RESOURCE SELECTION AND SPACE USE OF THE CRITICALLY ENDANGERED TUAMOTU KINGFISHER (*TODIRAMPHUS GAMBIERI*)

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by

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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

RESOURCE SELECTION AND SPACE USE OF THE CRITICALLY ENDANGERED TUAMOTU KINGFISHER (*TODIRAMPHUS GAMBIERI*)

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RESOURCE SELECTION AND SPACE USE OF THE CRITICALLY ENDANGERED TUAMOTU KINGFISHER (*TODIRAMPHUS GAMBIERI*)

Gabrielle L. Coulombe

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ABSTRACT

I investigated the ecological requirements of the critically endangered Tuamotu Kingfisher (*Todiramphus gambieri*), with the intent to provide management recommendations that could help prevent its extinction. The species is confined to the lowland forests on Niau Atoll in French Polynesia, with less than 250 individuals. I conducted a multi-scale resource selection study based on island-wide surveys and radiotelemetry relocation data from 2006-2008. The birds avoided undisturbed vegetation and appeared to rely on coconut plantations managed with prescribed burning for acquiring food resources. Managed plantations provided foraging habitat with open understory and visible ground where the kingfishers hunted lizards and other prey items. Such conditions might have resembled those of the original forest that no longer occurs on the island. I also tested factors that have the potential to influence space use, and found that variation was driven by the configuration of foraging habitat. The birds appeared to have a maximum territory length that was likely limited by their ability to effectively defend territory boundaries, guard the nest, and provision nestlings. Thus, regions where habitats occur in very linear or distant patches may be unsuitable. I recommended translocation as a potential conservation strategy for Tuamotu Kingfishers, and provided criteria for selecting an island for establishing a rescue population.

CHAPTER 1 – CONTEXT OF THE STUDY

TUAMOTU KINGFISHER CONSERVATION

The Tuamotu Kingfisher (*Todiramphus gambieri*) is one of the world's most threatened birds because it is restricted to an extremely small range and faces many potential threats (BirdLife International, 2010; IUCN, 2010). The nominate subspecies became extinct on Mangareva in the Gambier Islands in the late 19th century (Holyoak and Thibault, 1984), and the species now comprises less than 250 individuals, confined to Niau Atoll in the Tuamotu Archipelago. The species came to attention during the planning of the construction of an airport on Niau in 2002. Anne Gouni and the Ornithological Society of Polynesia (SOP Manu) initiated surveys and found that the Tuamotu Kingfisher population was extremely small, with preliminary estimates of only 39-51 individuals (Gouni and Sanford, 2003; Gouni et al., 2004). The numbers were alarming, especially considering a previous population estimate of 400-600 kingfishers in 1974 (Holyoak and Thibault, 1984) and that the species was described as "common" in 1990 (Seitre and Seitre, 1992).

The Tuamotu Kingfisher population might have been impacted by a series of destructive cyclones that occurred in 1983 (Dupon, 1985, 1986). Additionally, introduced rats (*Rattus exulans* and *R. rattus*; Gouni et al., 2006) and cats (*Felis catus*) may potentially impact the kingfisher population through predation and competition for food (Whitaker, 1978; McCallum, 1986; Towns et al., 2006). Further, the conversion of native habitat to plantations of coconut palms (*Cocos nucifera*), and agricultural management using prescribed burning, also generated concerns.

The SOP Manu and Dr. Dylan Kesler conducted further investigations to identify threats and preserve the Tuamotu Kingfisher. The collaboration led to the first scientific study of the species starting in 2006, to an ongoing conservation project, and to my research efforts. As very little was previously known about the species, information was required about its natural history, breeding biology, demography, and ecological requirements. For example, we documented an incubation period of approximately 23 days and a fledging age of approximately 26 days. We found that fledglings were usually excluded from the parental territory within a few weeks, which differs from cooperative breeding systems of some closely related species (Kesler and Haig, 2007; Kesler et al., 2010). We worked with a large portion of the Tuamotu Kingfisher population, as the most recent population estimate was 125 individuals and from 2006-2010 we banded 67 birds, radio-tagged 45 adults and 9 juveniles, observed 52 active nests, and conducted 32 hours of focal observations of foraging and nestling provisioning. A multidisciplinary team conducted additional studies on the plants, insects, and lizards of Niau Atoll.

The work resulted in the development of a conservation plan, including management recommendations for the birds on Niau and a series of criteria for selecting an island to form a “rescue” population of Tuamotu Kingfishers. Researchers already evaluated three islands (Mangareva, Makatea, and Anaa) for the potential introduction of translocated Tuamotu Kingfishers. Ongoing and future work includes translocation experiments with the contribution of Anne Gouni and the SOP Manu, James Mejeur and

Disney's Animal Kingdom, and Dr. Kesler's Avian Conservation Laboratory, a genetic study conducted by Dr. David Piquemal and Florian Noguier at Skuld-Tech, and an ecosystem level study on trophic interactions conducted by Dr. Eric Vidal and Diane Zarzoso-Lacoste at the University of Aix-Marseille. Knowledge from the Tuamotu Kingfisher project will likely aid conservation efforts for many other threatened kingfisher species on Pacific islands.

Our collaborative efforts also led to the development of an education and outreach program with the farmers and children of Niau Atoll. We held public meetings and conducted interactive workshops in classrooms and in the field, where local inhabitants learned about wildlife and research techniques. The method was effective, as it opened dialogs with landowners and people retained information from year to year. The children are aware of the biodiversity on their island, are enthusiastic about the environment, and are able to discuss biological and conservation concepts.

THESIS CONTENTS AND FORMAT

My research focused on identifying the ecological requirements of Tuamotu Kingfishers. I conducted island scale and home range scale studies to identify critical habitats and resources for survival and reproduction. I then further investigated factors influencing the movement and space use of individuals. My thesis chapters address complementary perspectives on Tuamotu Kingfisher ecology. The chapters each present essential introductory information and may contain some redundant material, as they were prepared for publication in separate peer-reviewed journals.

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CHAPTER 2 – AGRICULTURAL COCONUT FOREST AS HABITAT ON TROPICAL PACIFIC ISLANDS: MULTI-SCALE RESOURCE SELECTION OF A CRITICALLY ENDANGERED KINGFISHER

ABSTRACT

Anthropogenic modification of tropical forests is a primary threat to global avian diversity. Many lowland forests on tropical Pacific islands were converted to coconut (*Cocos nucifera*) plantations that still host native fauna. We evaluated resource selection of the critically endangered Tuamotu Kingfisher (*Todiramphus gambieri*) confined to the lowland forests on Niau Atoll in French Polynesia, with less than 250 individuals. At the landscape scale, kingfisher occurrence was best predicted by habitat features associated with foraging opportunities, including open agricultural coconut forest and low-vegetation wetland, exposed foraging substrate, and hunting perches. Conversely, kingfisher distribution was negatively associated with undisturbed vegetation, including primary feo forest and fallow coconut forest. At the home range scale, utilization distributions from radio-tracked kingfishers similarly indicated that they most preferred agricultural coconut forest and least preferred primary feo forest. Foraging opportunities seemed to underlie space use and habitat selection of Tuamotu Kingfishers on Niau at both spatial scales. Further, the birds may rely on coconut plantations managed with prescribed burning for acquiring food resources. The kingfisher is a rare example of a threatened tropical species benefited by agricultural management, and our findings provide support for conservation strategies based on establishing rescue populations of kingfishers on other islands with coconut agriculture. Our results further support

suggestions that agroforestry and other anthropogenic landscapes hold important potential conservation value, in particular for many insular kingfisher species that are threatened with extinction.

Keywords: coconut agriculture; foraging habitat; Pacific islands; prescribed burning; resource selection; Tuamotu Kingfisher.

1. INTRODUCTION

The conservation status of avifauna has been deteriorating over the past two decades (Butchart et al., 2004; IUCN, 2009) and will likely be further impaired in years to come (Jetz et al., 2007). The Pacific region holds the greatest number of threatened birds (Johnson and Stattersfield, 1990). On the islands of French Polynesia, for example, 18 of 25 endemic landbird species are threatened with extinction (Gouni and Zysman, 2007). Island birds account for only one fifth of avian species but for 90% of documented avian extinctions (Johnson and Stattersfield, 1990), as a result of introduced invasive species, habitat loss, and hunting (Milberg and Tyrberg, 1993; Steadman, 1997; Blackburn et al., 2004).

Anthropogenic habitat modification affects over 90% of threatened birds worldwide (BirdLife International, 2010a) and poses the greatest risk to island birds (Steadman, 1997; BirdLife International, 2000). Habitat loss was included in Jared Diamond's (1984) "evil quartet" of factors causing extinction and Edward O. Wilson's (2002) "HIPPO" list of primary threats to biodiversity. Some suggest that loss of avian habitat is occurring primarily through the expansion and intensification of agriculture and conversion of tropical forest (Jetz et al., 2007; BirdLife International, 2010a). On islands, most threatened landbirds inhabit forests (Johnson and Stattersfield, 1990) and many of those forests have already been impacted (Brooks et al., 1997; Fordham and Brook, 2010). For example, lowland forests on numerous Pacific islands were converted to agricultural coconut (*Cocos nucifera*) forests (Mueller-Dombois and Fosberg, 1998). Conservation of avifauna thus requires the identification and preservation of key forested habitats and greater understanding of avian interactions with anthropogenic landscapes (Chazdon et al., 2009; Gardner et al., 2009).

Conservation managers can attempt to reintroduce species to areas where they have been extirpated, or to introduce them outside the known historical range when limited native habitat remains (IUCN, 1998). There have been concerns about using translocation (sensu IUCN, 1987) as a conservation technique (Wolf et al., 1996; Armstrong and Seddon, 2008) and about the risks of planned introductions to recipient ecosystems (Ricciardi and Simberloff, 2009). However, translocation can be a viable rescue strategy for insular birds (Franklin and Steadman, 1991; Armstrong et al., 2002; e.g., Komdeur, 1994; Reynolds and Klavitter, 2006; Robertson et al., 2006), and may provide one of the only opportunities for preserving avian diversity in the Pacific region (Seitre and Seitre, 1992; Steadman, 2006). Oceanic islands tend to have fewer competitor species, and habitat features are shared across wide regions (Whittaker and Fernández-Palacios, 2007). Even in these relatively simple ecosystems, however, potential release sites must be carefully assessed because habitat quality is a primary determinant of translocation success (Griffith et al., 1989; IUCN, 1998; Wolf et al., 1998).

The Tuamotu Kingfisher (*Todiramphus gambieri*) is among the most threatened birds in the world (Critically Endangered, IUCN 2010), with only one extant population of approximately 125 individuals (BirdLife International 2010b). The nominate subspecies was extirpated from the Gambier islands in the late 19th century (Holyoak and Thibault, 1984), and the species is now confined to the small atoll island of Niau where tropical forest was extensively converted to coconut agriculture (Mueller-Dombois and Fosberg, 1998; Butaud, 2007). As is the case for many threatened tropical species, information about the natural history and ecological requirements of Tuamotu Kingfishers was previously almost nonexistent.

We studied resource selection of Tuamotu Kingfishers at the landscape and home range scales (Johnson, 1980; Block and Brennan, 1993) to gain insight into the effects of coconut agriculture, identify resources required for survival and reproduction, and provide information for the conservation management of the species. Forming rescue populations of Tuamotu Kingfishers on other islands has been considered as a possible conservation strategy to minimize extinction risks from catastrophic events, invasive species, or disease outbreaks (Gouni et al., 2006). Results from this study will thus also be helpful for evaluating potential islands for establishing a second population of the birds.

2. METHODS

2.1. Study site

Niau Atoll (16°10'S, 146°22'W; Fig. 1) is part of the Tuamotu Archipelago Endemic Bird Area (EBA 214; BirdLife International, 2003) and the UNESCO Man and Biosphere Reserve of Fakarava in French Polynesia. Niau is a raised atoll with a land area of 26 km^2 and a large enclosed lagoon (Andréfouët et al., 2005). Production of coconut pulp (copra) underlies Niau's economy and agricultural coconut forests cover most of the lowlands, which occur along the lagoon and ocean shores (Fig. 2). Coconut plantations range from fallow plots with dense understory vegetation, to heavily managed plots with exposed ground (Fig. 3). Wetlands dominated by *Sesuvium portulacastrum* and *Cladium mariscus* (Butaud, 2007) occur on the east fringe of the lagoon. The littoral zone consists of coral reef with low strand vegetation and sparse coconut trees. Inland areas are characterized by dense primary forest growing on jagged fossilized limestone coral (feo forest or makatea). Mixed coconut-feo forest occurs on the interior edge of the feo forest. The climate is tropical oceanic without pronounced seasons, with a mean annual temperature of 26 °C and annual rainfall of 1500-2000 mm (Mueller-Dombois and Fosberg, 1998).

2.2. Landscape-scale resource selection

We used an information-theoretic approach (Burnham and Anderson, 2002) to evaluate the association between landscape-scale resources and the spatial distribution of Tuamotu Kingfishers. We developed four *a priori* logistic regression models that relate the probability of kingfisher occurrence to nesting resources, foraging habitat, undisturbed vegetation, or a combination of these factors (Table 1). Tuamotu Kingfishers nest in standing dead trees (hereafter snags), their population may thus be limited by the number of available nest sites (Walters et al., 1992; Newton, 1994). From our observations of more than 50 active nests, we defined nest snags as coconut snags > 1.25 m tall and with sufficient decomposition to have lost the tree crown. Another model considered foraging habitat, because foraging resources potentially underlie habitat use (Block and Brennan, 1993) and limit population size in birds (Martin, 1987; Newton, 1998). Open habitat, hunting perches, and visible ground provide foraging opportunities for Tuamotu Kingfishers, which are opportunistic sit-and-wait predators of lizards and a wide variety of small arthropods (Marie, 2006). Our third model predicted that Tuamotu Kingfisher occurrence was negatively affected by human disturbance and modified vegetation (Block and Brennan, 1993) in agricultural coconut forest.

2.2.1 Tuamotu Kingfisher surveys

We surveyed Niau Atoll for Tuamotu Kingfishers at 145 locations in February 2006, and in November 2007 and 2008. Survey locations occurred throughout the island and were concentrated on the lowlands along the lagoon and the ocean because kingfishers were rarely detected in the feo forest interior during previous searches (Holyoak and Thibault, 1984; Gouni et al., 2006). Survey locations were spaced 300 m apart, except on the eastern ocean coast where they were spaced 500 m apart because of extensive stretches of uniform habitat. We recorded the geographic coordinates of each location with a hand-held global positioning system (GPS; Rino 520HCx; Garmin Ltd., Olathe, Kansas, USA).

We conducted surveys between 0500 and 0900 hours during clement weather (wind < 20 km/h and no rain). We broadcast Tuamotu Kingfisher calls from a hand-held stereo for 60 seconds and recorded audio and visual detections of Tuamotu Kingfishers during the subsequent 10 minutes. Based on previous behavioral observations in areas where birds were known to occur, we assumed that birds within 100 m responded to the playback calls. Tuamotu Kingfishers are territorial residents, thus we assumed that detections represented birds that were occupying the area. We defined the dependent variable in our logistic regression models by classifying survey locations as unoccupied if kingfishers were never detected, and as occupied if kingfishers were detected during the most recent (2008) survey and at least one other survey.

2.2.2. Resources

We evaluated resources in 2008 at stations consisting of the area within 100 m of Tuamotu Kingfisher survey locations. Stations that comprised > 25% of water (lagoon or ocean) were excluded from analyses because the Tuamotu Kingfisher is a terrestrial species. Remaining stations had a mean area of water of < 6%. We evaluated resources at randomly selected stations, 29 of which were occupied by Tuamotu Kingfishers and 29 of which were unoccupied. We used a land cover map of Niau (Butaud, 2007) and a geographic information system (ArcGIS 9.3; ESRI, Redlands, California, USA) to measure the proportional composition of vegetation types (agricultural coconut forest, non-agricultural forest including mixed coconut-feo forest and primary feo forest, and wetland) of each station.

We sampled nest snags, ground cover, and hunting perches based on linear transects centered on the survey locations, because habitats were configured linearly with well-defined boundaries consisting of water or primary feo forest. Uniform sampling methods were appropriate because resources were not clumped or uniformly distributed at the scale of sampling. We recorded the distance to the nearest nest snag from four points along the transect (at -50, -25, 25, and 50 m) to estimate nest-snag density ($1/[4*(\text{mean distance})^2]$; Waite, 2000). In agricultural coconut forest, we measured ground cover in six 100 m^2 quadrats positioned on each side of the linear transect (at -50, 0, and 50 m), and halfway between the transect line and the feo forest or water edge (measured with Bushnell Yardage Pro Sport 450 laser range finder). Ground cover was classified as percent visible ground (vegetation < 50 cm tall) and percent high vegetation (> 50 cm tall), and we multiplied the mean by the proportion of agricultural coconut forest to obtain an estimate for the station. As an indicator of the number of hunting perches, we measured the distance to a visual obstruction at eyelevel in 10 directions separated by 40°, from two points along each transect (at -50 and 50 m), using a compass and a laser range finder. Shorter mean distance indicated higher perch density. Finally, we categorized agricultural coconut forest as managed or fallow depending on whether the area was actively used to produce coconuts.

2.2.3. Model selection

We used Program R (glm function; R Development Core Team, 2005) to compute the maximum likelihood parameter estimates (MLE) and deviance (-2*[log-likelihood]) of our candidate models. We ranked candidate models based on a second-order Akaike

Information Criterion (AIC_c; Burnham and Anderson, 2002) and tested model fit with a Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow, 2000). We averaged parameter estimates across top-ranked models summing ≥ 90% of the Akaike weight (ω_i) (Burnham and Anderson, 2002), and calculated weighted unconditional standard errors (SE) and 95% confidence intervals (CI).

2.3. Home range scale resource selection

We defined a home range as the extent of area with a defined probability of use by a single bird during one breeding season (Kernohan et al., 2001). We radio-tracked kingfishers to model space use and habitat availability and test if birds used habitats disproportionally to the amount available (Johnson, 1980; Jones, 2001; Buskirk and Millspaugh, 2006). We conducted the home range scale study on the east side of Niau on a study area situated between the feo forest and the lagoon, and on a second study area between the feo forest and the ocean.

2.3.1. Radiotelemetry

Radiotelemetry work was conducted during the Tuamotu Kingfisher breeding season in Oct.-Nov. 2006, Oct.-Nov. 2007, and Sep.-Dec. 2008. We thoroughly searched the study areas to find all kingfishers and nests. We captured birds with a hoop-net at the nest cavity or using mist-nets. Birds were marked with numbered aluminum leg-bands and unique combinations of colored darvic leg-bands, and fitted with radio-transmitters (model BD-2; Holohil Systems, Ottawa, Canada) weighing 1.5 g (≤ 4% of body mass;

Gaunt et al., 1999). We used a modified leg harness that included a 1 cm length of rubber band, which functioned as a weak link so that equipment would shed from the bird after radio-tags lost functionality (Kesler, in review). We located radio-tagged birds throughout daylight hours (between approximately 0500 and 1800) because previous investigations of congener kingfishers found that nocturnal movements were unlikely (Kesler and Haig, 2007a). Birds were located approximately twice daily, with consecutive sampling separated by > 2 hrs to avoid serial correlation (e.g., Kesler and Haig, 2007b). We located birds using a hand-held Yagi antenna and telemetry receiver (model R-1000, Communications Specialists, Inc., Orange, CA) and recorded geographic coordinates with a GPS and a compass. When we could not observe birds visually, we used triangulation to estimate locations. Consecutive directional bearings were separated by < 10 min to minimize error due to potential movement of the birds. We estimated the maximum likelihood location for each bearing group using LOAS (Ecological Software Solutions, Urnäsch, Switzerland). We excluded triangulations that had a 95% error ellipse > 0.6 ha, which was approximately 10% of the mean Tuamotu Kingfisher territory size. We excluded relocation points within 10 m of nests to eliminate cluster bias on kernel density results (White and Garrott, 1990).

2.3.2 Habitat use versus availability

We derived utilization distribution (UDs) from the telemetry-based bird relocations to define habitat use. The UD provides a probabilistic and continuous measure of space use (Marzluff et al., 2001), and reduces concerns about independence of points and error related to telemetry and mapping (Marzluff et al., 2004; Thomas and Taylor, 2006). We derived the UDs using KernelHR (Version 4.27; Seaman et al., 1998) with a fixed kernel-density estimator and bandwidth selection based on least-square cross-validation (Seaman and Powell, 1996). We overlaid the UD grids on a vegetation cover map of Niau in ArcGIS. We included 95% of the UD by volume to reduce potential bias from the tails, and measured the proportion comprised of each habitat type.

We defined habitat availability for each study area (design 2 sensu Thomas and Taylor, 2006) using a minimum convex polygon that represents the maximum extent of where kingfishers were located. We derived the polygons from the telemetry relocation points and measured the proportion of each habitat type using Hawth's Tools extension (Beyer, 2004) in ArcGIS. We excluded areas covered by lagoon and ocean. We also excluded the urbanized zone from available habitat types because it was only available to one bird at the edge of one study area and the bird was never located there.

For each study area we ranked habitat types from most to least preferred, by comparing habitat use to habitat availability in a weighted compositional analysis (multivariate analysis of variance; Aebischer et al., 1993; Millspaugh et al., 2006) using Resource Selection for Windows (Version 1.00 Beta 8.4, F. Leban, 1999). We pooled data from males and females and from all years (2006-2008) because there was no gender or year effect on space use (see Chapter 2). Compositional analysis has been criticized for inflating Type I error rates from rare habitat types with zero use values (Bingham et al., 2007). However, in this case the method was robust because availability was $\geq 5\%$ for all habitat types. Further, replacing zero use values with 0.01 as recommended by Aebischer et al. (1993) or with 0.3-0.7 as recommended by Bingham and Brennan (2004) yielded identical ranking results. We used an α of 0.05 for all tests of significance.

3. RESULTS

3.1. Landscape scale resource selection

Tuamotu Kingfishers were detected at 26%, 21%, and 27% of survey locations in 2006, 2007, and 2008 respectively. We classified 36 (25%) locations as occupied by Tuamotu Kingfishers and 73 (50%) locations as unoccupied (Fig. 4). The birds occurred throughout Niau and were most common on the eastern portion of the island. All locations near *Sesuvium*-dominated wetlands were occupied. Locations that were occupied and situated within primary feo forest were in small patches of managed coconut groves not shown at the scale of the map.

Our model of foraging opportunities ranked first (ω_i = 0.854) and was > 7 times more likely to explain Tuamotu Kingfisher occurrence on Niau when compared to the second-ranked model (Table 2). Additionally, the foraging model was a good fit for the data (i.e., predicted values did not significantly differ from observed values; χ^2 = 8.138; df = 8; P = 0.420). The model of undisturbed vegetation ranked second (ω_i = 0.116) and was also a good fit (χ^2 = 10.422; df = 8; P = 0.237). However, parameter estimates indicated a relationship opposite of that expected, as kingfisher occurrence was negatively associated with undisturbed vegetation. The distribution of nest sites was unlikely to explain kingfisher occurrence on Niau (Δ AIC$_c$ = 10.22; ω_i = 0.004). We thus averaged the two top models to garner 97% of the Akaike weight (ω_i), and obtained the logistic equation:

$\text{logit}(\pi) = -1.729 + 2.280(\text{managed coconut forest}) - 0.075(\text{mean distance to perch in m}) + 0.061(\%\ \text{visible ground}) - 0.029(\%\ \text{non-agricultural forest}) - 0.024(\%\ \text{high vegetation}) + 0.011(\%\ \text{wetland}),$

where π is the predicted probability of Tuamotu Kingfisher occurrence. Kingfisher occurrence was significantly associated with managed coconut forest at the 95% confidence limit (Table 3). With all other variables held at their mean, agricultural management increased the probability of kingfisher occurrence by a factor of 5.6 (95% CI: 1.8-9.8). Mean perch distance and percent of visible ground also had significant effects on the probability of kingfisher occurrence (Table 3, Fig. 5).

3.2. Home range scale resource selection

We obtained telemetry relocations (Fig. 6.A) from visual observations (87%), triangulation (10%; median error ellipse: 0.06 ha), and biangulation (3%). We generated 28 UD home ranges (e.g., Fig. 6.B) with a mean of 34 (range: 15-51) telemetry relocations. They included 15 male and 13 female home ranges, and respectively 9, 12, and 7 home ranges from 2006, 2007, and 2008. Home ranges were composed primarily of agricultural coconut forest (Table 4).

Tuamotu Kingfishers from both study areas disproportionally preferred agricultural coconut forest and least preferred primary feo forest, when compared to other available habitat types (Table 5). On the lagoon study area, wetland habitat ranked second and was significantly selected over mixed coconut-feo forest. On the ocean study area, the littoral zone was significantly selected over primary feo forest.

4. DISCUSSION

The Tuamotu Kingfisher is a rare example of a threatened species benefited by agricultural management within its native range. The birds selected agricultural coconut forest both at the landscape scale and within individual home ranges. Further, they preferred managed compared to fallow coconut forest, and we observed that even some of the most heavily managed areas hosted successful breeding pairs. Agricultural areas therefore seemed to provide advantages that offset potential detrimental effects from fires and human disturbance during coconut harvest.

Managed coconut plantations likely provide more foraging opportunities for the kingfishers when compared to fallow plantations and primary feo forest. They feature open habitat and exposed ground where Tuamotu Kingfishers were often observed foraging. The use of fire for agricultural purposes in lowland tropical forests may have caused the extinction of many island birds (Olson and James, 1982). However, Niau farmers typically burn small piles of woody debris and the fires do not tend to propagate. Prescribed burning is therefore potentially compatible with preserving kingfisher nest snags and food resources, while providing foraging habitat for the birds.

We suggest that foraging habitat underlies space use and resource selection of Tuamotu Kingfishers on Niau. Landscape-scale kingfisher distribution was best explained by features associated with foraging opportunities, including open habitat, hunting perches, and visible ground. Additionally, birds near wetlands selected wetlands as the second most preferred habitat, likely exclusively for foraging. Birds selected *Sesuvium*-dominated wetlands, where they hunted for small invertebrates (Isopoda;

Marie, 2006) from perches along the margins. They were never observed using *Cladium*-dominated wetlands, which featured thick and tall vegetation that provided few foraging opportunities. Availability of foraging habitat could thus limit the number of Tuamotu Kingfishers.

Prey availability might also limit the number of Tuamotu Kingfishers. Skinks (Scincidae) and geckos (Gekkonidea; Ineich et al., 2007) are primary items for courtship feeding and provisioning nestlings of Tuamotu Kingfishers (pers. obs.) and other Polynesian kingfishers (e.g., Hayes, 1991; Rowe and Empson, 1996). Rats (*Rattus* spp.) introduced to islands have been documented to decrease lizard abundance and diversity through predation, competition for food, and ecosystem-level habitat modification (Whitaker, 1973; McCallum, 1986; Towns et al., 2006; Buckley and Jetz, 2007), and may therefore decrease prey availability for the kingfishers.

Broadleaf trees may enhance foraging habitat, as foliage provides an additional foraging substrate where we often observed kingfishers capture small prey items for consumption and provisioning nestlings. Further, broadleaf trees provide more hunting perches compared to coconut palms. Tuamotu Kingfishers also require perches for nest building, as they initiate excavation by flying from a nearby perch and colliding, bill-first, with the nesting substrate. They also use perches for stunning prey items, copulation, loafing, and guarding the nest. Broadleaf trees additionally provide shade and cover from the weather.

Despite Tuamotu Kingfishers' preference for agricultural coconut forest, it may be less suitable than the original forest that no longer exists on the island. Mixed tropical broadleaf forest occurred on the lowland areas of Niau before being converted to coconut agriculture (Mueller-Dombois and Fosberg, 1998; Butaud, 2007), and the birds likely used this habitat type. Further, the use of coconut snags for nesting might be a recent development in the Tuamotu Kingfisher's natural history (Butaud, 2007). Perhaps the kingfishers nested in tree species that were abundant prior to the introduction of coconut agriculture, such as *Pisonia grandis*, a soft-wooded tree used by other *Todiramphus* species (e.g., *T. cinnamominus*; Marshall, 1989; *T. chloris*; N. Johnson, unpublished results), or *Pritchardia pericularum*, which resembles the coconut palm (Butaud, 2007). Nonetheless, island-wide surveys conducted in three consecutive years indicated that there was no apparent decline of the Tuamotu Kingfisher population, and we observed that the kingfishers were able to reproduce successfully in coconut plantations. Managed coconut plantations may provide conditions similar to those of the original forest, which featured an open understory with canopy cover, contrarily to the extant primary feo forest which has dense understory vegetation.

5. MANAGEMENT RECOMMENDATIONS

Positive collaboration with Niau copra farmers is critical for the conservation of Tuamotu Kingfishers, as the extant kingfisher population occurs primarily in agricultural coconut forests and birds rely on those areas for acquiring resources for survival and reproduction. Small fires prescribed by farmers create foraging habitat. However, intensification of agricultural management could disturb nesting and decrease the abundance and diversity of kingfisher foods (Butaud, 2007). Retaining plant litter and ground cover might promote the abundance of lizards and other prey items (D. Zarzoso-Lacoste, unpublished results). Most importantly, farmers should preserve dead standing coconut trees as they are the kingfishers' sole nesting substrate. Applying rat guards (metal bands) to nest trees might reduce predation on eggs and nestlings. In addition, preserving broadleaf trees and dense vegetation would provide hunting perches and cover for juvenile kingfishers.

Introducing species to areas outside their known historical range for conservation purposes has been debated (Ricciardi and Simberloff, 2009). However, the Tuamotu Kingfisher provides an example of a species for which translocation to another island may be advisable. Many islands in French Polynesia are characterized by agricultural coconut habitats similar to those on Niau – for example the large island complex of Anaa. In addition to the recommendations above, conservation managers should ensure that coconut plantations support sufficient foraging habitat including hunting perches and visible ground. Assessing the availability of prey, in particular lizards, could also help evaluate the suitability of potential sites for introducing Tuamotu Kingfishers.

6. CONSERVATION IMPLICATIONS

Our research lends support to recent suggestions that conservation of tropical biodiversity requires the integration of human-modified landscapes, in addition to protected natural areas, and the formation of alliances with local stakeholders (Harvey et al., 2008; Chazdon et al., 2009; Garcia et al., 2009). Agroforestry holds potential conservation value for tropical species (Bhagwat et al., 2008), including forest birds (Sekercioglu et al., 2007). On the other hand, some authors have warned that investment for the conservation of tropical forest birds is better spent on natural areas than on enhancing agricultural landscapes (Edwards et al., 2010). Additionally, it has been suggested that large coconut plantations need to be replaced with native vegetation in order for translocated birds to survive (Franklin and Steadman, 1991). However, little unmodified native forest remains in Polynesia, and coconut is the main cash crop for the majority of Polynesian smallholder agroforesters (Clarke and Thaman, 1993). We alternatively suggest that consideration should be given to the use of coconut plantations, one of the most extensive types of agriculture on tropical Pacific islands (Mueller-Dombois and Fosberg, 1998), and other human-modified landscapes for the conservation of insular kingfishers.

Knowledge from one species often informs management decisions for other related species (e.g., Kesler and Haig, 2007c). However, case-by-case assessment is still required as managing human-modified landscapes for conservation could potentially lead to ecological traps (Schlaepfer et al., 2002). In addition to the Tuamotu Kingfisher, many *Todiramphus* species could potentially benefit from this approach. The Marquesan Kingfisher (*T. godeffroyi*; Critically Endangered) went extinct from one of the two islands it historically inhabited and has been observed in coconut plantations; the Mangaia Kingfisher (*T. ruficollaris*; Vulnerable) is also a single-island endemic, nests in coconut trees, and commonly occurs in disturbed forest; the Sombre Kingfisher (*T. funebris*; Vulnerable) resides in declining closed-canopy lowland forests often overlooking clearings and visits coconut groves; and the Chestnut-bellied Kingfisher (*T. farquhari*; Near Threatened) also appears moderately tolerant of habitat modification (IUCN 2010; BirdLife International, 2010b). Additionally, the Guam Micronesian

Kingfisher (*Todiramphus cinnamominus cinnamominus*; Endangered; US Fish and Wildlife Service, 1984) occurred in coconut forests before being extirpated from Guam due to introduced snakes (Jenkins, 1983).

Insular species are particularly vulnerable to anthropogenic interference (Vitousek, 1988), but may also be more tolerant of habitat modification when compared to more specialized mainland species. Many avian species on islands are considered generalists (Lack, 1970; Grant, 1998; Whittaker and Fernández-Palacios, 2007), including other tropical kingfishers (e.g., *Halcyon chloris*; Steadman and Franklin, 2000; *Halcyon recurvirostris*; Freifeld et al., 2001) and many insectivorous birds of Eastern Polynesia (Holyoak and Thibault, 1977; Thibault and Guyot, 1987). Further, birds surviving on islands long inhabited by humans might be less sensitive to human-induced changes (Pimm et al., 1994; Biber, 2002). Therefore, perhaps other insular birds can also benefit from minor changes to human-modified landscapes.

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FIGURES

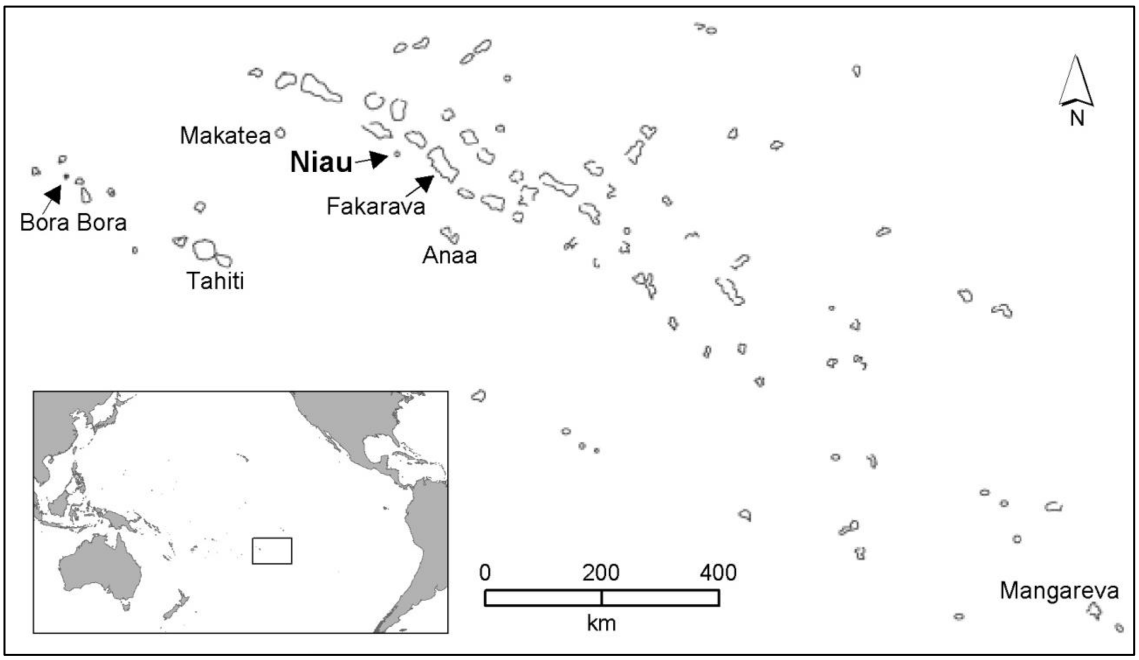

Fig. 1. Location of Niau Atoll in the Tuamotu Archipelago in French Polynesia.

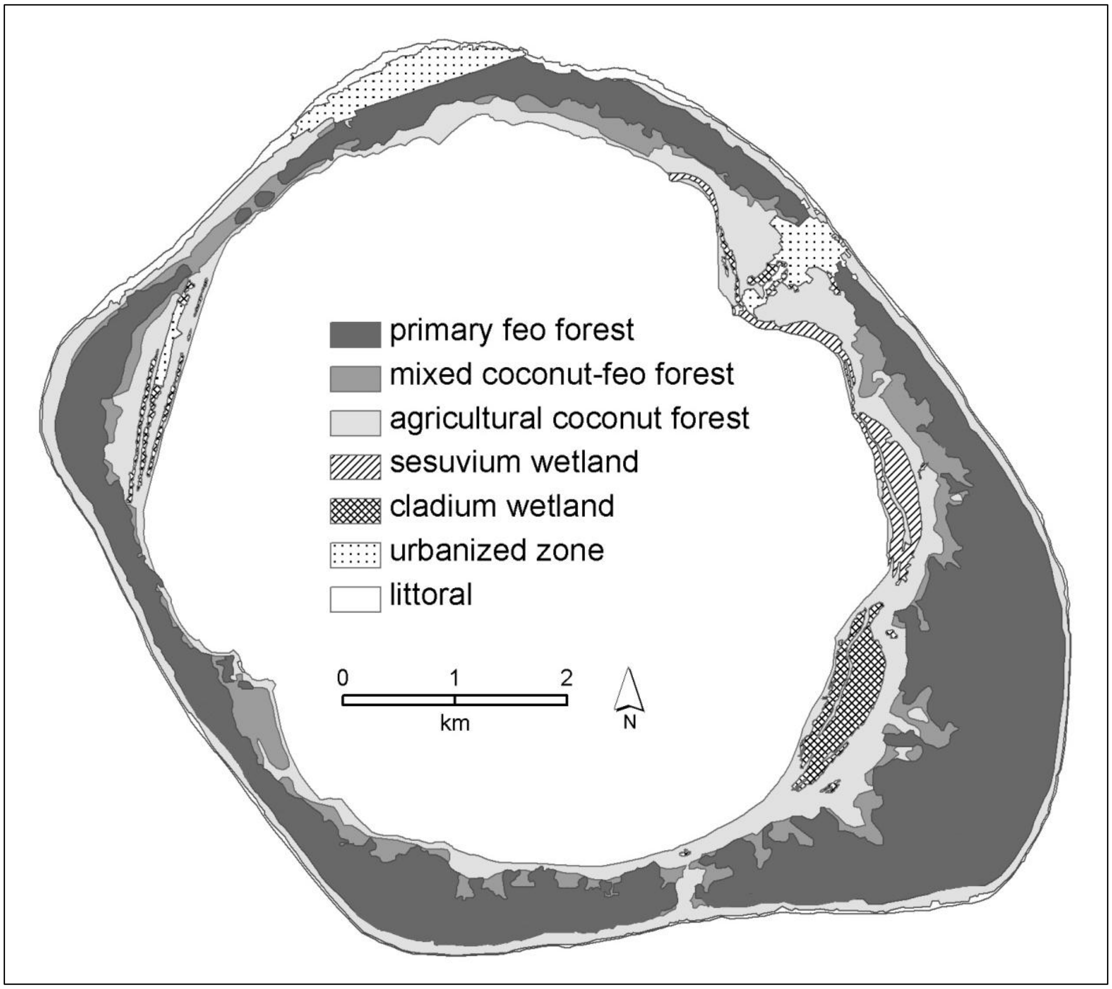

Fig. 2. Vegetation cover map of Niau Atoll (adapted with permission from Butaud (2007)).

Fig. 3. Agricultural coconut forest on Niau Atoll in 2008: fallow plot (A), and plot managed with prescribed burning (B).

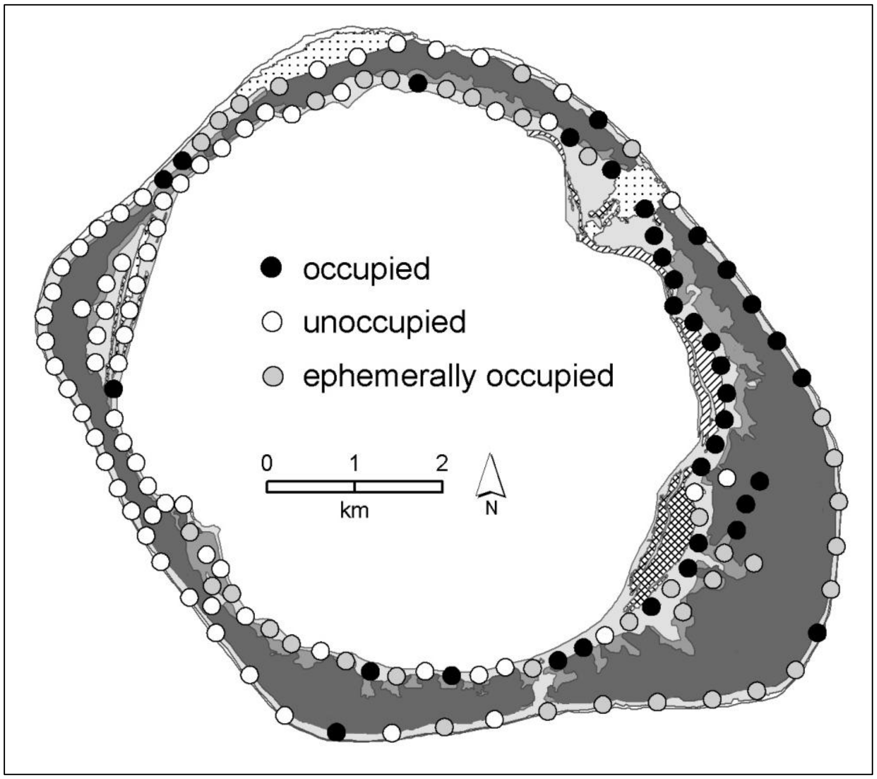

Fig. 4. Locations and results of Tuamotu Kingfisher surveys conducted on Niau Atoll in 2006-2008.

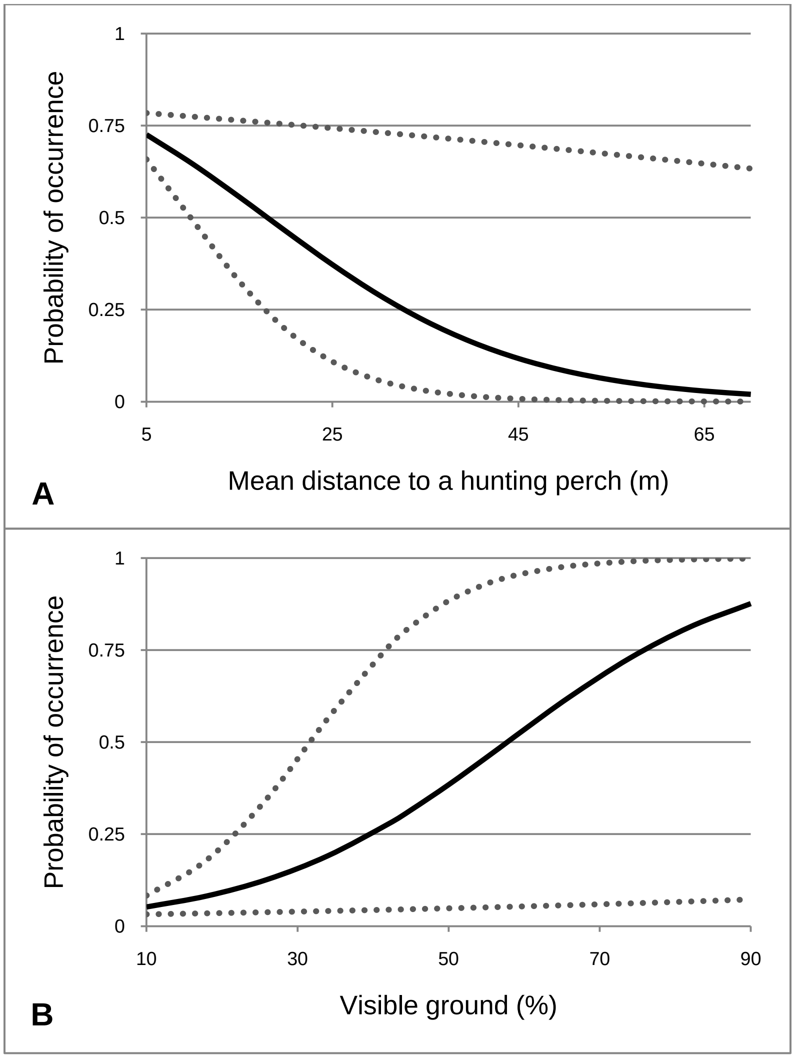

Fig. 5. Predicted effect of the mean distance to a hunting perch (A) and of the proportion of visible ground (B) on the probability of Tuamotu Kingfisher occurrence; dotted lines: 95% confidence interval.

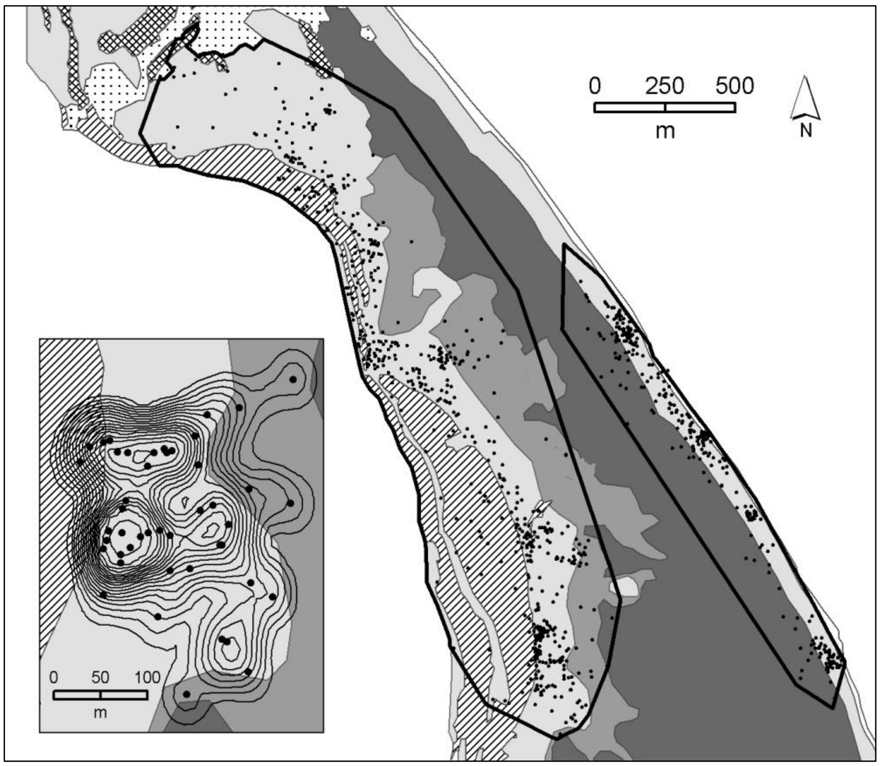

Fig. 6. Radiotelemetry relocations of Tuamotu Kingfishers on two study areas on Niau Atoll in 2006-2008. Insert: example of a Tuamotu Kingfisher home range represented by a kernel utilization distribution (95% contour by volume).

TABLES

Table 1.

Candidate logistic regression models of Tuamotu Kingfisher occurrence on Niau Atoll; π: predicted probability of kingfisher occurrence.

Model	Model structure	Expected relationship
Nest sites	$\text{logit}(\pi) = \beta_0 + \beta_1$(snag density)	$\beta_1 > 0$
Foraging opportunities	$\text{logit}(\pi) = \beta_0 + \beta_1$(managed coconut forest) + β_2(mean perch distance) + β_3(visible ground) + β_4(wetland)	$\beta_1 > 0$, $\beta_2 < 0$, $\beta_3 > 0$, $\beta_4 > 0$
Undisturbed vegetation	$\text{logit}(\pi) = \beta_0 + \beta_1$(high vegetation) + β_2(managed coconut forest) + β_3(non-agricultural forest)	$\beta_1 > 0$, $\beta_2 < 0$, $\beta_3 > 0$
Global	$\text{logit}(\pi) = \beta_0 + \beta_1$(high vegetation) + β_2(managed coconut forest) + β_3(non-agricultural forest) + β_4(mean perch distance) + β_5(snag density) + β_6(visible ground) + β_7(wetland)	

Table 2.

Ranked logistic regression models of the probability of Tuamotu Kingfisher occurrence on Niau Atoll; *K*: number of parameters, AIC_c: second-order Akaike Information Criteria, ω_i: Akaike weight (i.e., model probability given the set of candidate models).

Model	log-likelihood	*K*	AIC_c	Δ AIC_c	ω_i
Foraging opportunities	-30.55	5	72.27	0.00	**0.854**
Undisturbed vegetation	-33.84	4	76.45	4.18	**0.116**
Global	-30.15	8	79.30	7.03	0.025
Null (intercept only)	-39.50	1	81.07	8.80	0.010
Nest sites	-39.28	2	82.79	10.52	0.004

Table 3.

Model-averaged parameter estimates included in the logistic equation for the predicted probability of Tuamotu Kingfisher occurrence on Niau Atoll; SE: unconditional standard error, CI: confidence interval.

Parameter	Estimate	SE	95% CI
managed coconut forest [a]	2.280	0.815	**0.682, 3.878**
mean perch distance in m	-0.075	0.032	**-0.138, -0.011**
% visible ground	0.061	0.026	**0.011, 0.111**
% non-agricultural forest	-0.029	0.016	-0.061, 0.003
% high vegetation	-0.024	0.025	-0.073, 0.026
% wetland	0.011	0.027	-0.043, 0.064

[a] categorical variable

Table 4.

Mean proportion of habitat types included in Tuamotu Kingfisher home ranges on Niau Atoll in 2006-2008; Area: proportion of total surface used; UD: proportion of total intensity of use; habitat types: agricultural coconut forest, wetland, littoral zone, mixed coconut-feo forest, primary feo forest.

	Agricultural [a, b]		Wetland [a]		Littoral [b]		Mixed [a]		Primary [a, b]	
	Area	UD	Area	UD	Area	UD	Area	UD	Area	UD
Mean (%)	65	74	24	20	7	7	10	7	10	5
SD	13	11	13	12	4	5	11	10	15	8
Range (%)	39-88	54-93	6-55	3-43	0-16	0-16	0-35	0-30	0-55	0-31

[a] lagoon study area (*n* = 19 home ranges); [b] ocean study area (*n* = 9 home ranges)

Table 5.

Ranking matrix of habitat types included in Tuamotu Kingfisher home ranges on Niau Atoll, based on a weighted compositional analysis; + indicates a preference for habitat [a] when compared to habitat [b], and + + + indicates significance using $\alpha = 0.05$; habitat types: agricultural coconut forest, wetland, mixed coconut-feo forest, primary feo forest, littoral zone.

Lagoon study area					
	Agricultural [b]	Wetland [b]	Mixed [b]	Primary [b]	**Rank**
Agricultural [a]		+ + +	+ + +	+ + +	**1**
Wetland [a]	- - -		+ + +	+ + +	**2**
Mixed [a]	- - -	- - -		+	**3**
Primary [a]	- - -	- - -	-		**4**
Ocean study area					
	Agricultural [b]	Littoral [b]	Primary [b]	**Rank**	
Agricultural [a]		+ + +	+ + +	**1**	
Littoral [a]	- - -		+ + +	**2**	
Primary [a]	- - -	- - -		**3**	

CHAPTER 3 – LANDSCAPE CONFIGURATION LIMITS RESOURCE AVAILABILITY FOR A CRITICALLY ENDANGERED TROPICAL KINGFISHER

ABSTRACT

Tropical forest birds are primarily threatened by habitat conversion, yet we know little about how they use modified landscapes. Understanding factors influencing space use of threatened birds can improve their conservation management. We investigated space use in a tropical forest resident, the critically endangered Tuamotu Kingfisher (*Todiramphus gambieri*). We collected radiotelemetry data from 2006-2008 and estimated home ranges (n = 29) using a local convex hull method. Tuamotu Kingfisher home ranges were representative of their territories, as they were very similar between mates and consisted of areas defended against other conspecifics. Home range size varied greatly among individuals, but was not influenced by sex or seniority. Instead, differences in landscape structure, in particular the configuration of preferred foraging habitat, appeared to drive intraspecific variation in space use. In regions where preferred habitat occurred in a long narrow patch, home ranges were half the size and contained 50% less preferred habitat than home ranges where habitat patches were wider. Birds appeared to have a maximum territory length of approximately 500 m, likely because of fitness costs related to territory defense and nestling provisioning. The spatial arrangement of resources might therefore limit resource availability for Tuamotu Kingfishers in heterogeneous landscapes. The kingfishers appeared to maximize the amount of preferred habitat within the maximum travel distance threshold, rather than defend the minimum amount needed, and in some areas, breeding densities were likely limited by defense behavior rather than resource

abundance. We recommend allocating > 3.5 ha of habitat per breeding pair, and suitable regions should include > 2 ha of available foraging habitat within a 250 m radius.

Key words: economic defendability, home range, landscape structure, resource configuration, space use, territory size, Tuamotu Kingfisher

1. INTRODUCTION

On a global scale, avian diversity is most threatened by anthropogenic modification of tropical forests (Steadman, 1997; Jetz et al., 2007; BirdLife International, 2010), yet tropical forest birds are among the least studied (Stutchbury and Morton, 2001). Many are territorial year-round residents, and their population structure and dynamics may be strongly affected by variation in territory size and shape (Adams, 2001). However, we know little about how they use modified landscapes. Understanding space use and movement of threatened tropical forest birds can provide insight into their ecological requirements and improve their conservation management (Kernohan et al., 2001). For example, it can help with allocating appropriate spatial resources for sustaining a population.

Avian space use theory is largely based on temperate species that are ecologically distinct from those in the tropics (Stutchbury and Morton, 2001; Stutchbury and Morton, 2008). Nonetheless, there may be some commonalities across regions. The extent of avian territories, or defended areas, assumedly depends on resource benefits discounted for travel and defense costs (Fretwell and Lucas, 1970). Similarly, models of optimal home range size, or the areas used during regular daily activities, balance individual time and energy budgets. Space use strategies may vary among individuals, over time, and regionally (Lott, 1984), but relatively few studies addressed the dynamic nature of home range behavior and territoriality (Börger et al., 2008). Intraspecific variation of space use in birds may be explained by individual traits and ecological factors. In many temperate and some tropical species, males are more aggressive than their mate and may thus cover larger areas to defend territory boundaries (Fedy and Stutchbury, 2005). In addition, seniority, or the number of years that a bird has owned a territory, may influence territory size because more experienced birds might be better at defending against intruders. Ultimately, the distribution of limiting resources, particularly food, is often assumed to drive space use (Pyke, 1984). Many birds may adjust the extent of their home ranges and territories depending primarily on foraging habitat (Rolando, 2002; e.g., Tremblay et al., 2009). However, many studies found little or no effect of food availability on the size of animal territories (Adams, 2001).

Territory shape has been less studied compared to territory size, but may also interact with defense costs and foraging economics. Round territories are assumedly optimal in homogenous habitats, particularly for central place foragers such as birds provisioning nestlings (Andersson, 1978). In heterogeneous landscapes, territories may be shaped to minimize defense costs rather than optimize foraging (Eason, 1992).

We studied space use and territoriality in a tropical forest bird, the critically endangered Tuamotu Kingfisher (Todiramphus gambieri; IUCN, 2010). For the purposes of this study, a home range is the area used by an individual, and a territory is the area used by a breeding pair and dependant offspring and defended to exclude other conspecifics. We estimated the home ranges of radio-tagged kingfishers and investigated factors with the potential to influence intraspecific variation in space use. We tested for effects of individual bird traits, including sex and seniority. We also considered the effects of landscape structure, including composition, which is the relative amount of resources, and configuration, which is the spatial arrangement of resources (Fahrig, 2005). Niau Atoll provided the opportunity to test for potential effects of landscape structure because resources were continuous within clearly defined patches but differed in configuration and composition between regions. We previously found that Tuamotu Kingfishers selected agricultural coconut (*Cocos nucifera*) forest when compared to other available vegetation types, as it provided foraging habitat for the birds (see Chapter 1). We thus expected home ranges and territories to contain a minimum area of agricultural coconut forest, and to be more elongated where coconut forest was arranged in a narrow patch, compared to regions where coconut forest patches were wider. The species is endemic to Niau Atoll in French Polynesia with only one extant population of approximately 125 individuals (IUCN, 2010), and we intended for results from this study to help develop a conservation management plan aiming to form a second population of the birds on another island (Gouni et al., 2006).

2. METHODS

2.1. Study site

Niau Atoll (16°10'S, 146°22'W) is a small island in French Polynesia with a land area of 26 km^2 and a large enclosed lagoon (Andréfouët et al., 2005). The inland is characterized by dense primary forest growing on jagged fossilized limestone coral (feo forest or makatea). Coconut agriculture underlies Niau's economy, and plantations ring the island on the ocean and lagoon shores (Fig. 1). The climate is tropical oceanic without pronounced seasons (Mueller-Dombois and Fosberg, 1998).

We conducted research on two study areas situated by the ocean coast and the lagoon (Fig. 1). Coconut forests in both areas were regularly managed by farmers using prescribed burning to clear the understory vegetation. Coconut forest occurred in a narrow and continuous patch along the ocean coast, and was wider on the lagoon study area. The lagoon area was also comprised of mixed coconut-feo forest and wetlands dominated by *Sesuvium portulacastrum* (Butaud, 2007). A small littoral zone along the ocean coast consisted of coral reef with low strand vegetation and sparse coconut trees.

2.2. Radiotelemetry

Tuamotu Kingfishers were radio-tracked during the breeding season (September – December) in 2006, 2007, and 2008. We captured birds using a hand-held hoop-net at nest cavities or with a mist-net. They were marked with numbered aluminum leg-bands and unique combinations of colored darvic leg-bands. We collected a small blood sample from the brachial vein and used primers P2/P8 for molecular sex determination (Griffiths et al., 1998; Kesler et al., 2006). Adult birds were fitted with radio-transmitters (model BD-2; Holohil Systems, Ottawa, Canada) weighing 1.5 g (≤ 4% of body mass; Gaunt et al., 1999). We used a modified leg harness including a 1 cm length of rubber band which functioned as a weak link, so that equipment would shed from the bird after radio-tags lost functionality (Kesler, in review). We located radio-tagged birds throughout daylight hours (between approximately 05:00 and 18:00) because previous investigations of congener kingfishers found that nocturnal movements were unlikely (Kesler and Haig, 2007a). Birds were located approximately twice daily, with consecutive sampling separated by > 2 hr to avoid serial correlation (e.g., Kesler and Haig, 2007b). We located birds using a hand-held Yagi antenna and telemetry receiver (model R-1000; Communications Specialists Inc., Orange, CA), and recorded geographic coordinates with a global positioning system (GPS; Rino 520HCx; Garmin Ltd., Olathe, Kansas, USA) and a compass. When we could not observe birds visually, we used triangulation to estimate locations. Consecutive directional bearings were separated by < 10 min to minimize error due to potential movement of the bird. We estimated the maximum likelihood location for each bearing group using LOAS (Ecological Software Solutions, Urnäsch, Switzerland). We excluded triangulations that had a 95% error ellipse > 0.6 ha, which was approximately 10% of a Tuamotu Kingfisher territory.

2.3. Home ranges

We estimated home ranges using a geographic information system (ArcGIS 9.3; ESRI, Redlands, California, USA) with a local convex hull method based on a fixed number of nearest neighbors (k-LoCoH; Getz and Wilmers, 2004; Getz et al., 2007). The method constructs a minimum convex polygon (MCP) for each relocation point using that point and a given number of nearest neighbor points, and then the union of the polygons provides the estimated home range. For 25 home ranges we used a value of 10 nearest neighbors, because it was sufficiently large to obtain a continuous home range that covered the area where the bird was known to occur. For 4 home ranges, we used a larger value (12 or 14 nearest neighbors) to cover spurious "holes" where birds were not directly observed but which were contained within the home range boundaries. We used the k-LoCoH method because it could detect hard boundaries formed by the ocean and lagoon, and could include areas which birds did not use often or flew over, but which were part of the home range.

2.4. Statistical analyses

We conducted statistical analyses in Program R (R Development Core Team, 2005) and SAS software (SAS Institute Inc., Cary, NC). We log-transformed home range area to meet the assumption of normality, used a significance level of $\alpha \leq 0.05$ for all statistical tests, and presented 95% confidence intervals (CI) or standard deviations (SD). We tested the assumption of homogeneity of variance using Bartlett's test for analyses of variance (ANOVA), or with an *F*-test when conducting *t*-tests. We first tested for a year effect on home range size using an ANOVA and found no significant difference. We investigated the influence of sex and seniority on home range size using two-sample two-tailed paired *t*-tests. For sex, we compared home range size between mates. For seniority, we compared home range size between two consecutive years for birds that retained the same territory.

We investigated the potential influence of landscape structure on space use by comparing home ranges of birds in two study areas, situated by the lagoon and the ocean, which were characterized by markedly different landscapes (Fig. 1). We used two-sample two-tailed independent *t*-tests to test for differences in home range size and composition. We also assessed the relative variability of the amount of vegetation types included in home ranges using the coefficient of variation (CV = standard deviation * mean^{-1}) on the log of (1 + area in m^2). Finally, we used two-sample two-tailed independent *t*-tests to compare home range shape characteristics, which we measured in ArcGIS using ET GeoWizards (version 9.9; Tchoukanski 2009). Shape metrics included maximum length (length of the longest possible axis; Fig. 2), width (length of the shortest side of the bounding rectangle aligned with the longest axis; Fig. 2), and circularity ratio (= 1 for a circle).

3. RESULTS

We estimated 29 home ranges from 15 territories (Fig. 3), with a mean of 34 relocations (SD = 9). Most relocations (87%) were obtained from visual observations, 10% from triangulations with a median error ellipse of 0.06 ha, and 3% from biangulations. Home range size was independent of the number of relocations (number of relocations regressed on log area; $P = 0.99$; $R^2 = 0.022$). Four birds were radio-tagged during two field seasons and 21 birds were radio-tagged once. Nine home ranges were on the ocean study area and 20 were on the lagoon study area. They consisted of 15 female and 14 male home ranges.

3.1. Tuamotu Kingfisher home ranges

Home range size averaged 4.4 ha (geometric mean; CI: 3.4-5.7 ha) and varied considerably among individuals, ranging from 1.1 to 18.4 ha. Home ranges were composed primarily of agricultural coconut forest, accounting for 65% (range 29-100%) of the total home range area and averaging 2.7 ha (geometric mean; CI: 2.1-3.4 ha).

Our observations and radiotelemetry data confirmed previous suppositions that Tuamotu Kingfishers were socially monogamous and territorial residents. Home ranges were nearly the same as territories, as they overlapped greatly between mates and abutted home ranges of neighboring conspecifics or had small overlapping areas containing few relocation points (Fig. 3). As we previously defined, territories were used exclusively by the breeding pair and dependent offspring, and defended against intrusions from other conspecifics. However, some of the birds were observed "visiting" neighboring territories on rare occasions. Territories were fairly stable through years and vacancies were filled rapidly. Birds were generally faithful to their mate and territory, and many birds were still paired after our three-year study, but two color-banded females switched territories while the males continued to provision the nestlings.

3.2. Effect of sex and seniority

There was no difference in home range size between mates (Fig. 4; n = 7 breeding pairs, $t_6 = 0.19$, $P = 0.86$). We also found no effect of seniority on home range size of birds that held the same territory for two consecutive years (Fig. 4; n = 4 birds, $t_3 = -0.61$, $P = 0.59$).

3.3. Effect of landscape structure

Home ranges, and thus territories, generally followed the distribution of agricultural coconut forest (Fig. 3). Birds on the lagoon study area additionally included adjacent portions of wetland within their home range. On both study areas, agricultural coconut forest was the primary habitat component of home ranges, and comprised more area than all other habitat types combined (Fig. 5). Further, the coefficient of variation indicated that the amount of agricultural coconut forest included in home ranges was less variable than the amount of all other habitat types, either individually or combined (Fig. 5). However, home ranges on the lagoon study area included twice as much agricultural coconut forest compared to home ranges on the ocean study area ($t_{27} = 3.14$; $P = 0.004$; Table 1). They were also twice as large ($t_{27} = 2.50$; $P = 0.02$), twice as wide (*t*-test assuming unequal variances; $t_{26.88} = 4.49$; $P < 0.001$; Table 1), and more circular ($t_{27} = 4.18$; $P < 0.001$; Table 1). The maximum length of home ranges did not differ between the two study areas ($t_{27} = -0.19$; $P = 0.85$; Table 1).

4. DISCUSSION

The size of Tuamotu Kingfisher home ranges varied greatly among individuals but was not influenced by sex or seniority. Instead, landscape structure, or the composition and configuration of habitats on the landscape, appeared to drive intraspecific variation of space use. The kingfishers shaped their home ranges to include agricultural coconut forest, which is the preferred foraging habitat on Niau (see Chapter 1). Agricultural coconut forest was not only the most abundant, but it was also the most constant (least variable) component of home ranges. Home ranges were representative of territories, and these results thus suggest that the birds required a minimum amount of foraging habitat within their territory, and that the maximum amount may be limited by competition among conspecifics.

Where habitats occurred in long narrow patches, on the ocean study area, home ranges contained only half as much coconut forest as home ranges on the lagoon study area, where habitats occurred in wider patches. Birds on the ocean area could have increased the amount of coconut forest by increasing the length of their territories until they encompassed as much preferred habitat as territories on the lagoon study area. However, increasing territory length might also increase the costs of guarding territory boundaries. Additionally, although longer territories would add foraging habitat, the added areas might not be useful because increasing foraging distance from the nest could reduce rates of food delivery to the young and leave the nest outside visual range, and thus unguarded, for longer periods. We hypothesize that there may be a threshold for the maximum length of Tuamotu Kingfisher territories, above which territories may not be economically defendable. For Tuamotu Kingfishers, it may be more beneficial in terms of fitness to stay within a certain traveling distance from the nest or from the territory center, than to defend additional foraging habitat. Landscape configuration may thus potentially limit the amount of resources truly available to the birds. Birds might be unable to maintain suitable territories in regions where key habitats occur in very distant or linear patches. Management recommendations often address total area requirements of suitable and foraging habitats, but we suggest that the spatial arrangement of habitats should also be considered when allocating space for preserving territorial species.

Birds on the lagoon study area likely defended more resources than the minimum amount required for survival and reproduction. Their home ranges were twice as large and contained twice the amount of preferred foraging habitat as home ranges on the ocean study area, even though the quality of resources appeared to be identical. In addition, pairs on both areas bred successfully and there was no evident difference in survival. Tuamotu Kingfisher breeding densities on the lagoon study area may therefore be limited by defense behaviors and the ability of individuals to maintain territory boundaries, and may be lower than resources might support.

Theory suggests that animals can maximize resources within their home ranges, or use the smallest area that includes the minimum amount of resources required for survival or reproduction (Mitchell and Powell, 2004). Tuamotu Kingfishers seemed to maximize the amount of resources within a travel distance threshold, rather than minimize area. Many birds on the lagoon study area expanded their home ranges considerably by including wetland habitat. High-visibility areas, like the wetlands, might have lower defense costs when compared to coconut forest because intruders may be quickly detected (e.g., Eason, 1992). Wetlands provided additional foraging resources (see Chapter 1), but their utility might be limited due to the lack of hunting perches. Improving foraging habitat by increasing the number of hunting perches, as has been suggested for other avian species (e.g., Yosef and Grubb, 1994), could potentially reduce the amount of space required for Tuamotu Kingfishers.

5. CONSERVATION IMPLICATIONS

The formation of a second population of Tuamotu Kingfishers on another island has been proposed as a conservation strategy (Gouni et al., 2006). The composition of habitats selected by the kingfishers was defined in Chapter 1. Additionally, we recommend allocating > 3.5 ha of habitat for each breeding pair. Further, managers should consider the configuration of foraging habitat when evaluating potential translocation destinations, as it appeared to underlie space use on Niau. The birds might require a minimum amount of foraging habitat within a maximum distance threshold, above which they may be unable to guard nests and territory boundaries. Territories exceeding 500 m in maximum length may not be economically defendable. Birds may thus be unable to secure sufficient resources in landscapes with low density of foraging habitat. We suggest that suitable translocation destinations should include > 2 ha of available foraging habitat within a 250 m radius for each breeding pair of Tuamotu Kingfishers. Coconut plantations with exposed ground and hunting perches may provide foraging habitat similar to that found on Niau. Habitats on Niau were distributed in long continuous patches, but landscapes with patchy or clumped resources could potentially also be appropriate because Tuamotu Kingfishers were often observed flying over less preferred habitat within their home range.

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FIGURES

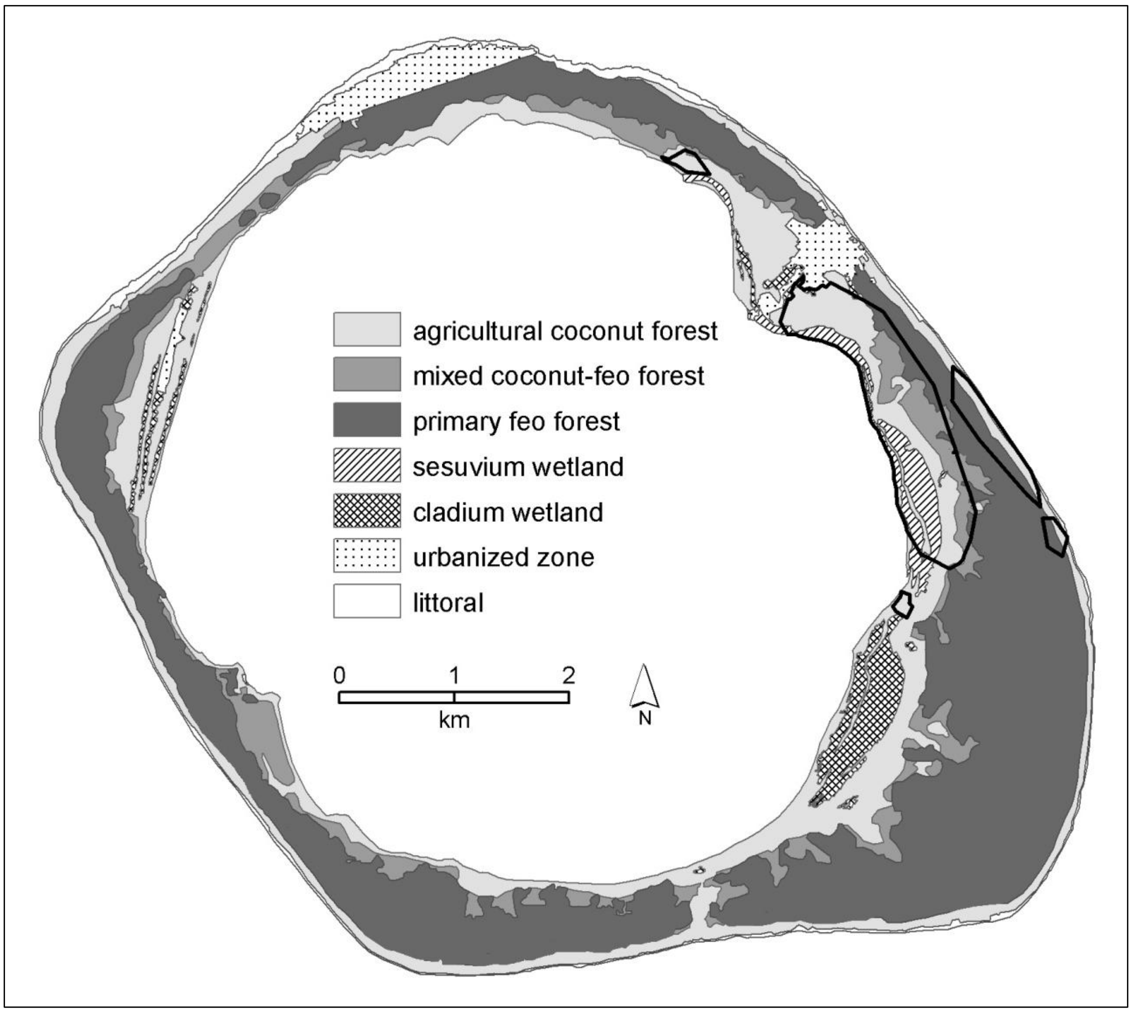

Fig. 1. Vegetation cover map of Niau Atoll (adapted with permission from Butaud (2007)), and areas (outlined) where we radio-tracked Tuamotu Kingfishers in 2006-2008.

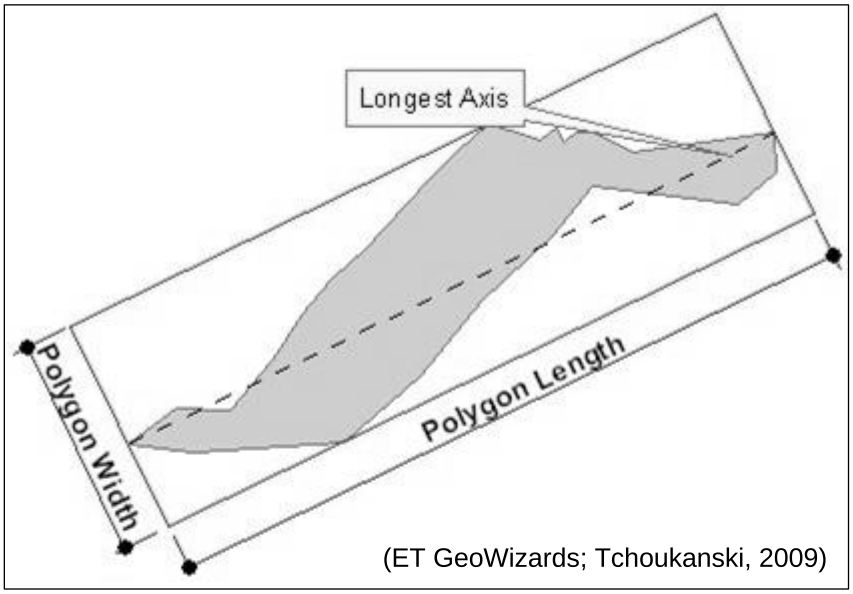

Fig. 2. Example of the determination of the maximum length and the width of a home range polygon using ET GeoWizards (version 9.9) for ArcGIS 9.3.

Fig. 3. Radiotelemetry relocations on Niau Atoll and Tuamotu Kingfisher home ranges (outlined) from 2006-2008 generated using a local convex hull method; filled polygons (alternating light grey and dark grey) are estimated territories represented by the union of individual home ranges.

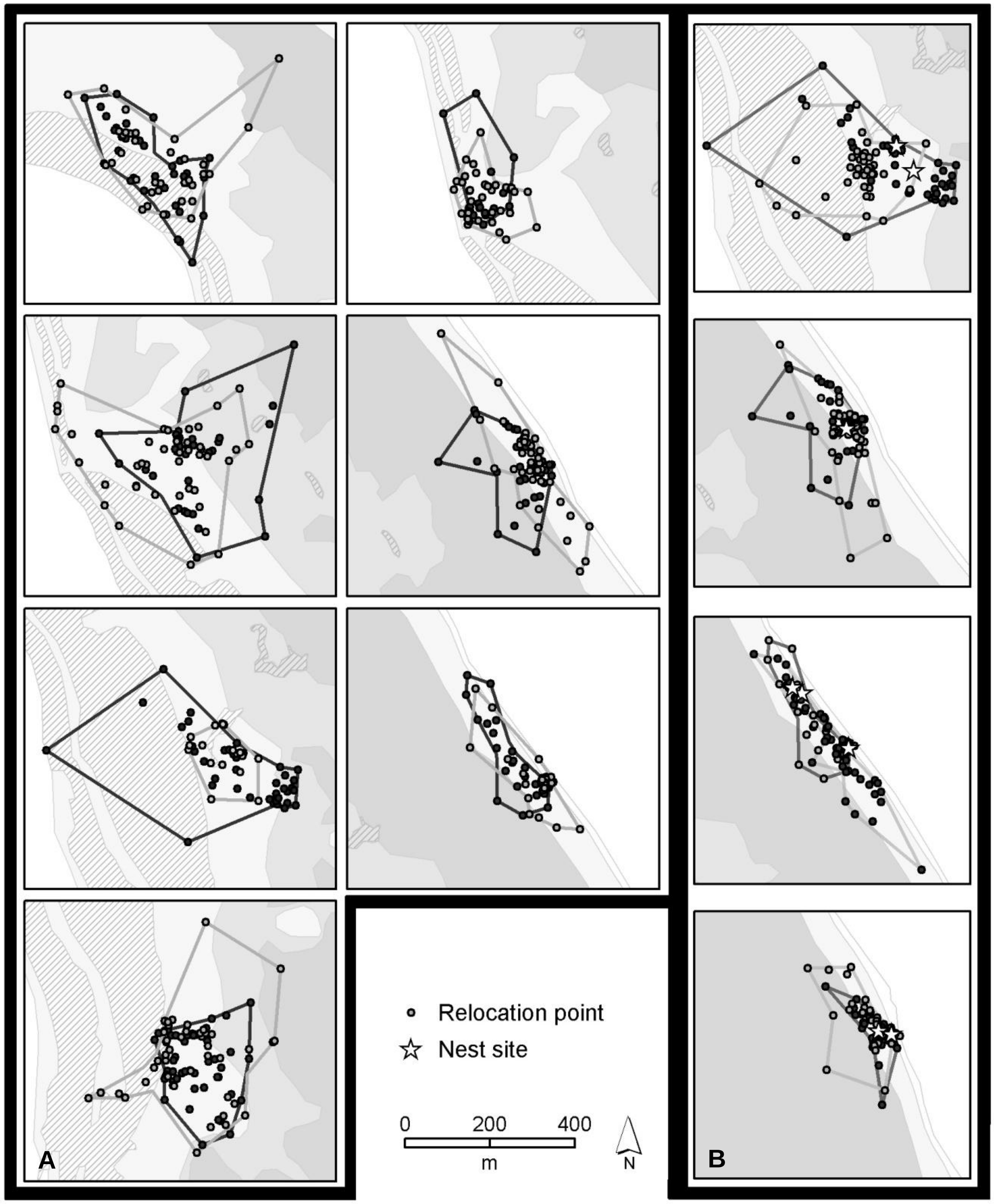

Fig. 4. Comparison of Tuamotu Kingfisher home ranges on Niau Atoll in 2006-2008; A: between mates (dark grey: male, light grey: female); B: between two consecutive years for birds that retained their territories (dark grey: first year, light grey: second year).

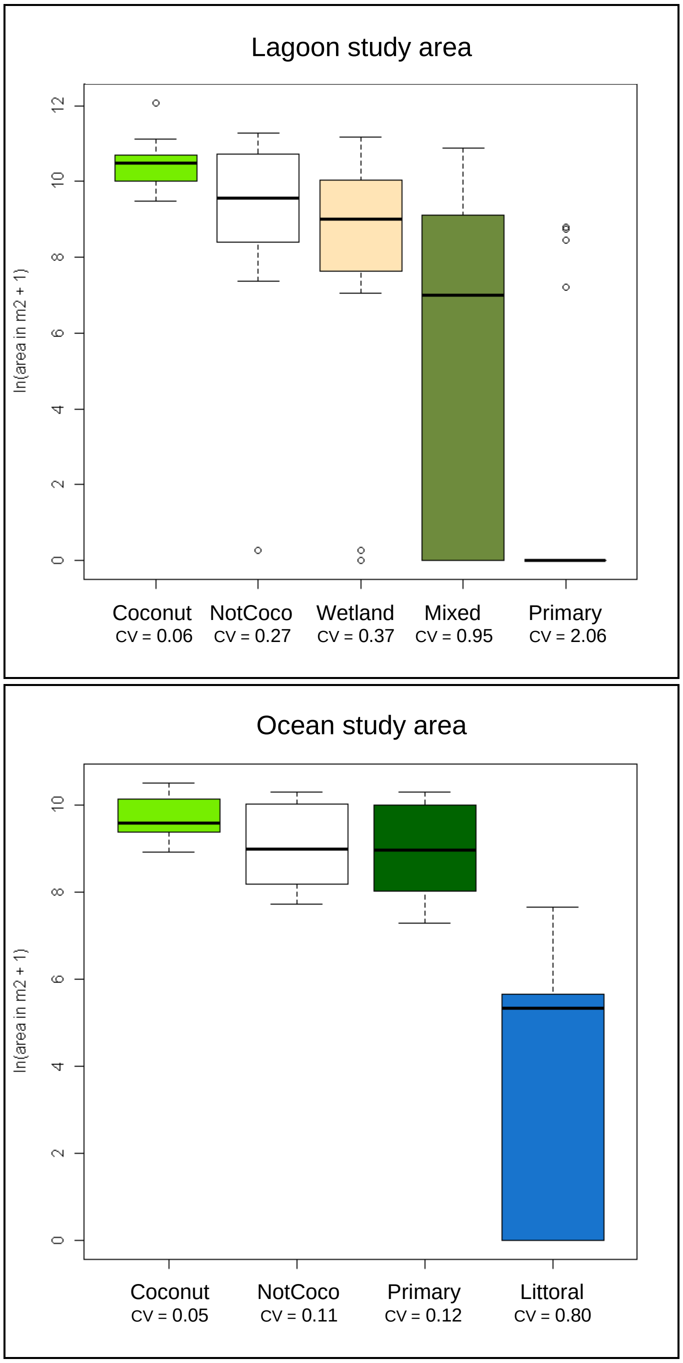

Fig. 5. Boxplots showing the median and quartiles of the amount of each habitat type composing Tuamotu Kingfisher home ranges on Niau Atoll in 2006-2008; CV: coefficient of variation; Coconut: agricultural coconut forest, NotCoco: all other habitat types combined, Mixed: mixed coconut-feo forest, Primary: primary feo forest.

TABLE

Table 1.

Comparison of the characteristics of Tuamotu Kingfisher home ranges on Niau Atoll in 2006-2008 between two study areas differing in landscape structure.

Study area	*N*	Home range [a]	Agricultural coconut forest [a]	Width [b]	Length [b]	Circularity ratio [b]
Lagoon	20	**5.4 ha** (3.7-8.1)	**3.4 ha** (2.2-5.1)	**277 m** ± 27	439 m ± 31	**0.60** ± 0.03
Ocean	9	**2.8 ha** (2.0-4.1)	**1.7 ha** (1.0-2.8)	**139 m** ± 16	449 m ± 43	**0.39** ± 0.04

[a] geometric mean and 95% confidence interval; [b] mean ± standard error