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Radley *et al.*

Habitat selection by Micronesian Scrubfowl

Breeding and feeding habitat selection by an island endemic bird may increase its vulnerability to climate change.

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Abstract

Understanding habitat use is important for understanding the ecology of a species and to apply conservation actions. Species restricted to low-lying islands are at greatest risk from climate change related sea level rise. Species autecology, especially choice of breeding and foraging habitat, may determine their risk from tidal inundation. The endangered Micronesian Scrubfowl (*Megapodius laperouse senex*) is a model species for understanding these impacts. It faces the cumulative challenges of tourist visitation, invasive species, and rising sea levels, yet little is understood about its habitat use in the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau. We studied the habitat requirements of this mound-nesting scrubfowl as a representative of a group of birds considered highly vulnerable to climate change. Analysis of 15 habitat variables at 24 incubation mounds and 26 randomly chosen sites, indicated that scrubfowl selected incubation sites that were close to shore, contained large trees, and exhibited greater canopy heights than the surrounding forest. Birds preferentially built mounds at the base of large ironwood trees (*Casuarina equisetifolia*) but selected sites with significantly more breadfruit trees (*Artocarpus mariannensis*) than random. Scrubfowl foraged in a non-preferential manner, making use of all littoral strand forest habitat. Anthropogenic habitat loss is not a major threat to scrubfowl in the RISL but breeding habitat is limited and within close proximity to the ocean, rendering them highly vulnerable to climate change driven sea level rise in coming decades.

Key Words: climate change; habit selection; habitat use; *Megapodius laperouse senex*; Micronesian Scrubfowl; mound nesting; Palau.

1. INTRODUCTION

Knowledge of a species use of habitat is essential to understanding its ecology and addressing many of the environmental challenges it faces (Kays et al., 2011). Numerous species of temperate and tropical island birds are confronted not only with current threats presented by introduced predators and habitat loss, but also by current and future threats posed by climate change (e.g., Blackburn, Cassey, Duncan, Evans, & Gaston, 2004; Sekercioglu, Primack, & Wormworth, 2012; Taylor & Kumar, 2016). Although the effects of climate change on birds in the world's temperate areas are relatively better studied, far more research on birds in the tropics is required (Sekercioglu et al., 2012). To formulate effective conservation action to these threats and to mitigate the impacts of climate change on tropical birds, it is essential to understand their habitat requirements; these data, however, are lacking for many species (Sekercioglu et al., 2012).

Climate change induced sea level rise will affect and drastically alter coastal habitats globally (IPCC, 2007), which will in turn affect many bird species that rely on them as sites for roosting, foraging and breeding (Clausen & Clausen, 2014). Numerous species of waterfowl, shorebirds and seabirds are increasingly threatened as their breeding habitat is predicted to be inundated or washed away by rising seas or storm surges (e.g., Galbraith et al., 2002; Craik, Hanson, Titman, Mahoney, & Tremblay, 2015; Ivajnsiĉ, Lipej, Škornik, & Kaligariĉ, 2017). The frequency and magnitude of such occurrences are expected to increase as a result of climate change (Collins et al., 2013). Eustatic sea level rise is predicted to have the greatest impact on terrestrial habitat in the tropical Pacific where terrestrial vertebrates are at risk of losing up to 22% of current habitable area to inundation (Wetzel, Beissmann, Penn, & Jetz, 2013). Not only will coastal habitat of this region be affected, but entire low-lying islands could be submerged

(Wetzel et al., 2013; Bellard, Leclerc, & Courchamp, 2014). Owing to their tendency to occur in relatively low numbers on small, isolated islands, endemic landbirds are thought to be the most vulnerable (Jetz, Wilcove, & Dobson, 2007; Wetzel et al., 2013; Taylor & Kumar, 2016). Some groups are particularly sensitive to the effects of climate change as a function of their habitat preferences, range and biology, and recent work has shown that the primarily mound-nesting scrubfowl are under particular threat (Radley et al., 2018).

Scrubfowl belong to the family Megapodiidae, which is confined to the tropics and subtropics of the Indo-Pacific and Australasia where many species occur on relatively small and remote islands (Jones, Dekker, & Roselaar, 1995). Nineteen of the 22 species in the family construct mounds as at least one strategy for incubating their eggs (Jones et al., 1995). Unique to scrubfowl, none use body heat for incubation but instead employ other naturally occurring sources of heat (Jones et al., 1995). Mound building species specifically use heat generated by microbial decomposition of the fine organic matter from which their mounds are constructed (Jones et al., 1995). This organic matter consists of leaves and small woody debris that is collected directly from the forested habitat in which scrubfowl build their mounds (Jones et al., 1995; Sinclair, 2002).

The Micronesian Scrubfowl (*Megapodius laperouse senex*) of Palau, which is listed as endangered by the International Union for the Conservation of Nature (IUCN) (Birdlife International, 2016), is threatened by habitat loss due to rising sea levels (Radley et al., 2018). Although this sub-species also faces the potential cumulative anthropogenic challenges of increasing tourism and introduced rats throughout its core-range (Radley, Davis, & Doherty, 2020), very little is understood about its breeding and foraging habitat needs, a situation that may diminish effective conservation planning for it. The sub-species is vulnerable to sea level rise

because the majority of scrubfowl in Palau breed only on the islands of the United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage listed Rock Islands Southern Lagoon Conservation Area (RISL) (Wiles & Conry, 2001; Olsen, Eberdong, Ketebengang, Blailes, & Chen, 2016). Furthermore, mounds in the RISL are commonly situated in littoral strand forest where they are generally constructed in well-shaded sandy areas just above high tide and just inland from the beach; elevation is typically no more than a few meters above sea level (Wiles & Conry, 2001; Olsen, Eberdong, Ketebengang, & Chen, 2013). Appropriate breeding habitat in the RISL is limited and typically occurs in relatively narrow strips of littoral forest that are generally sandwiched between beach and abrupt, near-vertical limestone hillsides (Pratt, Engbring, Bruner, & Berrett, 1980; Wiles & Conry, 2001). On some comparatively larger islands, such as Kayangel Atoll located in the very northern portion of the Palau archipelago, mounds may be located in more expansive areas of littoral strand habitat (Wiles & Conry, 2001; Olsen et al., 2016).

Other species of scrubfowl in the tropics construct their mounds in locations where microhabitat characteristics both increase the availability of organic matter and provide microclimate stability, decreasing the rate of mound desiccation and maintaining optimal incubation temperatures within (Jones, 1988; Sinclair, 2002). Similarly, scrubfowl in the RISL would be expected to non-randomly select sites for mounds based on habitat and microclimate variables that increase incubation effectiveness and breeding success.

While few specifics are known about the habitat selected by Micronesian Scrubfowl for incubation sites (i.e., for mound building), even fewer are known about the habitat they use for foraging. This is a common gap in research within the family with little published data pertaining to the use of habitat by scrubfowl away from incubation sites (Radley et al., 2018).

What data are available regarding their foraging habitat tend to be relatively coarse in detail (e.g., Broome, Bishop, & Anderson, 1984; Göth & Vogel, 2003; Sivakumar & Sankaran, 2012). Scrubfowl are generally omnivorous scratch-feeders and tend to range broadly through forested habitat opportunistically taking suitable food items as they uncover them (Jones et al., 1995). Regardless, the habitat they select for foraging can influence female fecundity and lead to overall greater reproductive output and, along with the habitat they choose for incubation sites, stimulate greater reproductive success (Jones et al., 1995; Sinclair, 2002). Knowing the characteristics of habitat in the RISL that are important to scrubfowl, for both incubation sites and foraging, is essential for their long-term conservation. It may allow conservation managers to employ engineered solutions to protect core breeding and feeding habitats from sea level rise or it may identify the need for habitat restoration to increase the availability of usable nesting and foraging habitat away from island edges.

Here we investigate what site- and habitat-specific variables are selected by scrubfowl in Palau, both when choosing incubation sites and while foraging. We hypothesized that scrubfowl select incubation and foraging sites based on specific features of habitat structure. We predicted that areas of denser understory or canopy that a) produce more organic debris useful for mound building, and b) maintain a more stable external microclimate for mound incubation, would be preferred to areas that are less dense. Similarly, we predicted that such areas of denser understory or canopy would provide denser and richer leaf litter that produced more invertebrate and plant food and would thus be selected for by foraging birds. We identify habitat variables that are the most important for the Micronesian Scrubfowl in Palau and compare our findings to those for other species of scrubfowl that occur throughout the Indo-Pacific and Australasia.

2. METHODS

2.1 Study site

Palau (7°30' N, 134°35' E; Figure 1), the westernmost archipelago in Micronesia, is comprised of 12 inhabited islands and over 500 smaller islands and islets that extends ~700 km from northeast to southwest (Olsen, 2009). Approximately 87% of the archipelago is forested, 75% of which is classified as native tropical lowland rainforest (Kitalong, DeMeo, & Holm, 2013). Our research focused exclusively on the islands of the RISL, which lies between Babeldoab to the northeast and Peleliu to the southwest (Figure 1). Comprised of ancient, uplifted reefs, most of these “rock islands” are uninhabited and characterized by sheer, highly fissured and eroded karst or limestone slopes undercut at the water’s edge and covered by dense forest, despite little or no soil development beneath (Pratt et al., 1980; Engbring, 1988). A number of these islands also exhibit fringing, sandy littoral zones where strand forest occurs on mostly level limestone soils immediately behind their beaches. These areas of littoral strand forest, in which our research was focused, fall under the category of “Limestone Forest” (Kitalong et al., 2013) and are almost exclusively preferred by scrubfowl for breeding in the RISL (Olsen et al., 2016). Some 55% of the known population breeds in the Rock Islands Southern Lagoon and an estimated 31% on the low-lying Kayangel Atoll (Olsen et al., 2016).

2.2 Incubation mound habitat sampling

We collected habitat data at 24 active scrubfowl incubation mounds and 26 randomly chosen sites on seven islands from 19 February to 2 April 2016 and on 17 January 2017. Nineteen of the sampled mounds were active or maintained and the remaining five were in the process of being

constructed. These represent all known active mounds on the islands to which our time was restricted for mound habitat assessment at the time of data collection (Figure 1).

We located scrubfowl incubation mounds either through use of a 2012 data set provided by Belau National Museum (pers. comm., A. Olsen), or by thorough search of littoral strand habitat on each island. Mound locations were acquired using a differential Global Positioning System (GPS) with an accuracy of approximately 1m. We measured mound diameters and heights with a forester's tape measure, and distances from the shore (the furthest upper reach of high tide) with either handheld laser rangefinder or forester's tape. If straight-line distances were too great or blocked by impenetrable obstructions to accurately measure on-site, we estimated necessary distances by measuring them in ArcGIS (ESRI, 2015).

We followed the methods of Sinclair (2002) for the measurement and collection of habitat data. Habitat characteristics were assessed only at maintained and active incubation mounds. Mounds were considered active when they were obviously maintained and clear of heavy leaf, vine, fern or grass cover, were not worn flat or obviously eroded, and showed signs of scrubfowl activity, or were obviously in a state of construction (Wiles & Conry, 2001; Olsen et al., 2013). We did not include unmaintained or inactive mounds because our inability to reliably and accurately age them left us uncertain about the relative age of the surrounding forest. We therefore could not determine the values of forest structural variables (e.g., ground cover, numbers of seedlings or saplings, and canopy cover) at the time these sites were chosen by scrubfowl for mound construction. We also measured habitat variables at randomly selected sites for statistical comparison to those measured at mounds. All but two random sites were associated with active incubation mounds and were selected based on a table of random bearings and distances (range = 20 – 100 m) from mound centers, as generated in Microsoft Excel 2016.

The remaining two random sites were associated with sampled mounds that were subsequently determined to be inactive. After completing data collection at a mound, we located its random site by choosing the next available pair of bearing and distance on the list and walked to it with the aid of compass and rangefinder or forester's tape measure. Random points were selected only within areas of beach and littoral strand habitat that occurred above high tide. An example of the mapped distribution of mound data and random points on four islands is seen in Figure 2.

We measured and collected habitat data at mounds and random points at two spatial scales: a 'base area' and the 'surrounding forest' (Sinclair, 2002). Together, the base area and the surrounding forest constituted a sampling plot or 'site'. The base areas consisted of everything within the mound perimeter, or a 3.5 m radius circle for random points. This radius was based on the mean diameter of 10 scrubfowl mounds previously measured by Wiles and Conry (2001) in the RISL. Variables of the surrounding forest (which corresponded to the area where birds logically collect the majority of litter and soil for their mounds) were measured in four separate 2-m radius sampling plots, each established at the four cardinal directions around the base area. The centers of these sampling plots were situated seven metres from the center of the mound base area, thus providing 1.5 m of distance between the edge of the base area and the edge of each sampling plot. At mound sites, this compensated for any mounds with a radius slightly larger than the mean of 3.5 m and avoided overlap between the base area and any of its four surrounding forest sample plots.

Seven habitat variables were measured within the base area of both mounds and random sites, 11 were measured in each surrounding forest and corresponding random sample plot, and three site-specific variables were measured or assessed to describe each site as a whole (Table 1; measured habitat variables include the category Dominant Tree Species, which is not included in

the table). We specifically selected variables that might exert some influence on the placement or function of mounds (Sinclair, 2002). Diameter at Breast Height (DBH) was measured for all trees in base areas and sample plots and then placed in one of three life-stage categories: seedlings (all trees under 4 cm DBH), saplings (those between 4 and 10 cm DBH) and mature trees (those over 10 cm DBH). Mature trees and saplings were considered within and measured if they at least touched the perimeter of base areas or sample plots. Stem counts were recorded for all seedlings, along with the dominant species in all three categories. All plants were identified to species and those that occurred in highest number in each life-stage category were considered dominant, although at some sites there was no obvious dominant species. Percent canopy cover was assessed with a spherical densiometer by averaging readings at each of the four cardinal directions around the centers of each base area and at the center of each surrounding forest sample plot. Canopy height was measured with a clinometer at base areas, and number of crowns in canopy was determined by the number of tree canopies that intersected or overlapped each 2-m radius plot boundary.

The cover of all shrubs, herbs and bare ground was estimated for surrounding forest sample plots only (given mounds are mostly unvegetated; Sinclair, 2002). For consistency, ground cover variables within the base area of random sites were not measured.

2.3 Foraging habitat sampling

Scrubfowl foraging habitat data were collected between 9 and 23 January 2017. We employed a modified version of ‘Instantaneous Sampling’ (e.g., O'Donnell & Dilks, 1994), focusing specifically on measuring and quantifying the habitat in which scrubfowl foraged, as opposed to gathering standardized descriptive observations of habitat use. Observers walked slowly through

231 littoral habitat using binoculars to scan ahead of them for scrubfowl. The uplifted limestone
232 formations ubiquitous to the islands were not surveyed because the sheer nature of their slopes
233 made them mostly inaccessible. When a bird was observed, the behavior it exhibited at first
234 sight was recorded. If the individual bird did not obviously notice the observer, it was watched
235 for foraging behavior until it either became aware of the observer or until it moved out of sight.
236 The observer then walked either to the location of first observation or to where the bird was seen
237 actively foraging. For birds that were observed only momentarily prior to flushing or otherwise
238 fleeing, the location of first visual observation became the center point of the data collection plot.
239 If birds were observed longer, the first observed location of actual foraging activity was used as
240 the center point.

241 Foraging habitat data were collected in the same manner as those at incubation mounds
242 and many of the same variables were assessed and measured (Table 1). Ten habitat variables
243 were measured within 1-m radius plots centered on both foraging locations and randomly chosen
244 points (Table 1). Randomly chosen points were selected based on a table of random bearings
245 and distances (range = 10 – 50 m) from foraging plot centers. Seedling stem counts, sapling and
246 tree DBH measures, shrub, herb, and ground cover assessments all followed the methods
247 described above for incubation mound data collection.

248 After completion of data collection at a given foraging site and its randomly chosen
249 point, the observer moved towards the opposite end of the beach or island to search for another
250 scrubfowl from which to collect data. Although not quantified, the observers commenced data
251 collection for a successive bird only if they were reasonably confident it was not the same one
252 for which they had just completed foraging habitat measurements. This approach was taken to

avoid successively collecting data for the same bird or pair, and to ensure the best possible independence between observations in the limited time we had.

2.4 Data analysis

For the purpose of analysis, all individual trees (≥ 11 cm DBH) were placed into four size classes: DBH of 11 to 30 cm; DBH of 31 to 50 cm; DBH of 51 to 70 cm; and DBH of > 70 cm. We first used two-sample *t*-tests to investigate the significance of differences in individual habitat variables between mound base areas, surrounding forest, and foraging sites (collectively referred to here as “target sites”) and their corresponding random sites. The program PRIMER v6 (Clarke & Gorley, 2006) was then used for multivariate testing and display (via ordination) of the differences in overall habitat structure between target and random sites. All continuous habitat variables were first normalized before multivariate analyses and then Euclidean distances between sites were calculated. We then used a one-way Analysis of Similarities (ANOSIM, a non-metric test) to determine the significance level for difference between target and random sites. We used non-metric Multi-Dimensional Scaling (nMDS) and Principal Co-ordinates Analysis (PCO) to represent Euclidean distances between samples in two dimensions, the latter with vectors added showing significant Spearman rank correlations of habitat variables in the ordination space. Similarity percentages analysis (SIMPER) was then used in PRIMER to determine which habitat variables contribute to the top 90% of the overall Euclidian distance dissimilarity between target and random sites.

To investigate the importance of dominant tree species to scrubfowl for selection of incubation and foraging sites, we used chi-squared tests to test for the differences in the frequency of dominant species of mature trees, saplings, and seedlings between target sites and

random sites. Given the low counts or null values for species in some of these life-stage categories, we used Fisher's Exact Test with Monte Carlo estimation to determine significance.

3. RESULTS

3.1 Mound habitat

Scrubfowl mound diameters ranged from 3.5 m to 9.6 m ($\bar{x}$ = 6.7 m) and only three mounds were situated on substrate that exhibited any sort of relief, with relatively gentle associated slopes of 3°, 5°, and 15°, and slope aspects of 70°, 218°, and 115°, respectively. We found four variables that were significantly different ($P < 0.05$) between mound base areas and random sites (Table 1). Mounds were constructed closer to shore ($\bar{x}$ = 41.9 m, range = 5–136 m) than random sites ($\bar{x}$ = 61.7 m, range = 11–167 m) (Figure 3), and mound base areas contained fewer trees in size class 31-50 cm DBH than random (Table 1). Reflecting the fact that 20 of the 24 mounds studied were constructed at the base of large trees, base areas also contained more trees over 70 cm DBH and exhibited significantly greater canopy height than random sites (Table 1). Eleven (45%) of these large trees at mounds were ironwood, one of which was a snag that had been “strangled” by a *Ficus* sp. Four (17%) other mounds were constructed at the base of large breadfruit trees *Artocarpus mariannensis*) and three (13%) were at the base of large snags or stumps that were in the later stages of decay and were identified as unknown species. The remaining two mounds were constructed at the bases of a coral (*Erythrina fusca*) and Indian beech (*Milletta pinnata*) tree. *T*-tests revealed no significant difference ($P > 0.05$) between individual habitat variables at surrounding forest sample plots compared to their random sites (Table 1).

Our ANOSIM comparing mound base areas and random sites yielded a significant ($P < 0.001$) difference in habitat variables between these two groups (Global $R = 0.131$). Although there is some overlap in the ordination space, the general separation of sites can be seen in our PCO (Figure 4). Vectors (Spearman correlations) in the PCO (Figure 4) indicate that the variables of trees over 70 cm DBH, distance to shore, and to a lesser extent canopy height and the number of crowns, were the most strongly correlated and played the largest role in explaining the difference between mound base areas and random sites. The SIMPER analysis further supported this and indicated that trees over 70 cm DBH and canopy height contribute to the top 19.5% of Euclidian distance dissimilarity between mound base areas and random (Table S1), and both these variables were significantly more prominent at base areas (Tables 1). SIMPER analysis also indicated that trees with DBH of 11 to 30 cm were more prominent at base areas, while those with a DBH of 31 to 50 cm were less prominent (Tables 1 and S1). Although random sites contained more seedlings and saplings, and were covered by more tree crowns and a denser canopy (Table S1), t -tests suggested that none of these variables were significantly different from base areas (Table 1). Random sites were, however, situated significantly farther from shore than mound base areas (Tables 1 and Figure 4). An ANOSIM comparing surrounding forest at mounds to random sites indicated no significant difference between these two groups (Global $R = -0.019$, $P = 0.844$), which was further supported by the nMDS (Figure 5).

We identified 22 species of seedlings, saplings and mature trees as dominant at mound base areas and their surrounding forest plots, compared to 17 species identified as dominant at corresponding random sites (Table S2 and S3). The frequency of site species dominance was significantly different between mound base areas and random sites for trees only ($\chi^2 = 21.21$, $P =$

0.020; Table S2). No other tree life-stage category in base areas and random sites and no category in surrounding forests sites and random sites showed a significant difference in species dominance ($P > 0.05$; Table S2). Of the two mature tree species that occurred at both mound base areas and random sites, Coconut palm (*Cocos nucifera*) and Java-apple (*Syzygium samarangenses*) were more likely to be dominant at the latter, while breadfruit was more likely dominant at the former. Forty-six percent of base areas contained no dominant species compared to 11% of random sites, a difference which is significant ($X^2 = 5.29$, $DF = 1$, $P = 0.021$). This difference also drove the overall difference between mound base areas and random sites as reported above, with base areas much less likely to exhibit a clear dominant species compared to the surrounding forest.

3.2 Foraging Habitat

We collected microhabitat data at 62 scrubfowl foraging sites and 62 randomly chosen sites on five islands in the RISL (Figure 1). *T*-tests yielded no significant difference ($P > 0.05$) in individual habitat variables between these two groups (Table 1). An ANOSIM likewise yielded no significant difference between these two groups (Global $R = -0.007$, $P = 0.804$) and this was further demonstrated by nMDS (Figure 5).

We identified 13 species of seedlings, saplings and mature trees as dominant at scrubfowl foraging sites, while 18 species were identified as dominant at corresponding random sites (Table S4). There was no significant difference ($P > 0.05$) in the frequency of species dominance of seedlings, saplings or mature trees between foraging or random sites (Table S4).

4. DISCUSSION

4.1 Habitat at mounds

Micronesian Scrubfowl in the RISL preferentially selected incubation sites that were relatively close to shore, contained large trees, and exhibited greater canopy heights than the surrounding forest. This preference for large trees and high forest canopies at mounds is consistent with findings for populations of the Wattled Brush-Turkey (*Aepypodius arfakianus*), Australian Brush-Turkey (*Alectura lathami*), Brown-collared Talegalla (*Talegalla jobiensis*), New Guinea Scrubfowl (*Megapodius decollates*), and Philippine Scrubfowl (*Megapodius cumingii*) (Jones, 1988; Sinclair, 2002; Sinclair, O'Brien, & Kinnaird, 2002). Both Jones (1988) and Sinclair (2002) suggested that incubation sites in Queensland and New Guinea, respectively, were selected based on the presence of large trees, the latter postulating that they provide more organic litter and microclimate enhancing shade for proper mound function, and that they may serve as a base against which mounds can be supported while being built. Forty-five percent of the active scrubfowl mounds in the RISL from which we collected habitat data were constructed at the base of large ironwood trees. This salt-tolerant species of tree is native to Southeast Asia and the Western Pacific and is a common component of littoral strand habitat throughout the region (Orwa, Mutua, Kindt, Jambadass, & Anthony, 2009). In terms of the scrubfowl breeding habitat assessed in our study, this species of tree was only present at mound base areas (Table S2), a factor that strongly contributed to the overall higher canopies at mounds.

As a separate study (Radley, 2018), we collected GPS locations of 198 active, inactive, and mounds under construction in the RISL (including those in our analysis here), 30% ($n = 59$) of which were built at the base of moderate to large trees; 64% ($n = 38$) of these were identified as ironwood. In most instances during surveys, this species was the largest and most prominent tree in the strand forests of the RISL, with DBH measures of well over 100 cm (pers. obs., P.

Radley). In a previous study of scrubfowl mounds in Palau, Wiles and Conry (2001) found that 10 of 12 active mounds in strand habitat were constructed at the base of relatively large trees, the most common of which was lantern tree (*Hernandia nymphaeifolia*), followed by ironwood. This difference may in part be attributed to the fact that much of their data were collected either outside of the RISL or in the highly restricted Ngerukuid Islands Wildlife Preserve (Wiles & Conry, 2001), to which we were not permitted access.

Other studies of mound building scrubfowl have determined that a denser or more closed canopy is a significant factor in the selection of incubation sites (Jones, 1988; Sinclair, 2002). While forest canopy at mound base areas in the RISL approached 100% coverage, canopies at mounds were not significantly denser or more closed than random. Canopy cover across all target and random sites in our study (i.e., from 224 data collection points across nine islands) yielded a mean for each that ranged from 96.3 – 97.2% (Table 1). This strongly suggests that canopy cover of the littoral strand forests in the RISL is uniformly high and generally closed, and evenly suitable for mound incubation throughout in terms of microclimate maintenance and enhancement of conditions favourable to vegetative decomposition (Sinclair, 2002).

Studies by Jones (1988) and Sinclair (2002) showed that other species of scrubfowl selected incubation sites based specifically on habitat features of the surrounding forest that both increased the availability of organic matter for mound construction and moderated sub-canopy microclimate, which prevents mounds from desiccating. There were no significant differences, however, in habitat variables between forest immediately surrounding mound base areas and random sites in our study. This suggests that scrubfowl in the RISL do not necessarily select incubation sites based on the presence of readily available leaf litter and fine organic matter to provision their mounds. Considering the evenly dense, closed canopy over the vast majority of

their preferred breeding habitat throughout the RISL, the availability of ‘fuel’ for incubation may not be a driving concern for the species. Instead, our data suggest that they choose sites based on specific variables pertaining to where the mound itself will be placed in littoral strand forest. The significantly lower density of medium-sized trees (31 to 50 cm DBH) within base areas could be a function of very large trees at mounds severely suppressing surrounding trees, or may reflect gap-phase recruitment of saplings following tree fall or forest disturbance, both common scenarios in lowland tropical forests (Hartshorn, 1980; Swaine, Lieberman, & Putz, 1987). Although our analysis found them not significant, a greater density of smaller DBH (11 to 30 cm size class, $\bar{x} = 18.6$ cm) and thus generally lower stature trees at base areas may provide a denser forest sub-canopy that helps maintain a moister microclimate closer to the mound at ground level.

Nearly half of all mound base areas at which we measured habitat in the RISL lacked a species of dominant tree (Table S2). Our results showed that base areas were more likely to exhibit a mix of tree species with no clear dominant present. A more mixed selection of tree species may provide a more diverse variety of organic matter for mound construction. As scrubfowl in Palau may breed year-round (Jones et al., 1995), this may also ensure the availability of material for maintenance throughout the year. Regardless of the fact that the majority of scrubfowl apparently chose ironwood when selecting a tree around which to build their mounds, this tree species was dominant at only one base area. Although our results do suggest that scrubfowl choose sites based on the presence of breadfruit, this tree species was present at only four base areas and in all cases it had been selected specifically for mounds to be constructed against. Perhaps more notable, birds in the RISL may have selected incubation sites that lacked or were not in the immediate vicinity of mature coconut palms. Jones (1988) found

that Australian Brush-turkeys specifically avoided dense areas of eucalypts (*Eucalyptus* sp.) when choosing incubation sites, likely owing to the decomposition resistant properties of their leaves. The older fallen fronds of coconut palms are large, relatively heavy, and may be challenging for scrubfowl to move, perhaps leading them to simply select incubation sites that are free of fallen fronds and, consequently, coconut palms. While not specifically a study of habitat use but rather an analysis of species density and abundance by habitat cover type, Amidon, Marshall, & Kessler (2011) found abundances of Micronesian Scrubfowl (*M. l. laperouse*) in the Mariana Islands to be greater in coconut dominated forests compared to native forests. These reported differences, however, were not statistically significant and their study did not necessarily concern breeding birds but pertained to all detected individuals. While Java-apple was likewise significantly avoided by scrubfowl in the RISL, this species was the second most common tree at or within mounds of Nicobar Scrubfowl (*Megapodius nicobariensis*), following Pandanus (Sivakumar & Sankaran, 2012).

4.2 Foraging habitat

In terms of structure and species composition, our results indicate that scrubfowl in the RISL foraged in a non-preferential manner, apparently making use of all littoral strand forest habitat. Although not significant, our data suggest that birds tend to forage under dense canopy cover in open locations away from trees and saplings and with sparse herb cover, yet relatively dense in seedlings and with a moderate litter cover approaching 60% (Table 1 & 6). While this description is suitable for much of the littoral areas where scrubfowl forage in the RISL, the apparent lack of saplings and trees may in part be a result of our sampling method. We measured all habitat variables within 1 m radius plots centered on the observed locations of

scrubfowl, either where birds were seen to be actively foraging or where they were first seen prior to being flushed. In the latter case, we assumed birds had been foraging prior to being flushed. Although not quantified, saplings and trees were often within relative close proximity to foraging locations, but not close enough to fall within the relatively small radius of the sample plot. Given this, we suggest that the random sites associated with mound base areas and surrounding forest plots may more accurately reflect the structural make-up of the forests in which scrubfowl forage.

There are relatively few studies that focus on the use of habitat by scrubfowl outside of that which they require for breeding. Broome et al. (1984) found that the Melanesian Scrubfowl (*Megapodius eremita*) dispersed to lowland rainforest in western New Britain during the non-breeding season. While this cover type constitutes their primary foraging habitat, Melanesian Scrubfowl also made light use of swamp and hill forests and areas of garden regrowth (Broome et al. 1984). Although their study did not explicitly consider foraging habitat use of the Nicobar Scrubfowl, Sivakumar and Sankaran (2012) observed the majority of the species in cover types of pagoda tree (*Clerodendrum peniculatum*) and pandanus and found that they preferred microhabitats dominated by pandanus and kenda (*Macaranga peltata*), regardless of season. Most Nicobar Scrubfowl were also observed during the non-breeding season in sandy-loam substrates, which Sivakumar and Sankaran (2012) hypothesized was because it may have been richer in invertebrate food resources than the strictly sandy substrate on which the species constructs its mounds. Like all other scrubfowl, the Micronesian Scrubfowl in the RISL is omnivorous, consuming various small invertebrates and arthropods, snails, larvae, seeds, small fruits and other plant matter (Jones et al., 1995). This generalist feeding behavior might be reflected in their non-specific use of foraging habitat.

The modified form of instantaneous sampling we employed was appropriate and adequate for our assessment of foraging habitat use by scrubfowl in the RISL. We suggest, however, that measuring variables in 2 m radius sampling plots may better capture a more accurate representation of the habitat in which they forage by potentially including more saplings and trees in samples. Larger sampling plots, and counting the number of crowns above their centers, would also have made possible a direct comparison with the habitat variables collected at sample plots in the surrounding forest at incubation mounds. This would allow for a more accurate and informative assessment of the overall structure of littoral forest in the RISL, and perhaps allowed for a more nuanced assessment of the use of this cover type for foraging by scrubfowl.

4.3 Sea level rise and conservation implication for the Micronesian Scrubfowl in Palau

Although human-caused habitat loss may not be a major threat to scrubfowl in the RISL, climate change driven sea level rise could have serious implications for their breeding by the end of the current century. The strand forest habitat that scrubfowl prefer for breeding is vulnerable to future scenarios of eustatic rise predicted by the Intergovernmental Panel for Climate Change (IPCC) (Church et al., 2013; Radley et al., 2018). Terrestrial vertebrate species of Oceania may be the most impacted by rising seas and are predicted to lose up to nearly a quarter of their current ranges (Wetzel et al., 2013). Landbirds throughout this region may be at particular risk given their tendency to occur on small, remote Pacific islands (Wetzel et al., 2013; Taylor & Kumar, 2016). The scrubfowl in our study non-randomly selected low lying incubation sites that were located on average 42 meters from shore (Table S1), and the vast majority of mounds are within close proximity to sea level at high tide (Olsen et al., 2013; Olsen et al., 2016). Wiles and

Conry (2001) previously reported distances of 5–15 m from shore for eight scrubfowl mounds in the RISL, but these all occurred on narrow beaches compared to many that we surveyed for our study.

The Nicobar Scrubfowl is the only other mound nesting species that usually chooses coastal forest incubation sites on well-drained, sandy soils that are close to shore, the vast majority of which are within 100 m of the beach (Sankaran, 1995; Sivakumar & Sankaran, 2012). This species, however, has the option of readily establishing incubation sites further from the shore and has been recorded doing so with mounds documented as far as 15 km inland on Grand Nicobar Island (Sankaran, 1995). While scrubfowl in the RISL may have the opportunity to forage in the higher limestone areas, the option of selecting breeding habitat in strand forest at a safer distance from the ocean is exceedingly limited within the conservation area. (There is potentially only one incubation mound, constructed solely of leaf litter, documented in uplifted limestone in the RISL [Wiles & Conry, 2001; Olsen et al., 2016], highlighting the rare use of these areas for incubation by scrubfowl). On the island of Dmasech in the Ngemelis Complex (Figure 1), for example, we documented one mound at 136 m from the shore, representing nearly the farthest from the water a scrubfowl can establish an incubation site in apparently preferred littoral strand forest habitat in the RISL. The 2004 Indian Ocean tsunami devastated the Nicobar Islands and greatly affected scrubfowl populations, extirpating the species from two islands, and decreasing coastal breeding habitat by about 60% (Sivakumar, 2010). Aside from sea level rise, similar abrupt stochastic events in the form of storm surges associated with increased storm intensity and frequency that are predicted as a part of climate change could pose at least equally serious consequences for scrubfowl in the RISL.

504 Our findings suggest that the Micronesian Scrubfowl in Palau has broad preferences in
505 terms of foraging habitat, which is likely a reflection of its broad and non-specialized diet (Jones
506 et al., 1995). This species, however, does specifically select locations to construct their mounds
507 that contain large trees with DBH exceeding 70 cm, which provide high canopy cover, and that
508 are situated relatively close to shore. Our findings help to further characterize and identify
509 necessary or likely important habitat for the Micronesian Scrubfowl in Palau, and will help to
510 inform modelling exercises that are intended to measure the effects of climate change driven sea
511 level rise on the subspecies in the archipelago and other island restricted species.

TABLE 1. Means ($\pm$ *SD*) of untransformed data for habitat variables collected at scrubfowl mound base areas (BA), surrounding forest (SF) at mounds, scrubfowl foraging plots (FP), and all associated random sites in the Rock Island Southern Lagoon Conservation Area (RISL), Palau.

Habitat Variables	BA Mound (<i>n</i> = 24)	BA Random (<i>n</i> = 26)	SF Mound (<i>n</i> = 24)	SF Random (<i>n</i> = 26)	FP Site (<i>n</i> = 62)	FP Random (<i>n</i> = 62)
<i>Canopy and Understory</i>						
No. of Seedlings	28.8 $\pm$ 43.6	36.3 $\pm$ 29.2	68.2 $\pm$ 61.7	70.4 $\pm$ 48.9	8.8 $\pm$ 8.3	10.2 $\pm$ 11.1
No. of Saplings	1.5 $\pm$ 1.5	2.3 $\pm$ 2.5	2.7 $\pm$ 2.4	4.5 $\pm$ 4.4	0.4 $\pm$ 0.8	0.3 $\pm$ 0.6
Trees 11 to 30 cm DBH ¹	1.6 $\pm$ 1.7	0.8 $\pm$ 1.4	2.0 $\pm$ 1.9	1.9 $\pm$ 1.7	0.1 $\pm$ 0.3	0.2 $\pm$ 0.4
Trees 31 to 50 cm DBH ¹	0.08 $\pm$ 0.3**	0.5 $\pm$ 0.7	0.6 $\pm$ 1.2	0.6 $\pm$ 0.9	0.1 $\pm$ 0.4	0.1 $\pm$ 0.3
Trees 51 to 70 cm DBH ¹	0.08 $\pm$ 0.3	0.1 $\pm$ 0.4	0.04 $\pm$ 0.2	0.1 $\pm$ 0.3	-	-
Trees > 70 cm DBH ¹	0.8 $\pm$ 0.6*	0.1 $\pm$ 0.3	0.1 $\pm$ 0.3	0.1 $\pm$ 0.3	-	-
% Canopy Cover	96.6 $\pm$ 2.3	97.2 $\pm$ 2.9	96.3 $\pm$ 2.6	96.3 $\pm$ 4.2	97.1 $\pm$ 2.1	96.6 $\pm$ 3.6
Canopy Height	26.0 $\pm$ 8.1*	19.2 $\pm$ 7.1	-	-	-	-
No. of Crowns	2.1 $\pm$ 0.9	2.4 $\pm$ 1.2	1.7 $\pm$ 0.3	1.6 $\pm$ 0.6	-	-
<i>Ground Cover</i>						
% Shrub Cover	-	-	0.1 $\pm$ 0.5	0.3 $\pm$ 1.0	-	-
% Herb Cover	-	-	9.5 $\pm$ 13.1	12.1 $\pm$ 13.9	6.8 $\pm$ 13.7	9.9 $\pm$ 19.2
% Bare Ground	-	-	22.6 $\pm$ 21.5	18.5 $\pm$ 16.9	37.9 $\pm$ 28.8	33.9 $\pm$ 27.9
% Litter Cover	-	-	77.0 $\pm$ 21.3	77.9 $\pm$ 20.8	56.2 $\pm$ 29.9	60.9 $\pm$ 29.8
% Limestone Cover	-	-	0.4 $\pm$ 2.0	3.9 $\pm$ 16.5	5.5 $\pm$ 16.8	3.7 $\pm$ 12.0
<i>Site Specific</i>						
Distance to Shore	41.9 $\pm$ 27.7**	61.8 $\pm$ 40.6	-	-	-	-
% Slope	0.9 $\pm$ 3.2	1.3 $\pm$ 2.6	-	-	-	-
Slope Aspect	16.8 $\pm$ 50.6	40.7 $\pm$ 81.6	-	-	-	-

¹ = Falls under the single forest habitat variable category "Tree DBH"

* Significantly different for *P* = 0.05 to 0.01

** Significantly different for *P* < 0.01

Figure Legends

FIGURE 1. Map of the study area within the Rock Islands Southern Lagoon Conservation Area (RISL) of Palau, and the locations of islands on which Micronesian Scrubfowl habitat data were collected. A ¹ denotes those islands on which only breeding habitat data were collected, and a ² those on which only foraging habitat were collected. Both breeding and foraging habitat data were collected on the remaining three such labelled islands.

FIGURE 2. Map of four of the main Rock Island study sites showing location of active mounds, mounds under construction and random locations. The concentration of points on some islands relates to the limited availability of littoral habitat.

FIGURE 3. Measured distances to shore of scrubfowl incubation mounds compared to randomly chosen sites in the Rock Islands Southern Lagoon Conservation Area, Palau.

FIGURE 4. Results of Principal Co-ordinates Analysis (PCO) for scrubfowl mound base areas as compared to random sites in the Rock Islands Southern Lagoon Conservation Area (RISL), Palau. Only variables with a Pearson Correlation of > 0.40 are included in the graph and length of the generated line is proportional to the strength of the correlation.

FIGURE 5. Results of non-metric Multi-Dimensional Scaling (nMDS) for surrounding forest sample plots at mounds (top) and scrubfowl foraging sites (bottom), as compared to their random sites.

Figure 1

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Figure 4

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552 Figure 5

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564 **Data Availability Statement**

565 Data for this study will be available at the ECU institutional repository if the manuscript is
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