



Contributed Paper

The importance of incorporating functional habitats into conservation planning for highly mobile species in dynamic systems

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Abstract: *The distribution of mobile species in dynamic systems can vary greatly over time and space. Estimating their population size and geographic range can be problematic and affect the accuracy of conservation assessments. Scarce data on mobile species and the resources they need can also limit the type of analytical approaches available to derive such estimates. We quantified change in availability and use of key ecological resources required for breeding for a critically endangered nomadic habitat specialist, the Swift Parrot (*Lathamus discolor*). We compared estimates of occupied habitat derived from dynamic presence-background (i.e., presence-only data) climatic models with estimates derived from dynamic occupancy models that included a direct measure of food availability. We then compared estimates that incorporate fine-resolution spatial data on the availability of key ecological resources (i.e., functional habitats) with more common approaches that focus on broader climatic suitability or vegetation cover (due to the absence of fine-resolution data). The occupancy models produced significantly ($P < 0.001$) smaller (up to an order of magnitude) and more spatially discrete estimates of the total occupied area than climate-based models. The spatial location and extent of the total area occupied with the occupancy models was highly variable between years (131 and 1498 km²). Estimates accounting for the area of functional habitats were significantly smaller (2–58% [SD 16]) than estimates based only on the total area occupied. An increase or decrease in the area of one functional habitat (foraging or nesting) did not necessarily correspond to an increase or decrease in the other. Thus, an increase in the extent of occupied area may not equate to improved habitat quality or function. We argue these patterns are typical for mobile resource specialists but often go unnoticed because of limited data over relevant spatial and temporal scales and lack of spatial data on the availability of key resources. Understanding changes in the relative availability of functional habitats is crucial to informing conservation planning and accurately assessing extinction risk for mobile resource specialists.*

Keywords: dynamic resource availability, habitat specialist, *Lathamus discolor*, migration, rich patch exploiter, species-distribution modeling, threatened species

La Importancia de la Incorporación de los Hábitats Funcionales dentro de la Planeación de la Conservación para las Especies Altamente Móviles en Sistemas Dinámicos

Resumen: *La distribución de las especies móviles en los sistemas dinámicos puede variar enormemente con el tiempo y el espacio. Estimar el tamaño de la población y la extensión geográfica puede ser problemático y afecta la certeza de las valoraciones de conservación. Los datos escasos sobre las especies móviles y los recursos que necesitan también pueden limitar el tipo de estrategias analíticas disponibles para derivar dichos estimados. Cuantificamos el cambio en la disponibilidad y el uso de los recursos ecológicos clave requeridos para la reproducción en un especialista nómada y en peligro de extinción crítico: el periquito migrador (*Lathamus discolor*). Comparamos los estimados del hábitat ocupado derivados de los modelos climáticos dinámicos de presencia-segundo plano (es decir, datos de sólo-presencia) con los estimados derivados de*

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los modelos de ocupación dinámica que incluyeron una medida directa de la disponibilidad de alimento. Después comparamos los estimados que incorporan datos espaciales de alta resolución sobre la disponibilidad de recursos ecológicos clave (es decir, los hábitats funcionales) con estrategias más comunes que se enfocan en una idoneidad climática más general o en la cobertura vegetal (debido a la ausencia de datos de alta resolución). Los modelos de ocupación produjeron estimados más pequeños significativamente ($p < 0.001$) y más discretos espacialmente del área total ocupada que los modelos con base climática. La ubicación espacial y la extensión del área ocupada total fueron altamente variables entre años ($131\text{--}1498 \text{ km}^2$) con los modelos de ocupación. Los estimados que representan el área de los hábitats funcionales fueron más pequeños significativamente (2–58% [DS 16]) que los estimados basados solamente en el área total ocupada. Un incremento o disminución en el área de un hábitat funcional (búsqueda de alimento o anidación) no correspondió necesariamente con un incremento o disminución en el otro. Así, un incremento en la extensión del área ocupada puede no ser igual a un incremento en la función o calidad del hábitat. Argumentamos que estos patrones son típicos para los especialistas en recursos móviles pero son ignorados comúnmente debido a los datos limitados sobre las escalas espaciales y temporales relevantes y a la falta de datos espaciales sobre la disponibilidad de recursos clave. Entender los cambios en la disponibilidad relativa de los hábitats funcionales es crucial para informar a la planeación de la conservación y valorar con certeza el riesgo de extinción de los especialistas en recursos móviles.

Palabras Clave: disponibilidad de recursos dinámicos, especialista de hábitat, especies amenazadas, explotador de fragmento rico, migración, modelo de distribución de especies, *Lathamus discolor*

Introduction

Predicting the distribution of nomadic migrants that respond to dynamic pulses in resource availability by exploiting rich patches is a major challenge for conservation planners (Woinarski et al. 1992). These species vary markedly in life history-strategies, movement patterns, and settlement cues (Dean 2004; Newton 2006), and their settlement patterns are poorly understood. They are often also resource specialists, which can make them vulnerable to resource bottlenecks in time and space (Runge et al. 2014). Conservation of nomadic migrants depends on understanding where and when resources are available and how populations respond to resource configuration (Runge et al. 2015a). Ecologically relevant and spatiotemporally explicit estimates of these species distributions are needed to guide conservation planning (Gaston & Fuller 2009) and accurately assess exposure to threatening processes (Runge et al. 2015b).

Species distribution models (SDMs) are increasingly used to guide conservation planning by characterizing a species' ecological requirements and projecting this over unsampled areas (Guisan & Zimmerman 2000). The relative benefits of different modeling approaches have received considerable attention (Hastie & Fithian 2013; Guillera-Arroita et al. 2015). Models derived from systematically collected data on species' presences and absences perform better in terms of avoiding false positive and false negative errors than those based on less robust sampling designs (Guillera-Arroita et al. 2015). However, few nomadic migrants in dynamic environments have been studied using systematic sampling designs at ecologically relevant, large spatial scales, partly due to logistic, or funding constraints. Hence, limited data availability, especially the lack of absence records, can limit mod-

eling approaches to less-accurate presence-background techniques (Phillips et al. 2006). Another common limitation when modeling species distributions is that the resolution of spatial data layers used to predict a species' distribution may not reflect the resolution of the species' habitat use. Most SDMs are derived from macroscale environmental characteristics (e.g., temperature, rainfall, and vegetation cover) (Gaston & Fuller 2009) because continuous fine-scale data on specific resources (e.g., food) are rarely available and often impractical to collect. If fine-scale habitat features determine species occurrence (hereafter functional habitats), a species' occupancy of the landscape is likely to be overestimated in SDMs that do not account for them (Gaston & Fuller 2009). For habitat specialists this effect is magnified because broad-scale environmental data rarely capture higher-resolution heterogeneity of functional habitats (Jetz et al. 2008). Species also often require spatial and temporal co-occurrence of different resources (e.g., food near nests [Brambilla & Sapopetti 2014]). Incorporating functional habitats and presence and absence data into SDMs is likely to improve model estimates and transferability of predictions to unsampled areas, but published examples are rare (e.g., Araújo & Luoto 2007; Vanreusel et al. 2007).

Despite these challenges, there is increasing demand for accurate and fine-scale distribution maps to guide conservation planning for threatened species. We explored factors affecting accurate distribution modeling for a critically endangered nomadic migrant, the Swift Parrot (*Lathamus discolor*) (Heinsohn et al. 2015). Settlement patterns of Swift Parrots are determined by local pulses of food availability over a large potential range (Webb et al. 2014). This dynamic and unpredictable system has proven a major challenge for implementing effective conservation action (Allchin et al. 2013) that accounts for

spatial variation in the location and availability of breeding habitat, as well as likely changes in the relative availability of functional habitats. Deforestation of Swift Parrot breeding habitat continues (Supporting Information) without a clear understanding of the implications of the loss of particular sites and the effect on local habitat quality. Information about the spatial ecology of Swift Parrots is fundamental to their conservation because managing anthropogenic and predator impacts (Stojanovic et al. 2014a; Heinsohn et al. 2015) on their population depends on understanding how Swift Parrots move through their large range. In this context, the implications of using different modeling approaches to estimate dynamic distributional changes in occupied functional habitats is crucial to conservation planning (Jetz et al. 2008).

We used data from a unique multiyear Swift Parrot monitoring program to quantify change in the use and availability of functional habitats over the breeding range. Using data sampled from each functional habitat, we aimed to compare estimates of occupied habitat derived from presence-background modeling that incorporated climatic predictors with estimates from occupancy modeling that incorporated absence data and a direct measure of food; quantify changes in the relative availability of different functional habitats over time; and determine whether variation in occupancy rates in one functional habitat is associated with changes in the other. We considered our results in the context of knowledge gaps for mobile species that exploit rich patches of food in dynamic systems and the potential shortcomings for conservation planning when data on functional habitats are limited.

Methods

Study System and Species

Swift Parrots are nectarivorous, nomadic migrants that move between their wintering range on mainland Australia to the island of Tasmania to breed during the austral summer (Higgins 1999). Breeding Swift Parrots need the flower of eucalyptus trees for food (Webb et al. 2014) and tree cavities for nesting (Webb et al. 2012). Variable but spatially structured flowering events of blue (*Eucalyptus globulus*) and black gum (*Eucalyptus ovata*) determine settlement patterns of nesting Swift Parrots (Webb et al. 2014), meaning that nesting locations change annually and can be separated by up to hundreds of kilometers.

Standardized surveys in potential foraging habitat were carried out for Swift Parrots over their entire core breeding range (Natural Values Atlas 2015) between 2009 and 2014. Survey methods are outlined by Webb et al. (2014). Briefly, several hundred sites (range 771–1034) were surveyed in eastern Tasmania (approximately 10,000 km²) during October each year (i.e., the early breeding sea-

son) to collect presence-absence data through repeated 5-minute counts. Survey sites were in potential foraging habitat (i.e., ≥1 food tree within 200 m of the site centroid). Food trees were surveyed for flowering and scored on a scale of 0 to 4 (0, none; 1, light; 2, moderate; 3, heavy; 4, very heavy).

Comparison of Distribution-Estimate Approaches

To derive the distribution of Swift Parrots with a standard presence-background-data approach, we fitted annual models of habitat suitability with Maxent version 3.3.3 (Phillips et al. 2006). We built annual time-sliced distribution maps for November 2009 to November 2012. We matched species occurrence data with site-specific environmental conditions over the preceding 12 months before each observation. Daily weather data were unavailable for 2013 and 2014, and these years could therefore not be included in this component of the analysis. This resulted in 4 annual distribution maps. (See Runge et al. [2015b] for further details of the modeling approach.) A 12-month time lag was chosen because this lag had the strongest predictive power (3-, 6-, 9-, and 12-month lags were compared using the area under the curve [AUC]). We used annual time-sliced models because we suspected the use of an area in 1 year was independent of habitat use in previous years (i.e., no site fidelity), a characteristic of many mobile species that rely on fluctuating resources.

The annual distribution maps were created by first populating fine-resolution monthly rasters with 6 different weather variables for each 100 × 100 m grid cell in Tasmania over the preceding 12 months: total rainfall, average rainfall, maximum temperature, minimum temperature, average maximum daily temperature, and average minimum daily temperature (Xu & Hutchinson 2011). A spatial layer of eucalypt forest was also converted to a 100 × 100 m resolution raster to represent potential habitat (TASVEG 3.0) (DPIPWE 2013). All variables were checked for correlations. We considered other weather variables, but they correlated with at least one of the above variables. Next, a global model of Swift Parrot responses to environmental conditions based on all Swift Parrot occurrences from 2009 to 2012 ($n = 477$) was created using Maxent. Ten percent of records were reserved for model validation. We projected the global model across the environmental conditions in the study region over the 12 months preceding November each year (approximate midpoint of the Swift Parrot nesting season).

We used equal sensitivity and specificity threshold values for each year to reclassify the Maxent logistic output into predictions of presence or absence (Liu et al. 2013). This resulted in a map of predicted presence or absence for each year from 2009 to 2012.

To estimate species distribution based on presence-absence data and food availability, we used occupancy

models published by Webb et al. (2014). We updated these models to include 2 additional years of data (resulting in a time series from 2009 to 2014). Using data from each year we modeled annual occupancy probabilities (Ψ) and incorporated imperfect detection (p) in zero-inflated binomial models (ZIB) with the EM Algorithm to allow the inclusion of a generalized additive model (GAM) in the occupancy component of the ZIB (Webb et al. 2014). Flower score and a bivariate smoothed spatial term (latitude, longitude) were used as covariates in the Ψ component; flower score was the single covariate in the p component. Model predictions were interpolated across the study area with kriging at 0.02° resolution (approximately 1.6 × 1.6 km) and a neighborhood search radius of 0.05° (approximately 5 km) (Webb et al. 2014). We considered these scales ecologically relevant based on the degree of spatial autocorrelation in each year (Webb et al. 2014). Again, we assumed the species' distribution in each year was resource driven and therefore independent of other years.

To produce a binary map of Swift Parrot occurrence, we reclassified Ψ into predictions of presence or absence using a minimum threshold value for each annual model that represented the midpoint between average Ψ values for occupied and unoccupied sites from our monitoring data (Fielding & Haworth 1995).

Estimating Temporal Change in Occupied Habitat

Using species-distribution outputs from the habitat suitability and occupancy models, we derived annual estimates of occupied habitat based on 2 scenarios that reflected different underlying assumptions about habitat availability: total area (area of all cells identified as suitable or occupied) and forest (area of all eucalypt forest and woodland in cells identified as suitable or occupied). Areas outside the Swift Parrot breeding range (Natural Values Atlas 2015) were excluded from estimates.

To better account for Swift Parrot habitat specialization, we estimated occupied habitat within the species' 2 key functional habitats: foraging habitat containing blue or black gums, and nesting habitat containing mature cavity-bearing trees (i.e., functional habitat area). For these analyses, we used 2 different spatial layers that identified each functional habitat. For foraging habitat, we used a spatial polygon layer that categorizes the contribution of blue or black gum to forest canopy cover (DPIPWE 2010). For nesting habitat, we used a spatial polygon layer of mature forest that reflects the probability of the presence of tree cavities (Forest Practices Authority 2011). To reduce uncertainty, we excluded foraging—habitat polygons with <5% blue or black gum and polygons where tree diameter at breast height was <40 cm (young trees produce few flowers and rarely provide an attractive resource [Brereton et al. 2004]). Polygons of the mature forest layer were included in

the analysis if they were categorized as low (5–20%), medium (20–40%), or high (>40%) density of mature tree crowns (Stone 1998). The mature-forest-cover layer was updated using the 30 × 30 m remotely sensed Global Forest Change Layer (Hansen et al. 2013) to account for recent deforestation (also see Supporting Information).

Three estimates of functional habitat area were derived from both the habitat suitability models and the occupancy models. We intersected the final output of each model in each year with the foraging-habitat layer or the mature-forest layer to derive estimates of foraging habitat and nesting habitat, respectively. Then, we derived another estimate of nesting habitat, adjusted nesting habitat, to account for variation in the density of mature trees and thus the likely density of tree cavities. To do this, we reclassified the crown cover category for each polygon of the mature forest layer by dividing the area of each polygon by the median value of its crown cover (12.5%, 30%, and 60%, respectively). Total functional habitat area was then calculated by summing foraging habitat and adjusted nesting habitat.

We compared different estimates of occupied habitat derived from habitat maps versus occupancy maps with Pearson's product-moment correlations. To determine whether these estimates followed the same trends over time when derived from different models, we used analysis of covariance (ANCOVA) to compare trends in the slopes of regressions of the estimates from different modeling approaches.

Estimating Occupancy Rates in Nesting Habitat

To validate our models and estimate occupancy rates in nesting habitat, we also surveyed potential nesting habitat of Swift Parrots annually from November through December from 2009 through 2014 (i.e., after the survey of foraging habitat described above and timed to coincide with the middle of the nesting period). Sampling locations were established in the nearest potential nesting habitat (i.e., mature forest) to foraging sites where Swift Parrots were detected. After marking an initial sampling location, the observer moved >200 m away on a random compass bearing to mark the next site. Sampling locations had at least one potential nest tree (described in Webb et al. [2012]). Swift Parrot presence-absence data were recorded within a 100-m radius around each sampling location. Provisioning Swift Parrots forage mostly within a 5-km radius of their nests (D.S., personal observation), so we included nesting survey sites if they were within 5 km of the boundary of each occupancy model (with the threshold applied).

For each year, we estimated Swift Parrot occupancy (Ψ_n) and detectability (p_n) (MacKenzie et al. 2002) in nesting habitat captured by the respective threshold occupancy model in PRESENCE (Hines 2012). We achieved spatial replication (with replacement) by placing a 1-km²

grid over sampled areas. Each sampling location was treated as a repeat visit to each grid cell. The mean number of 1-km² cells sampled each year was 128 (SD 45), and the mean number of sampling locations per cell was 3.6 (SD 2.4) (Supporting Information). The number of sampling locations per cell was primarily influenced by the occurrence of potential nesting trees and access. Estimates of Ψ_n are conditional on the presence of potential nest trees because no surveys were conducted where likely nest trees were absent.

Results

Presence-Background Versus Presence-Absence Approaches

Habitat suitability models produced substantially different distribution maps relative to the occupancy models in terms of the locations predicted to be suitable or occupied over time (Figs. 1 & 2). Distribution maps based on habitat suitability models also captured significantly larger areas of the landscape than those based on occupancy models (i.e., 2–12 times larger depending on the measure of habitat) (Table 1, Fig. 3). There was no significant correlation between habitat extent estimates based on the 2 different modeling approaches (Pearson's product-moment correlation $P > 0.05$ [Supporting Information]). Model summaries and the location of Swift Parrot detections are in Supporting Information.

Habitat suitability models captured 16–30% more occupied sites than the occupancy models in the 4 years climate data were available (Supporting Information), but they also predicted large areas (2618–4827 km²) to be suitable in locations where the occupancy models provided strong evidence that Swift Parrots were either absent or present in only very low numbers. Mean occupancy probability outside areas captured by the occupancy models from 2009 to 2012 was 0.109 (SD 0.099) (Supporting Information). Occupancy models had a high degree of overlap with the habitat suitability models (mean 78% [SD 8.7]) (Supporting Information) but identified more spatially discrete regions of occupied habitat that reflected patterns of flowering in each year (Fig. 2).

Temporal Change in Occupied Habitat

There were large differences in the location of occupied habitat estimated using the occupancy models in each year (Fig. 2). Habitat extent derived from the occupancy models also varied dramatically between some years, particularly for functional habitats (up to 3 orders of magnitude) (Fig. 3; individual estimates in Supporting Information), although there was no significant trend over time ($P > 0.05$) (Table 1). Compared with the occupancy models, annual estimates of habitat extent derived from habitat suitability models varied less (Fig. 1

& Supporting Information). Estimates of functional habitat areas were consistently and substantially smaller than other estimates for both modeling approaches, often by several orders of magnitude (Fig. 3). For the occupancy models, an increase or decrease in total area or forest did not correspond to a significant respective increase or decrease in foraging habitat ($P > 0.05$, Supporting Information). Furthermore, an increase or decrease in availability of one functional habitat did not necessarily correspond to a significant increase or decrease in the other ($P > 0.05$) (Fig. 3 & Supporting Information). Poor flowering conditions in 2014 resulted in only small isolated patches of foraging habitat being available and a dramatic reduction in all estimates of occupied habitat (Figs. 2 & 3). At a handful of sites (<10) captured by the 2014 occupancy model, unusually high abundances of Swift Parrots (estimated >300 individuals) appeared to be constantly present while local flowering persisted.

Occupancy Rates in Nesting Habitat

Predicted Swift Parrot occupancy (Ψ_n) in nesting habitat was high in all years (0.69–0.94) except 2014, and detectability (p_n) remained relatively constant (0.49 [SD 0.09]) (Table 2). Large annual variations in estimates of nesting habitat and adjusted nesting habitat (Fig. 3) were not reflected in the respective annual changes in Ψ_n (Pearson's $r = -0.33$, $P = 0.58$; Pearson's $r = -0.45$, $P = 0.45$, respectively). Although the very restricted functional habitat areas identified by the 2014 occupancy model were associated with very high densities of birds in a small area of foraging habitat (see above), this did not translate into high Ψ_n (or p_n) in nearby nesting habitat.

Discussion

By linking estimates of geographic range size to changing availability of functional habitats for a nomadic migrant, we have provided a means to better understand the consequences of dynamic variation in species geographic distributions. The method we used to derive functional habitat area from dynamic occupancy models can be used to identify where and when resource bottlenecks may occur. For example, although Swift Parrot breeding had previously been recorded at several locations we identified, we found that in some years most of the population is forced to rely on small areas of habitat. Our approach provides a sound basis for targeting conservation resources and allows spatially explicit thresholds to be set for functional habitats in the context of ongoing habitat loss and dynamic pulses in resource availability that can result in very small areas of breeding habitat. We also found that assessment of spatiotemporal variation in exposure to other threats (e.g., nest predation) may be improved with modeling approaches that account for

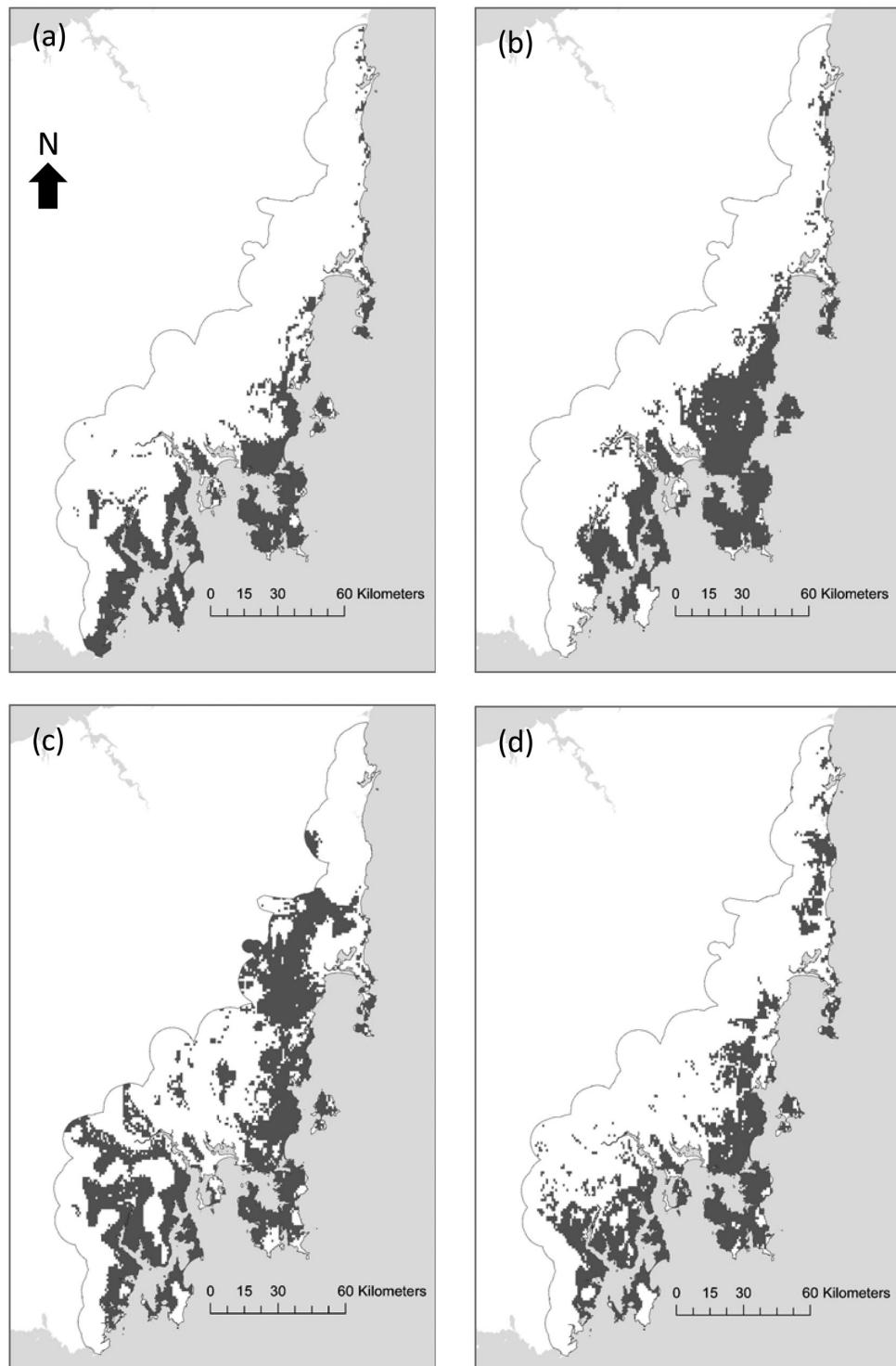


Figure 1. Estimates of areas occupied by Swift Parrots (gray) in eastern Tasmania, Australia, in (a) 2009, (b) 2010, (c) 2011, and (d) 2012 based on habitat suitability models implemented in Maxent with equal sensitivity and specificity thresholds applied (gray line, Swift Parrot breeding range [Natural Values Atlas 2015]). Threshold values for each year are 0.1557, 0.2070, 0.2481, 0.1670, respectively.

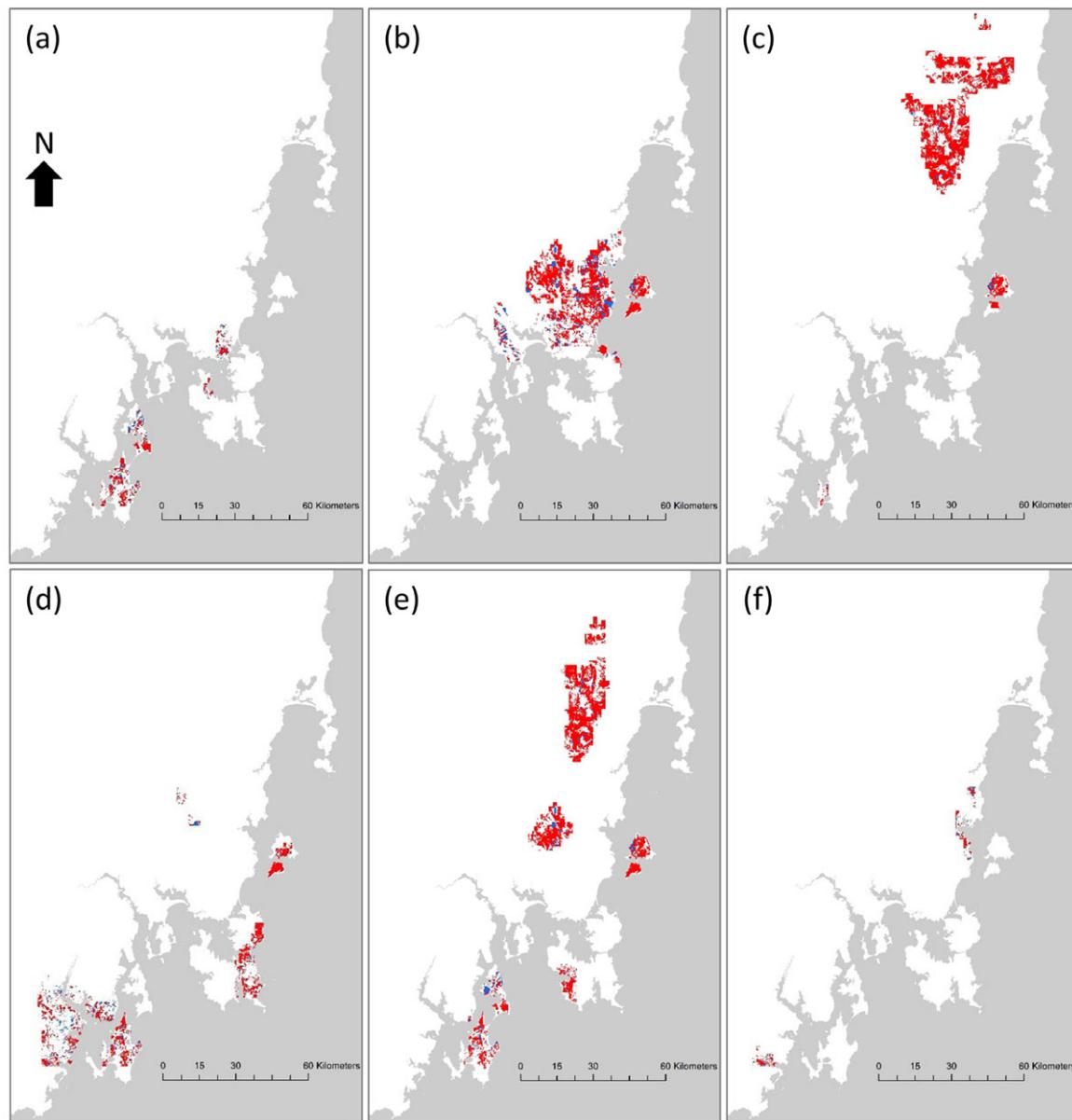


Figure 2. Estimates of areas of functional habitat occupied by Swift Parrots based on occupancy models (red, nesting habitat; blue, foraging habitat) in eastern Tasmania, Australia, from (a) 2009, (b) 2010, (c) 2011, (d) 2012, (e) 2013, and (f) 2014. Threshold values for each year are 0.3637, 0.3904, 0.4305, 0.3932, 0.3635, 0.2926, respectively.

ecologically relevant information (i.e., presence and absence of target species and functional habitats).

By modeling change in species occupancy and selecting only the functional habitat from annual distributions, we detected dynamic variation in ecologically relevant habitats that was not detected by more commonly applied habitat suitability models (Fig. 3). Significant differences between estimates of occupied habitat depended on the type and function of habitat considered and the modeling technique and illustrated how the method used to calculate geographic range size can in itself cause non-trivial variation and uncertainty in occupancy estimates

of potential habitat (Jiménez-Valverde et al. 2008). This may have important implications for assessing extinction risk of nomadic migrants because scarce data often limit modeling approaches that can be used to achieve conservation-planning and -assessment objectives (Jetz et al. 2008; Runge et al. 2015b; Tulloch et al. 2016). In particular, the high rate of type I errors (i.e., false positives) inherent in our habitat suitability models limits their application to conservation planning in a landscape with multiple competing land uses (e.g., industrial-scale logging) and to detection of trends over time. There will always be trade-offs between the rate of type I and type II

Table 1. Results of analysis of covariance testing for the effect of modeling approach and year on estimates of habitat occupied by the Swift Parrot (habitat suitability model versus occupancy model).

Measure of habitat	Variable	F	P
Total area	model	46.5	0.006
	year	1.2	0.48
Forest	model	36.4	0.009
	year	2.0	0.31
Nesting	model	36.1	0.009
	year	2.1	0.29
Adjusted nesting habitat	model	29.9	0.012
	year	2.3	0.26
Foraging habitat	model	74.1	0.003
	year	1.1	0.51

errors (Field et al. 2007); however, our occupancy models provide strong evidence on which to base conservation planning in an environment where habitat protection often has considerable economic implications for competing interests. Furthermore, our results demonstrate the importance of incorporating direct measures of resource availability into species distribution predictions, as well as distinguishing functional habitats in the environmental matrix.

Readily available presence-only data may be sufficient to understand the distributions of well-studied species, providing occurrence records cover important environmental gradients (Lentini & Wintle 2015). However, we found this may not be the case for specialized species with dynamic distributions. Our presence-background models were based on occurrence data collected in a spatially stratified, systematic sampling design but yielded much larger estimates of Swift Parrot distribution over time relative to occupancy models. Sensitivity analyses revealed that these differences remained even when the threshold assigning species' presence or absence to the occupancy model results was reduced by 50% (Supporting Information). The strong overprediction (i.e., higher type I error rate) of the presence-background models occurred because they did not explicitly account for food availability or spatial location and hence spatial structuring of the population each year (Estrada et al. 2016). Because flowering is also typically spatially structured (Webb et al. 2014) and is likely influenced by climatic variability, explicitly modeling flowering patterns (Giles et al. 2016) rather than birds may be an interesting area of future research to predict changes in food availability and the occurrence of Swift Parrots (Woinarski et al. 2000).

We suggest the greater percentage of occupied sites captured by these models is a reflection of the species realized niche (while breeding) being greater than its fundamental niche (Pulliam 2000), likely resulting from limitation of one or both functional habitats. Alternatively, this may also be attributable to records of Swift Parrots that had not yet settled to breed. Unfortunately, most data for species with similarly variable distribu-

tions consist of presence-only records that have not been collected in a structured sampling design (Runge et al. 2015b). Our study highlights the value of investing in the acquisition of high-quality (i.e., repeated, standardized) presence-absence data for threatened nomadic migrants.

The small estimates of functional habitat area represent a sobering reality for a species experiencing widespread anthropogenic landscape change (Supporting Information) and spatially heterogeneous threats like nest predation. Although the spatial location and extent of functional habitat areas varied considerably between years (Fig. 3), nesting occupancy remained consistently high until 2013 (up to 94%). This suggests either the abundance-occupancy relationship in nesting habitat varied between years or some birds did not breed due to nesting-site limitation, particularly in 2014 (Table 2). Moreover, even our detailed estimates of functional habitat area are likely to overestimate occupied habitat (e.g., Stojanovic et al. 2012, 2014b). Accurately quantifying resources at such fine resolutions is often not possible, but it is important to consider irrespective of the sophistication of modeling approaches (Collier et al. 2012).

The relative availability and spatial configuration of functional habitats for mobile species has important ramifications for the fitness of individuals and carrying capacity within occupied areas (Brambilla & Saporretti 2014; Olsson & Bolen 2014). The fitness of Swift Parrots is improved by breeding in the richest patch of food available in the landscape (Stojanovic et al. 2015), but nest-site availability will determine how many birds will be able to breed in a given patch. For example, as Swift Parrot settlement patterns changed over time, an increase or decrease in one functional habitat did not necessarily correspond to an increase or decrease in the other (Fig. 3). For species that experience dynamic change in geographic distribution, an increase in the extent of occupied area may not equate to improved habitat quality or function. Rather, habitat quality is contingent on the relative availability and overlap of key functional habitats. Our results indicated that the temporal availability of one functional habitat (e.g., nesting sites) can be restricted due to the absence of another key resource (e.g., foraging resources). When the availability of one or both functional habitats for the Swift Parrot falls below an (as yet undefined) threshold it may restrict settlement options and limit breeding participation. We argue that many nomadic migrants experience resource bottlenecks due to limitation of one or more functional habitats, but these bottlenecks go unmeasured due to data deficiency and lack of rigorous research (Newton 2012).

By incorporating a direct measure of food availability and high-resolution mapping of functional habitat features, we derived ecologically relevant and mechanistically informed estimates of occupied Swift Parrot

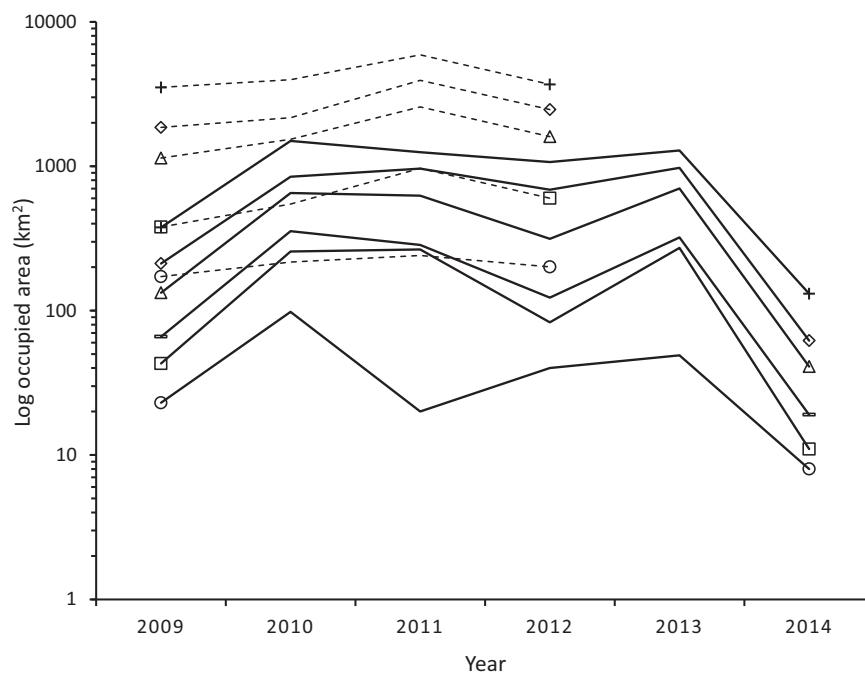


Figure 3. Annual estimates of occupied Swift Parrot habitat from suitability models (dashed lines) and occupancy models (solid lines) in the species' breeding range over 6 years (plus sign, total area; diamond, forest; triangle, nesting habitat; square, adjusted nesting habitat; circle, foraging habitat; short horizontal bar, total functional habitat area).

Table 2. Swift Parrot occupancy (Ψ_n) and detectability (p_n) rates in surveyed nesting habitat.

Parameter	Year					
	2009	2010	2011	2012	2013	2014
Naïve Ψ_n^a	0.66	0.66	0.51	0.59	0.65	0.29
Ψ_n	0.74	0.83	0.69	0.94	0.74	^b
SE	0.07	0.05	0.06	0.07	0.05	
p_n	0.4	0.57	0.55	0.49	0.57	0.35
SE	0.03	0.03	0.04	0.03	0.03	0.04

^aObserved occupancy.

^bCould not be estimated due to poor model fit.

breeding habitat. Even when a species appears to occupy a large area, resource dependence may mean only a small fraction of that area can actually be exploited (e.g., Jetz et al. 2008). Hence, the loss of small areas of one (or both) functional habitats can have profound effects on the population and negate potential benefits from conservation actions elsewhere (Runge et al. 2015a). Given the spatial and temporal scale at which habitat loss and disturbance are occurring in the Swift Parrot breeding range (Supporting Information), we argue that spatially discrete regions should be managed in a way that reflects the availability of functional habitats at ecologically relevant scales and their importance to the population in a given year. For example, the foraging range of Swift Parrots from a nest site is one relevant scale to consider. Similarly, the scale (and location) at which breeding aggregations occur, such as those we identified, is important at the population level. The availability of functional habitats at these 2 scales, in combination with changing flowering conditions, de-

termined the carrying capacity of the breeding range in a given year, particularly during resource bottlenecks. Therefore, habitat management that does not consider the spatial location, scale, and relative availability of specific habitats is likely to be relatively less effective.

Nomadic migrants are a chronically understudied species guild but represent an important component of animal movement strategies (Dingle 1996). Many nomadic species require urgent conservation attention (Faaborg et al. 2010), but a lack of robust data can be a serious impediment to conservation assessment and effective conservation actions. We encourage conservation agencies to recognize the limitations of using distribution models derived from incomplete data (see also Tulloch et al. 2016) and to develop conservation plans that account for functional habitats where possible. Integrating temporal change in resource availability into conservation planning for mobile species is challenging but critical to identifying key locations, dependencies among habitats and sites, and exposure to other threats (Runge et al. 2016). To address this challenge, investing in the collection of both high-quality occupancy and environmental data to estimate species distributions should be a priority. In the absence of such information, many knowledge gaps for nomads will continue to go unaddressed and will result in inaction or poorly directed resources that provide little conservation benefit.

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Supporting Information

Map of forest loss and disturbance from 1997 to 2013 (Appendix S1); occupancy models showing sites where Swift Parrots were observed in each of the 6 years (Appendix S2); occupancy model and Maxent model summaries; information on number of sampling locations for surveys in nesting habitat; comparison of estimates from different modeling approaches; percentage of occupied sites captured by habitat suitability and occupancy models; mean occupancy probabilities outside areas captured by occupancy models; annual estimates of occupied habitat from each modeling approach (Appendix S3); sensitivity analysis examining the effect of reducing the threshold assigning species' presence or absence to the occupancy models (Appendix S4) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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