

Research Article

Foraging Habitat Distributions Affect Territory Size and Shape in the Tuamotu Kingfisher

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I studied factors influencing territory configuration in the Tuamotu kingfisher (*Todiramphus gambieri*). Radiotelemetry data were used to define territory boundaries, and I tested for effects on territory size and shape of landscape habitat composition and foraging patch configuration. Tuamotu kingfisher territories were larger in areas with reduced densities of coconut plantation foraging habitat, and territories were less circular in the study site that had a single slender patch of foraging habitat. Maximum territory length did not differ between study sites, however, which suggested that the size of Tuamotu kingfisher territories might be bounded by the combined influence of maximum travel distances and habitat configurations. Results also suggested that birds enlarge territories as they age. Together, results supported previous work indicating that territory configurations represent a balance between the costs of defending a territory and gains from territory ownership.

1. Introduction

Understanding how territories are formed, shaped, and maintained is key to elucidating how individuals interact with conspecifics and with landscape resources. Previous work suggests that the spatial extent of animal territories depends upon resource benefits, discounted for travel and defense costs [1–4]. Resources Among birds, which can be strongly associated with the survival and reproductive needs of individuals. Among birds, which are often strongly territorial, perch availability [5] and food and nesting sites appear to be particularly relevant to territory configuration [4, 6]. The availability and distribution of resources differs across space; therefore, variation is expected to occur among territories in different regions [7–10]. The characteristics of territory holders also affect territoriality, as larger individuals can hold larger territories [11, 12]. Male birds are often more aggressive than females, and thus they also defend larger territories in some species [13]. Similarly, age and experience may influence territory size because older individuals might be better at defending against intruders.

Despite the development of theoretical concepts in space use, relatively few have used quantitative methods to study the dynamic nature of territoriality [14]. Most previous investigations have focused on the total area used, or on the relationship between habitat distributions and movements [4, 15]. Shape and configuration of bird territories have been less studied, even though territory shape may also be influenced by resource distributions and defense costs [9, 16–18]. Circular territories are optimal in homogenous habitats because of minimized edge-to-area ratios and transit distances [19, 20]. Circles can be perturbed into flat-sided hexagons when there is competition with neighboring individuals, as hexagons most efficiently balance edge-to-area ratios and they fit together to entirely cover landscapes. Circular or hexagonal territories may also benefit central-place foragers if movement gravitates around the territory center, which is very often the nest site for birds [7, 21]. On the contrary, the boundaries of long slender territories or territories with narrow extensions might be difficult to defend because of exaggerated edge-to-area ratios. In patchy or heterogeneous landscapes, however, territories of

noncircular shape might also minimize defense and transit costs if they encompass irregular-shaped patches of high value habitat [9].

Much of the work on avian territoriality is based on migrant birds that are ecologically distinct from resident species (e.g., [22, 23]). Migrants settle territories during each breeding season, whereas many resident species are territorial year-round and exist in high population densities that tax resources and promote intraspecific competition and aggression. On tropical oceanic islands, the situation is often even more exaggerated, with limited space, robust resources, high population densities, and few predators. Interactions among conspecifics can be extremely intense for the same reasons, which have apparently driven the evolution of social systems and associated population dynamics [24–26].

I studied territoriality in a tropical island terrestrial forest bird, the Tuamotu kingfisher (*Todiramphus gambieri*). This critically endangered species [27] is endemic to Niau Atoll in French Polynesia with only one extant population of approximately 125 individuals [28, 29]. The birds select for coconut plantation habitat, which has been associated with nest sites and abundant foraging opportunities [28], and with elevated kingfisher survival [29].

I estimated the boundaries of territories of radio-tagged kingfishers and investigated factors that have the potential to influence variation in territory size and shape. I was particularly interested in studying whether variation in territory size and shape was associated with interindividual differences, or whether it aligned with resource distributions at the local or larger study site scale. I predicted that if the characteristics of individual Tuamotu kingfishers underpin variation in territories than territories would enlarge as birds aged and became more experienced [30, 31]. I anticipated that the more aggressive males and older birds would have, respectively, larger territories than females or younger birds. I also evaluated effects of resources on Tuamotu kingfisher territory size and shape by studying habitat types (composition), and the spatial arrangement of habitat patches (configuration) [32]. I predicted that if resources influence territory shape, or configuration, kingfisher territories would be larger in areas with less coconut plantation foraging habitat, and territories would be long and thin on the study site with a single narrow band of coconut plantation habitat.

2. Methods

2.1. Study Site. Niau Atoll ($16^{\circ}10' S$, $146^{\circ}22' W$) is a small island in French Polynesia with a land area of 26 km^2 and a large enclosed lagoon ([33], Figure 1). The inland is characterized by dense primary forest growing on jagged fossilized coral (atoll forest), and mixes of coconut trees and atoll forest [34]. Coconut agricultural plantations ring the island on the ocean and lagoon shores, and most are managed by farmers that clear understory vegetation with hand tools and burning. The coconut plantation areas were likely historically characterized by a native palm ([34], *Pritchardia pericularum*). Wetlands characterized by shoreline purslane (*Sesuvium portulacastrum*) and Jamaica

swamp sawgrass (*Cladium mariscus*) occur along the lagoon and on the inside of the island ([34], Figure 1). The climate is tropical oceanic without pronounced seasons, and it is stable among seasons and years [35].

I conducted research on two study sites on the eastern portion of Niau, situated by the ocean coast and the lagoon (hereafter referenced as the *coast* and *lagoon* study sites, Figure 1). Study site boundaries were defined by minimum convex polygons (MCP, [36]) encompassing all radiotelemetry locations for adult kingfishers from within each site. The coast study site encompassed 38 ha and the lagoon study site encompassed 167 ha. Habitat composition and configuration differed substantially between the two sites. Habitat compositions on the lagoon study site included coconut plantation forest (44%), mixed coconut atoll forest (21%), atoll forest (7%), and wetland (26%) (classifications derived from 34). The coast study site included coconut plantation forest (33%), atoll forest (64%), and a littoral zone (4%) along the water. No wetlands or mixed forest occurred on the coast study site. Coconut plantation forest occurred in a narrow and continuous configuration along the ocean coast, and coconut plantation habitat was wider on the lagoon study site. I used an edge-to-area ratio to evaluate coconut plantation foraging habitat configuration in the study sites, and the ratio was $0.030 \text{ m edge/area m}^2$ on the coast study site and $0.021 \text{ m edge/area m}^2$ on the lagoon site, illustrating the long sinuous nature of the coast coconut plantation habitats when compared to the wider coconut plantation habitat patches on the lagoon study site (Figure 1).

2.2. Radiotelemetry. I captured Tuamotu kingfishers with mist-nets or using hand-held hoop-nets placed over nest cavities [37]. Each individual was weighed and marked with a numbered aluminum leg-band and unique combinations of colored plastic leg-bands. I collected $<0.1 \text{ mL}$ of blood (one drop) from the brachial vein using a 27-gauge needle, and I used previously described techniques [38] and primers P2/P8 for molecular sex determination. Each bird was also fitted with a radio-transmitter (model BD-2; Holohil Systems, Ottawa, Canada) weighing 1.5 g ($\leq 4\%$ body mass; [39]) that was attached with a leg harness that allowed equipment to shed from birds after radio-tags lost functionality [40].

Adult (after hatch year) Tuamotu kingfishers ($n = 30$) were radio-tracked during February–March 2006 (2 males), September–December 2006 (4 females and 5 males), September–December 2007 (5 females and 5 males), and September–December 2008 (5 females and 4 males). Birds were tracked for the 4–6 week battery life of the radio-transmitters. One bird was radio-tagged during three field seasons, four birds were radio-tagged during two field seasons, and 19 birds were radio-tagged once. I defined territories for each bird during each field season (bird*season) and used mixed models analyses to account for repeated observations of individual birds. Territory boundaries and territory membership were previously documented to be relatively stable within and among seasons [20, 29]. Nine territories were located on the smaller coast study site and

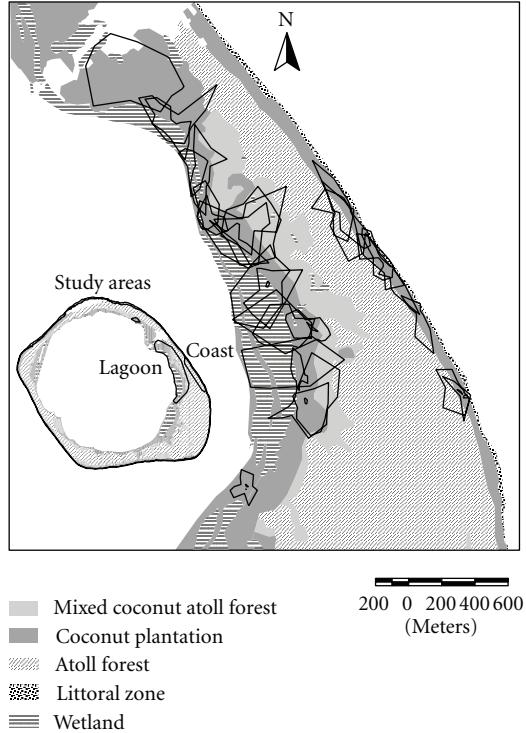


FIGURE 1: Niau Atoll study sites and territory boundaries for Tuamotu kingfishers radio-tracked in 2006–2008 (outline).

21 territories were on the more extensive lagoon study site. I excluded one female tracked in 2007 from analyses because of substantial territory overlap with modified anthropogenic habitats in the nearby village.

I located radio-tagged kingfishers during daylight hours (between approximately 05:00 and 18:00) because previous investigations of congeneric kingfishers found that nocturnal movements were unlikely [41]. Radio tracking techniques were fully described previously [28]. Tuamotu kingfishers were located using a hand-held Yagi antenna and telemetry receiver (model R-1000; Communications Specialists Inc., Orange, CA), approximately twice daily, with consecutive sampling separated by >2 hrs. (e.g., [28, 41–45]). The location of each bird was recorded with a global positioning system (GPS; Rino 520HCx; Garmin Ltd., Olathe, KS, USA). When birds could not be visually observed, I used previously described triangulation techniques (see [28, 43, 44]) to estimate locations. Briefly, consecutive directional bearings were separated by <10 min to minimize error from bird movements. I estimated the maximum likelihood location for each triangulation using LOAS software (Ecological Software Solutions, Urnäsch, Switzerland). I excluded triangulations that had a 95% error ellipse >0.6 ha, which was approximately 10% of a Tuamotu kingfisher territory.

2.3. Territory Boundaries. I used a geographic information system (GIS; ArcGIS 9.3; ESRI, Redlands, California, USA) and a local convex hull method to define territory boundaries [45, 46] for each bird*season [46]. I used the local convex hull method because it detected boundaries formed by the

ocean and lagoon. The method has been fully described elsewhere [36, 46], but in short, for each bird it amalgamates small polygons formed by subsets of telemetry locations. I used subsets of 10 nearest neighbor point locations to generate the small polygons. I intersected polygons defined by territory boundaries with vegetation cover [34] in the GIS to evaluate habitat composition and configuration within territories. I also reported the amount of overlapping area (ha) within territories of mated pairs ($n = 7$ dyads), and the amount of overlap area shared by neighboring individuals ($n = 21$ dyads). I did not observe any solitary individuals in the current study, and most pairings were identified by banded birds tending the same nests. I tested for differences in the mean amount of territory overlap of pairs versus overlap of neighbors using a Wilcoxon-Mann-Whitney test (proc nonpar1way; SAS Institute Inc., Cary, NC).

2.4. Individual Effects on Territory Size. I compared the total area and the amount of coconut plantation habitat within territories of males ($n = 16$) and females ($n = 13$) with generalized linear mixed models (proc glimmix; SAS Institute Inc., Cary, NC). Random effects variables were included for individual birds and study site, to account for repeated observations of birds during subsequent years and to counter differences among the sites. I also compared the size of territories of mated Tuamotu kingfisher pairs ($n = 7$ pairs) using a paired *t*-test (proc means; SAS Institute Inc., Cary, NC). Pairs shared the same space, so the paired test effectively evaluated differences in individual birds while controlling for the resource characteristics of

TABLE 1: Characteristics of Tuamotu kingfisher territories on two study sites differing in landscape structure on Niau Atoll in 2006–2008. Mean values and ranges are shown for each metric.

Study site	<i>n</i>	Territory	Coconut plantation forest	Length	Width	Length-to-Width ratio
Lagoon	20	6.1 ha (1.5–12.2)	3.2 ha (1.2–6.7)	424 m (219–626)	271 m (98–455)	0.63 (0.36–0.87)
Coast	9	3.3 ha (1.0–5.2)	2.0 ha (0.7–3.9)	460 m (312–652)	140 m (90–190)	0.36 (0.21–0.67)

the location. No pair-members were observed for multiple years. I further compared territories held by five birds that were tracked for two seasons each to evaluate potential changes in territoriality that are associated with age. Four birds were tracked for two seasons, and a fifth was tracked for three seasons. I included only the first two seasons for the fifth bird to avoid bias from individual overrepresentation. I used a nonparametric Wilcoxon signed-rank test (proc univariate; SAS Institute Inc., Cary, NC) to compare territory size change because the size distribution of territories was left-skewed.

2.5. Habitat Composition and Territory Size. To test for an association between the size of Tuamotu kingfisher territories and the composition of coconut plantation habitat resources, I compared kingfisher territory size with the proportion of coconut plantation encircled by territories using generalized linear mixed models. Tuamotu kingfisher territory size was modeled as a response variable, individual bird identification and study site were included as random effects variables, and the proportion of coconut plantation habitat within territories was included as an explanatory variable.

2.6. Habitat Patch Configuration Effects on Territory Shape. I investigated how landscape configuration might influence territory shape in the two study sites, which were characterized by markedly different coconut plantation patch configurations. I predicted that if kingfishers shaped territories to encompass more coconut plantation habitat, territories on the coast study site, where there was a narrow band of coconut plantation habitat, would be less circular than those on the lagoon study site. I used ET GeoWizards (version 10.1, ET Spatial Techniques, Pretoria, South Africa) extension for GIS to calculate the maximum length of each territory and the maximum perpendicular width. Territory length was defined as the maximum length line bisecting the territory center and external boundaries. Territory lengths on coast territories were compared to those on lagoon territories with generalized linear mixed models. The length was included as a response variable, study site was included as an explanatory variable, and individual bird identification was included as a random effects variable to account for multiple observations of some individuals. I further evaluated the relative circularity of territories. More circular territories have a width-to-length ratio of 1, whereas the ratio for elongated territories is closer to 0. The width-to-length ratio was compared among field sites with similarly implemented generalized linear models. Results for all analyses are presented as means with SD, and tests were considered statistically suggestive at $\alpha < 0.10$ and significant at $\alpha < 0.05$.

3. Results

I derived 29 territories (Figure 1), with a mean of 35 (SD 9) radio telemetry relocations each. Mean territory size was 5.3 ha (SD 3.4), and territories were composed primarily of agricultural coconut plantation, which accounted for 61% (range 29–99%) of the total territory area (Table 1). Radiotelemetry data and visual observations of color banded birds supported previous suppositions that Tuamotu kingfishers were socially monogamous and territorial residents [28]. Territories of neighboring Tuamotu kingfishers overlapped by a median area of 0.26 ha and 0.11 ha of coconut plantation area. Territories of mates overlapped by median of 2.2 ha total area, and a median of 1.8 ha coconut plantation habitat area, which was more overlapped than among neighbors ($Z = 4.0226, P < 0.0001$). The mean total territory area used by the 7 pairs that were simultaneously marked was 8.9 ha (SD 4.4), and the mean total coconut plantation habitat within the amalgamated territories was 4.6 ha (SD 1.6).

3.1. Individual Effects on Territory Configuration. Mean territory size (5.3 ha, SD 3.4 ha) and the amount of coconut plantation forest within territories (2.8 ha, SD 1.5 ha) did not differ between males and females (resp., $F_{1,6} = < 0.001, P = 0.9666$ and $F_{1,6} = 1.42, P = 0.2777$), and there was no difference in the size of territories ($t_6 = 0.018, P = 0.9860$) or in the amount of coconut plantation habitat ($t_6 = -1.63, P = 0.1540$) held by mates during the same year. All birds that were observed over two seasons increased territory size (range 0.4 to 2.6 ha increase) and coconut plantation habitat within territories (range 0.4 to 1.7 ha increase) in the second year of observation, although the Wilcoxon signed-rank test reported that the difference was only suggestive ($S = -7.5, P = 0.0625$).

3.2. Habitat Composition and Configuration. Tuamotu kingfisher territory size was strongly associated with the composition of habitat resources (Table 1). Model results indicated that Tuamotu kingfisher territories were smaller when they encircled areas with higher densities of coconut plantation habitat. Parameter estimates indicated that, after accounting for study site and the effects of individual birds, Tuamotu kingfisher territory size decreases by 0.84 ha (95% CI 0.21 ha to 1.46 ha) for each added 10% of coconut plantation habitat density ($F_{1,5} = 12.0, P = 0.0180$).

Results further suggested that Tuamotu kingfishers shaped their territories to encircle coconut plantation foraging resources. Territories on the lagoon study site were more circular (mean width-to-length ratio 0.63, 0.16 SD) than those on the coast study site (mean width-to-length

ratio 0.36, 0.15 SD; $F_{1,6} = 20.14$, $P = 0.0042$). However, the length ($F_{1,6} = 0.32$, $P = 0.5934$) and total area ($F_{1,6} = 2.40$, $P = 0.1725$) of territories on the lagoon study site did not differ from those on the coast area.

4. Discussion

Optima theory suggests that animals balance the costs of defending a territory with gains from territory ownership [47–50]. However, the activities and resources comprising the cost-benefit equation are often difficult to identify [51]. My results suggest that the condition of individual birds at least partially underpinned territory characteristics. Territory size did not differ by sex, and mates held similarly sized territories, but there was evidence that territory size increased as birds aged.

Composition and configuration of foraging habitats were also closely associated with territory size and shape. Tuamotu kingfishers held smaller territories when coconut plantation habitat was more abundant in the immediate surrounding area. Further, territories on the coast study site were long and slender, where coconut plantation habitat patches were also long and slender. Although habitat patch shape and resource distributions differed, resource quality appeared to be similar at both sites, as pairs on both sites bred successfully and there was no evident difference in survival [29, 40] and both sites were managed similarly by the same coconut plantation farmers. The sites were also positioned within 1 km and thus likely to have similar predator (*Rattus spp.*) densities.

Interestingly, birds on the coast did not extend territory boundary lengths to make extremely long and thin territories. Perhaps birds on the coast site did not, or could not, increase foraging habitat within their territories by elongating boundaries because they had already reached a maximum length. Beyond the maximum length, territories may not be economically defendable because the ability to detect intruders in other parts of the territory might be reduced, or because travel costs associated with food gathering are too great. These results align with previous models predicting that resource values decline with distance from a central location [48], and that territories are configured to maximize detection of conspecific intruders [9].

Factors underpinning territory size and shape have long been fodder for speculation among biologists. Results presented here support previous suppositions that the distribution of resources influences territory size and shape, and that territories may change dynamically as birds age. However, much remains to be learned about the finite behavioral mechanisms associated with territory establishment and maintenance, and about how those differ among taxa and regions. This investigation was aimed at long-term resident forest birds that occupy the same areas for multiple years [29], but migrant birds that establish territories during each breeding system may be even more responsive to the resources key to reproductive success. Much additional work is needed in order to develop broad theory about the interplay between spatial resource distributions, behavior, and territory size and shape.

On a global scale, tropical avian diversity is most threatened by anthropogenic modification of forested landscapes [52–54], yet we know little about the mechanisms by which habitat alteration affects birds [22]. Tuamotu kingfishers are among the most endangered birds (listed as Critical; [27]), and they occur only on the highly modified island of Niau. Assisted colonization is being considered for several Pacific kingfishers (e.g., *T. cinnamominus*, [54]), and the establishment of a second population of Tuamotu kingfishers on another island has been proposed [55]. My results indicate that coconut plantation habitat configuration might be key to the selection of sites where a second population could be established. Such sites should include >4.6 ha of coconut plantation habitat for each breeding pair of Tuamotu kingfishers, and coconut plantation resources should be configured so that they can be encompassed within territories with maximum diameters of 455 m.

Acknowledgments

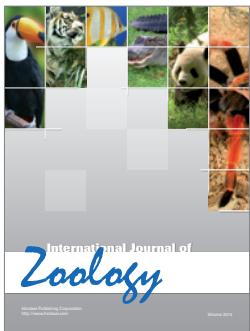
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