and comparing using ANOVA. Due to overdispersion a quasi-poisson error distribution was used in all glms.

Results

Of the 53 colonies monitored from 2006-20007 to 2013-2014, 42 were active in at least one year and were included in analyses. An additional four monitored colonies, all located outside the national park, were precluded from analyses due to missing data. Of the 22 monitored colonies located inside the protected area, 8 were located < 1 km of the boundary and 14 were located > 1 km from the boundary. All 20 colonies monitored outside the national park were located in the surrounding unprotected forest. Overall, colonies were mostly small (average 2.8 ± 3.6 nests), but three larger colonies had > 10 active nests in most years, and up to 20 active nests. The average number of complete nests in each colony location category is shown in Table 1. There was no difference in the mean number of complete nests between colony location category ($\chi^2 = 0.500$, df = 2, $P = 0.78$).

Colony occupancy

Over all breeding seasons, mean colony occupancy was 78%. Mean occupancy was higher within the national park compared to outside (Table 1) although there was no significant difference between the three categories ($\chi^2 = 0.046$, df = 2, $P = 0.98$).

Ranking of colony occupancy models found six models were similarly supported with a ΔAICc < 2 Table 2), and so model averaging was performed. After averaging, models which included colony location and rock surface area were the best supported and highest ranked, with the effect size and weight of evidence for these two variables in the global model much higher than all other variables that were retained in the averaged model (Table 3). In the final averaged

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Table 1. Summary for each category of colony location of mean colony occupancy and the number of active nests, mean rock surface area, mean distance to forest edge, village, stream, and the mean proportion of colonies where evidence of forest clearance or hunting was found across all surveyed breeding seasons. Standard deviations are shown in parentheses.

Variable	Outside park	Within park < 1 km	Within park > 1km
Colony occupancy (%)	67.2	93.5	87.7
Number of active nests	2.5 (4.0)	4.1 (3.9)	2.6 (2.5)
Rock area (m^2)	151.8 (156.6)	78.2 (95.7)	121.0 (267.1)
Distance to forest edge(m)	693.2 (328.2)	712.5 (714.6)	2037.4 (824.5)
Distance to village (m)	1456.4 (822.2)	2626.9 (806.2)	3475.5 (1665.0)
Distance to stream (m)	441.5 (244.3)	406.9 (404.8)	396.9 (223.2)
Forest clearance (%)	76.8	15.2	6.8
Hunting (%)	15.2	6.5	4.1

model, colony location was the only significantly important predictor of colony occupancy, with occupancy most likely within the national park irrespective of location in relation to the boundary. Coefficients from the averaged model show that occupancy was high within the national park but nearly 25% lower outside in unprotected forest. Rock surface area was also an important predictor (relative variable importance of 0.75 in the averaged model) with occupation more likely on larger rock faces. Mean rock surface area significantly differed between the colony location categories ($\chi^2 = 23.306$, df = 2, $P < 0.0001$; Table 1).

Temporal change in the colony size

Over all colonies, the average number of active nests was 3.3 ± 0.7 at the start of the study in 2006–2007 and 2.2 ± 0.5 by the end of the study in 2013–2014 (Figure 2). A generalised linear model controlling for rock surface area was run to examine change in colony size over time which showed that overall colony size declined significantly over the eight-year time period (slope = -0.0964, SE = 0.03, t =-3.033, $P < 0.003$). Adding a colony location*year term to this model showed that declines occurred in all three colony location categories but only colonies located outside the national park showed a significant decline (outside $P = 0.020$, within < 1 km from boundary $P = 0.187$, within > 1 km from boundary $P = 0.164$; Figure 2). There was no significant difference between slopes of the three colony location categories (ANOVA: $\chi^{2,1}$, $P = 0.947$, $n = 243$).

A total of 18 colonies (43%) had farms or forest cleared for farming within 100 m of them by the 2013–2014 season, with seven colonies having new farms created near to colonies between

Table 2. Top ranked colony size models within 2 ΔAICc units of the top model according to AICc values and AICc differences. LR-R^2 gives the likelihood-ratio based pseudo-R^2 adjusted for the number of model parameters; K indicates the number of parameters; AICc the Akaike's Information Criterion for small samples; ΔAICc the scaled AICc relative to the top ranked model; W_i the Akaike model weight; $\sum\omega$ the summed cumulative model weight. Model terms include distance to forest edge, distance to village, distance to stream, forest clearance, colony location (park) and park*village. Colony identity and breeding season were included as random effects.

Model parameters	LR-R^2	K	AICc	*ΔAICc*	W_i	$\sum\omega$
Rock area + park	0.279	6	219.1	0.00	0.075	0.075
Rock area + park + forest edge	0.284	7	220.1	1.03	0.045	0.120
Rock area + park + forest clearance	0.283	7	220.3	1.22	0.041	0.161
Park	0.261	5	220.4	1.33	0.038	0.199
Rock area + park + hunting	0.283	7	220.4	1.34	0.038	0.237
Park + forest edge	0.269	6	221.0	1.95	0.028	0.265

Table 3. Summary of the averaged model, averaged from the top 95% confidence set (∑ω = 0.95), testing for the effect of factors influencing colony size. Models used a Poisson error distribution and a logit link function. Unconditional confidence intervals of each variable are given, and the relative importance of each variable to the final averaged model.

Parameter	Estimate	Coefficient slope	SE	95% CI lower	95% CI upper	Relative importance
Park OUTSIDE	0.718		0.681	0.365	0.919	1.00
Park WITHIN <1km	0.973		0.740	0.821	0.996	1.00
Park WITHIN >1km	0.932		0.705	0.710	0.987	1.00
Rock area	0.501	+	0.501	0.500	0.502	0.75
Forest edge	0.637	+	0.627	0.387	0.830	0.28
Forest clearance	0.340	-	0.668	0.115	0.671	0.15
Hunting	0.360	-	0.657	0.135	0.669	0.14

2006–2007 and 2013–2014 (two within the national park and close to the park boundary, and five in unprotected forest). During this period four colonies were apparently abandoned (colonies where no active nests were found in any of the last three years of the study), with three of these colonies having farming or forest clearance recorded in these years. Although there was some inter-annual variation, no colony increased in activity over the study period, and of 34 colonies monitored throughout the time period, 18 (34%) had a lower number of active nests recorded in 2013–2014 compared with 2006–2007.

Discussion

Gola is of global importance to White-necked Picathartes, containing a significant population and the largest protected area of forest where the species occurs, which includes further colonies on

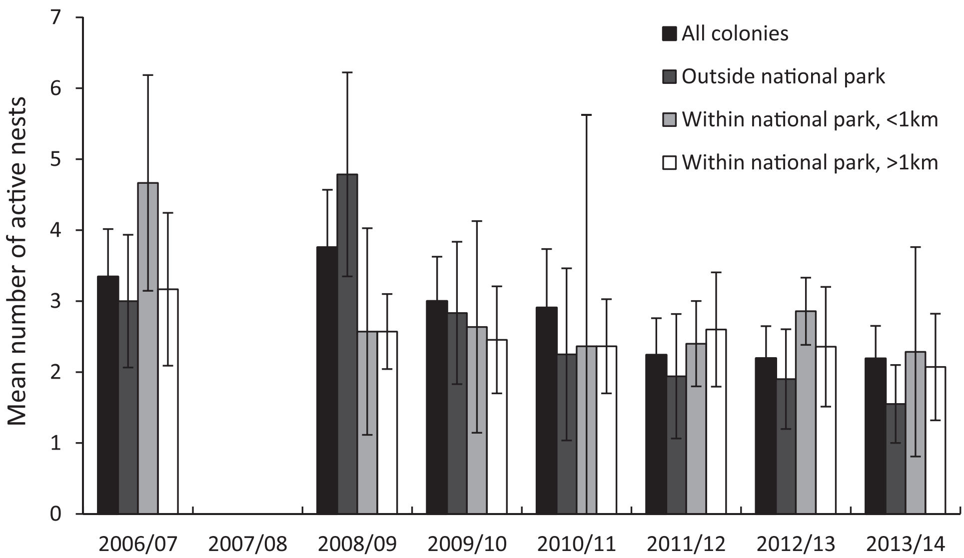

Figure 2. Mean number of active nests for 42 colonies monitored across Gola Rainforest National Park and surrounding community forest 2006–2014 (black bars), and for each colony location category: outside the Gola Rainforest National Park, inside the national park and < 1 km from the boundary and within the national park and > 1 km from the boundary. Standard errors are shown.

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the Liberian side of the forest reserve not monitored for the present study. We show that the probability of colony occupation is strongly influenced by colony location, with colonies located within the protected area having a higher probability of occupation. The surface area of colony rock faces was also an important predictor of colony occupation, with larger rock faces able to support larger colonies. Importantly, we also found a significant temporal decline in the overall number of active nests (active colony size) over the eight-year study. However, although colonies in all location categories showed a decline, only colonies located outside the protected area showed a significant decline suggesting negative pressures on picathartes are greatest in unprotected areas. Active colony size inside the national park, in both distance categories, only declined in the early period of the study and subsequently remained stable, and with similar average colony size, from 2008–2009 until 2013–2014 suggesting protected area status whether close to, or far from, the reserve boundary buffered these colonies from significant decline.

Colony occupation was also predicted by the surface area of colony rocks. We expected rock surface area to be important, as rock faces with a greater surface area are more likely to contain suitable faces for locating nests and support a higher density of nests. Previous work shows that picathartes have particular requirements for rock faces that can be important in determining their suitability including the rock angle, and presence of vegetation and water (Thompson 2007, Awa II 2008, Monticelli *et al.* 2011).

The best models that investigated occupancy also included the distance to the nearest forest habitat, presence of cleared forest and evidence of hunting as predictors, with occupancy more likely closer to forested habitat and less likely where forest clearance or hunting had occurred within 100 m of colonies. Although these habitat and disturbance related variables were of a lower relative importance in the final averaged model it does suggest that reasons for lowered colony occupation are related to indirect anthropogenic disturbance, through encroachment of non-forested habitat reducing habitat availability and increased levels of human disturbance close to colonies. This is supported by our observations of colony abandonment, which occurred to colonies subject to forest clearance. Picathartes do not use non-forest habitats and so colonies located closer to the forest edge will have reduced foraging habitat availability, and in many cases reduced connectivity between the colony and areas of more extensive forested habitat. Increased time away from nests may affect provisioning rates to young, and adult fitness, thereby reducing breeding success (Weimerskirch *et al.* 2000). Hunting activity close to colonies is likely to be irregular and not centred on colonies, so its effect is likely to be indirect unless specifically targeted at picathartes which has not been recorded at Gola. Camping by hunters, using the colony rocks as a camp, did occur but too infrequently to be included in our analysis but is a known cause of picathartes colony abandonment (Atuo *et al.* 2014).

There is a suggestion in other picathartes populations that colonies can remain occupied when subject to disturbance and loss of habitat from forest clearance and farming, even if colonies become largely surrounded by farmland. In Cameroon, Grey-necked Picathartes colonies remained occupied if connected by riparian forest to more extensive areas of forest and radio-tracking of adults at these colonies indicated that still dependent fledglings were led away from colonies at the time of fledging to these higher quality areas (Awa II *et al.* 2009a). This suggests that breeding in colonies close to non-forest habitat is sub-optimal but does not necessarily prevent occupation, perhaps because of the local scarcity of alternative nest sites.

Testing for temporal change in the number of active nests 2006–2007 to 2013–2014 showed a significant overall decline, but when examined by colony location a significant decline only occurred in colonies located outside the national park. Active colony size was relatively high outside the park in 2008–2009 but declined in every subsequent season, which was not driven by a decline in only the larger colonies. In the first season of the present study, 2006–2007, colony size was highest in colonies situated within the national park but close to the boundary, but these colonies had nearly halved in size by 2008–2009 after which time they remained stable. Colonies located further within the national park remained the most stable over the study and changed very little. Together, this strongly suggests both colony occupancy and active colony size are influenced by the level of protection from human related disturbance which may have been higher during some of the early years of the study. This may be explained by changes in the protected status of Gola during the study period, which was made a national park in 2010. However, prior to 2010 protection as a Forest Reserve was mainly in name and levels of protection were little different from the surrounding unprotected community forest until 2010. Earlier work on the same Gola population, using a subset of colonies monitored since 1988, showed stability from 1988 to 2008 (Monticelli *et al.* 2011). This study spanned 11 years of a civil war, 1991–2001, during which time the region saw a reduction in the rural human population reducing pressures on the forest from hunting, logging, farm creation and other subsistence related activities (Lindsell *et al.* 2011). Anthropogenic disturbance may then have increased as the human population and farming activities steadily grew following repopulation after civil war ended, and this may especially have contributed to reduced colony occupation outside the national park. It is therefore difficult to determine how levels of forest protection and disturbance levels influenced colony occupation and activity when pressure on the forest was not constant and the level of protection changed.

Even in the most protected locations some decline in colony size was evident from our monitoring. Environmental factors such as weather might be important as shown for other tropical forest birds (Senapathi *et al.* 2010). White-necked Picathartes in Sierra Leone breed during the dry season, in contrast to Grey-necked Picathartes that predominantly breed during rainy seasons. Although picathartes breeding has been associated with seasonal rainfall (Thompson and Fotso 2000) it is not clear why the two species have such contrasting associations, but changes in rainfall could influence colony size over time. Weather is relatively poorly monitored in Western Africa, including in the region of our study, and this precluded including rainfall in models as we had incomplete data collected within the national park and no other locally available data. Interpolated monthly rainfall data is available for the region in 0.5° x 0.5° grid squares (http://badc.nerc.ac.uk), which has been used in larger scale studies of birds (Finch *et al.* 2014). We obtained rainfall data from the 0.5° x 0.5° grid square that best represented Gola but these data showed little variation between years and no temporal change over the duration of our study.

Conservation implications and future research

Our study shows that non-protected areas can remain important for species of conservation concern, even though occupancy and colony activity was reduced compared to protected areas. Picathartes are colonial species with traditional breeding sites occurring in both protected and unprotected areas, and even in non-protected areas where colonies are subject to some loss of habitat and increased levels of disturbance they are still able to retain occupation in most years. In the Gola landscape, the size of the colony rocks is very important and some of the largest colonies happen to be situated along the national park boundary, including many outside the park, and these colonies may be some of most important in maintaining population size and facilitating dispersal to colonies inside and outside the protected area. The extent of forest habitat may be less important, providing colonies are in the vicinity of a (currently unknown) threshold of suitable and connected forest habitat.

Long term monitoring of the Gola population has been very valuable in identifying changes in colony occupation and activity, and recording evidence of human activities has enabled us to include these in our investigations. However, a lack of more detailed ecological studies of picathartes prevents understanding of the mechanisms involved, hindering conservation and forest management recommendations. The monitoring of picathartes at Gola, in common with most other studies of both species of picathartes, consists of single annual colony visits which is a crude metric of population size and provides no information on breeding productivity, population demographics or spatial population dynamics which is an urgent priority for future picathartes research.

Picathartes species show some tolerance of human activities but it is unknown how changes to habitat and human related disturbance in close proximity to colonies affects demographics and consequently populations. The picathartes literature currently lacks information on site fidelity of individuals to colonies, and dispersal and recruitment of young between breeding colonies. As a consequence, we are unable to determine if colony abandonment results in breeding individuals moving to another colony or skipping breeding in some years, or is the result of mortality without replacement from recruitment. We are also unable to determine if colonies subjected to higher levels of disturbance produce fewer recruits and are effectively population sinks, and likewise the potential importance of colonies located in more protected forest as potential source populations. Detailed nest and demographic monitoring, in conjunction with resource use studies, could help shed light on some of these.

In unmodified forest larger colonies would be expected to be the most important source of recruits to the wider breeding population, but at Gola the larger colonies are located close to the edge of the protected area where they are subject to increased levels of habitat modification and disturbance. A conservation recommendation that can be made from our work is to minimise colony disturbance and ensure continued occupancy. In particular reducing forest clearance around existing colonies and maintaining connected forest habitat should help maintain colony occupancy and prevent abandonment. A 4-km wide 'leakage belt' surrounding the protected area boundary was established in 2015 under the Gola REDD (Reducing Emissions from Deforestation and Forest Degradation) project, which may in future provide greater protection to previously unprotected areas. A programme of village mentoring and educational activities is also proposed to help achieve greater protection for picathartes colonies located in the unprotected community forest.

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