

## 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, with serious implications for 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. Here we quantify dynamic change in availability and use of key ecological resources required for breeding (i.e. food and nesting sites) for a critically endangered nomadic habitat specialist,

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the swift parrot (*Lathamus discolor*). We compare estimates of occupied habitat (km<sup>2</sup>) derived from dynamic presence-background data climatic models to those derived from dynamic occupancy models that include a direct measure of food availability. We also compare estimates that incorporate fine resolution information on key ecological resources (i.e functional habitats) into distribution maps with more common approaches that typically focus on broader climatic suitability. For all models, both the extent and spatial location of occupied areas varied dramatically over the study period. The occupancy models produced significantly smaller (up to an order of magnitude) and more spatially discrete estimates of occupied habitat than climate-based models. Estimates accounting for the area of functional habitats were also significantly smaller than estimates based only on occupied habitat. Importantly, an increase (or decrease) in one functional habitat did not necessarily correspond to changes in the other, with consequences for overall habitat functionality. We argue that these patterns are typical for mobile resource specialists, but currently go unnoticed due to limited data on (1) species' presence/absence and (2) 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.

## 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 planning (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. In addition, they are often 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).

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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-Aroita 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-Aroita 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 modeling 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 macro-scale environmental characteristics (e.g. temperature, rainfall, 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 (eg. food near nests - Brambilla & Saporetti 2014). Incorporating functional habitats into SDMs together with both presence and absence data is likely to improve model estimates and transferability of predictions to unsampled areas, but published examples are rare (eg. Vanreusel et al. 2007; Araújo & Luoto 2007).

Despite these challenges, there is increasing demand for accurate and fine-scale distribution maps to guide conservation planning for threatened species. We explore 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

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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. 2014; Heinsohn et al. 2015) on their population is dependent 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 use data from a unique multi-year 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, our aims were to: (1) compare estimates of occupied habitat derived from presence-background modeling incorporating climatic predictors, with estimates from occupancy modeling incorporating absence data and a direct measure of food, (2) quantify changes in the relative availability of different functional habitats over time, and (3) determine if variation in occupancy rates in one functional habitat is associated with changes in the other. We discuss 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, tree cavity nesting nomadic migrants that move between their wintering range on mainland Australia to the island of Tasmania to breed during the austral

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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 (*E. ovata*), determine settlement patterns of nesting swift parrots (Webb et al. 2014), meaning that the 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), but briefly, several hundred sites (range: 771-1034) were surveyed in eastern Tasmania (~10,000 km<sup>2</sup>) during October each year (i.e. the early breeding season) to collect detection/non-detection data using repeated five-minute counts. Survey sites were located in potential foraging habitat (i.e.  $\geq 1$  food tree within 200 m of the site centroid). Food trees were surveyed for flowering and scored on a scale of 0 to 4, where 0= no flower, 1= light, 2= moderate, 3= heavy and 4= very heavy.

### **Comparing distribution estimates using presence-background vs. presence-absence approaches**

#### *(i) Habitat suitability models*

To derive the distribution of swift parrots using a standard presence-background data approach we fitted annual models of habitat suitability using Maxent v3.3.3 (Phillips et al. 2006). We built annual time-sliced distribution maps for the period November 2009 to November 2012, matching 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 four 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 suspect the use of an area in one year was

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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 six different weather variables for each 100m x 100m grid cell in Tasmania over the preceding 12 months: total rainfall (mm), average rainfall, maximum temperature (° Celsius), minimum temperature, average maximum daily temperature, average minimum daily temperature (Xu & Hutchinson 2011). A spatial layer of eucalypt forest was also converted to a 100m x 100m resolution raster to represent potential habitat (TASVEG 3.0; DPIPW 2013). All variables were checked for correlations - other weather variables were considered but were 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, with 10% of records reserved for model validation. This global model was then projected across the environmental conditions in the study region during the 12 months preceding November each year (approximate midpoint of the swift parrot nesting season).

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

(ii) *Occupancy models representing functional requirements*

To estimate species distribution based on detection/non-detection data and food availability we used occupancy models published by Webb et al. (2014), updating them to include two additional years of data (resulting in a time series from 2009-2014). Using data from each year we modelled annual occupancy probabilities ( $\Psi$ ) and incorporated imperfect detection ( $p$ ) in zero-inflated binomial models (ZIB) using 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  $\Psi$  component, with flower score as the single covariate in the  $p$  component.

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Model predictions were interpolated across the study area using kriging at 0.02° resolution (~1.6x1.6 km) with a neighborhood search radius of 0.05° (~5 km) (sensu Webb et al. 2014). We considered these scales to be 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 to be resource driven and therefore independent of other years.

To produce a binary map of swift parrot occurrence we reclassified  $\Psi$  into predictions of presence or absence using a minimum threshold value for each annual model that represented the mid-point between average  $\Psi$  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 two scenarios that reflected different underlying assumptions about habitat availability : (1) TOTAL AREA (area of all cells identified as suitable or occupied), and (2) FOREST (area of all eucalypt forest and woodland in cells identified as suitable or occupied). Areas falling 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' two key functional habitats: (1) foraging habitat containing blue or black gums, and (2) nesting habitat containing mature, cavity bearing trees (i.e. functional habitat area). For these analyses we used two different spatial layers that identified each functional habitat. For foraging habitat, we used a spatial polygon layer categorizing 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 a higher 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 those where tree diameter at breast height was <40 cm (flowering of young trees is weak and rarely provides an attractive resource - Brereton et al. 2004).

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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 x 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. Firstly, 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 (i) FORAGING HABITAT and (ii) NESTING HABITAT respectively. Then, we derived another estimate of nesting habitat, (iii) 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 first 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 category (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 suitability maps versus occupancy maps using 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 'true' occupancy rates in nesting habitat, we also surveyed potential nesting habitat of swift parrots annually during November-December between 2009 and 2014 (i.e. after the survey of foraging habitat described above and timed to coincide with the mid 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 using the descriptions

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outlined in Webb et al. (2012). Swift parrot detection/non-detection 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. Stojanovic, unpublished data) 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 nesting occupancy ( $\Psi_n$ ) and detectability ( $p_n$ ) (MacKenzie et al. 2002) in nesting habitat captured by the respective threshold occupancy model using program PRESENCE (Hines 2012). We achieved spatial replication (with replacement) by placing a 1 km<sup>2</sup> grid over sampled areas, and each sampling location was treated as a repeat visit to each grid cell. The mean number of 1 km<sup>2</sup> 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. Importantly, estimates of  $\Psi_n$  are conditional on the presence of potential nest trees because no surveys were conducted where likely nest trees were absent.

## Results

### Presence-background vs. presence-absence approaches to mapping distribution

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

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Habitat suitability models captured 16 to 30% more occupied sites than the occupancy models in the four years climate data were available (Supporting Information), but they also predicted large areas (2618 – 4827 km<sup>2</sup>) 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 2009-2012 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 three orders of magnitude, Fig. 3; see Supporting Information for individual estimates), although there was no significant trend over time (Table 1,  $p > 0.05$ ). Compared to the occupancy models, annual estimates of habitat extent derived from habitat suitability models varied less (Fig. 1, Table S5). Estimates of functional habitat areas were consistently and substantially smaller than other estimates using 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 ( $p > 0.05$ , Table S2). Furthermore, an increase or decrease in availability of one functional habitat did not necessarily correspond to a significant increase or decrease in the other ( $p > 0.05$ , Table S2, Fig. 3). 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 (Fig. 2 & 3). Notably, 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.

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## Occupancy rates in nesting habitat

Predicted swift parrot occupancy  $\Psi_n$  in nesting habitat was high in all years (0.69 to 0.94) except 2014, with a relatively constant detection rate of 0.49 (SD 0.09, Table 2). Interestingly, large annual variations in estimates of NESTING HABITAT and ADJUSTED NESTING HABITAT (Fig. 3) were not reflected in the respective annual changes in  $\Psi_n$  (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  $\Psi_n$  (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 provide a means to better understand the consequences of dynamic variation in species geographic distributions. Our estimates of functional habitat area from dynamic occupancy models provide a method for identifying where and when resource bottlenecks may occur. For example, although swift parrot breeding had previously been recorded at several locations identified in this study, we reveal 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 suitable breeding habitat. Our study also demonstrates that assessment of spatiotemporal variation in exposure to other threats (eg. nest predation) may be improved with modeling approaches that account for ecologically relevant information (i.e. presence/absence of target species and functional habitats).

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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 were dependent on the type and function of habitat considered and the modeling technique, and illustrated how the method utilized 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 utilized for achieving 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 detecting trends over time. There will always be tradeoffs between the rate of Type I and Type II 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 show this may not be the case for specialized species with dynamic distributions. Our presence-background models used occurrence data collected in a spatially stratified, systematic sampling design, but yielded much larger estimates of swift parrot distribution over time compared to occupancy models. Sensitivity analyses revealed that these differences remained even when the threshold assigning species' presence/absence to the occupancy model results was reduced by 50% (Supporting Material). The strong over-prediction (i.e. higher Type I error rate) of the presence-background models is because they do 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

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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 distributions 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 data *and* 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. While 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 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

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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/decrease in one functional habitat did not necessarily correspond to an increase/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 better habitat quality or function. Rather, habitat quality is contingent on the relative availability and overlap of key functional habitats. Our study indicates 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 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 (eg. 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 identified in this study, are important at the population-level. The availability of functional habitats at these two scales, in combination with changing flowering conditions, determines the carrying capacity of the breeding range in a given year, particularly during resource bottlenecks.

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Therefore, habitat management that does not consider the spatial location, scale and relative availability of specific habitats is likely to be 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, leading to inaction or poorly directed resources that provide little conservation benefit.

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### **References**

Allchin R, Kirkpatrick J, Kriwoken L. 2013. On not protecting the parrot: Impact of conservation and planning legislation on an endangered species in Tasmania. *Journal of Wildlife Law and*

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Policy **16**:81-104.

Araújo MB, Luoto M. 2007. The importance of biotic interactions for modelling species distributions under climate change. *Global Ecology and Biogeography* **16**:743-753.

Brambilla M, Saporetti F. 2014. Modelling distribution of habitats required for different uses by the same species: Implications for conservation at the regional scale. *Biological Conservation* **174**:39-46.

Brereton R, Mallick SA, Kennedy SJ. 2004. Foraging preferences of Swift Parrot on Tasmanian Blue-gum: tree size, flowering frequency and flowering intensity. *Emu* **104**:377-383.

Collier BA, Groce JE, Morrison ML, Newnam JC, Campomizzi AJ, Farrell SL, Mathewson HA, Snelgrove RT, Carroll RJ, Wilkins RN. 2012. Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. *Diversity and Distributions*, **18**:158-167.

Dean WRJ. 2004 *Nomadic desert birds*. Springer-Verlag, Berlin, Heidelberg.

Department of Primary Industries Parks, Water and Environment (DPIPWE). 2010. *GlobMap, The swift parrot foraging habitat map*. Biodiversity Conservation Branch, Tasmanian Government, Hobart.

Department of Primary Industries, Parks, Water and Environment (DPIPWE). 2013. *TASVEG 3.0. Tasmanian Vegetation Monitoring and Mapping Program*, Tasmanian Government, Hobart.

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Dingle H. 1996. Migration. The Biology of Life on the Move. Oxford University Press Inc., New York.

Estrada A, Delgado MP, Arroyo B, Traba J, Morales MB. 2016. Forecasting large-scale habitat suitability of European Bustards under climate change: The role of environmental and geographic variables. PLOS ONE **11**: (e0149810) DOI: 10.1371/journal.pone.0149810

Faaborg J, et al. 2010. Conserving migratory land birds in the New World: Do we know enough? Ecological Applications **20**:398-418.

Field SA, O'Conner PJ, Tyre AJ, Possingham HP. 2007. Making monitoring meaningful. Austral Ecology **32**:485-491

Fielding A, Haworth, PF. 1995. Testing the generality of bird-habitat models. Conservation Biology **9**:1466-1481.

Forest Practices Authority. 2011. Potential hollow availability map, Fauna Technical Note No. 2. Forest Practices Authority, Hobart.

Gaston KJ, Fuller, RA. 2009. The sizes of species' geographic ranges. Journal of Applied Ecology **46**:1-9.

This article is protected by copyright. All rights reserved.

Giles JR, Plowright RK, Eby P, Peel AJ, McCallum H. 2016. Models of Eucalypt phenology predict bat population flux. *Ecology and Evolution* **6**:7230-7245

Guillera-Aroita G, Lahoz-Monfort JJ, Elith J, Gordon A, Kajula, H, Lentini PE, McCarthy MA, Tingley R, Wintle BA. 2015. Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography* **24**:276-292.

Guisan A, Zimmerman N. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* **135**:147-186.

Hansen MC, et al. 2013. High-Resolution Global Maps of 21<sup>st</sup> Century Forest Cover Change. *Science* **342**:850-853.

Hastie T, Fithian W. 2013. Inference from presence-only data; the ongoing controversy. *Ecography* **36**:864-867.

Heinsohn R, Webb M, Lacy R, Terauds A, Alderman R, Stojanovic D. 2015. A severe predator-induced population decline predicted for endangered, migratory swift parrots (*Lathamus discolor*). *Biological Conservation* **186**:75-82.

Higgins PJ. (Ed.), 1999. Handbook of Australian, New Zealand and Antarctic Birds, Volume 4, Parrots to dollarbird. Oxford University Press, Melbourne.

Hines JE. 2012. PRESENCE 10.4 – Software to estimate patch occupancy and related parameters. USGS-PWRC. Available from: <http://www.mbr-pwrc.usgs.gov/software/presence.html>

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Jetz W, Sekercioglu CH, Watson JEM. 2008. Ecological correlates and conservation implications or overestimating species geographic range sizes. *Conservation Biology* **22**:110-119.

Jiménez-Valverde A, Lobo JM, Hortal J. 2008. Not as good as they seem: the importance of concepts in species distribution modelling. *Diversity and Distributions* **14**:885-890.

Lentini PE, Wintle BA. 2015. Spatial conservation priorities are highly sensitive to choice of biodiversity surrogates and species distribution model type. *Ecography* **38**:1101-1111.

Liu C, White M, Newell G. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* **40**:778-789.

MacKenzie D, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**:2248-2255.

Natural Values Atlas ([www.naturalvaluesatlas.tas.gov.au](http://www.naturalvaluesatlas.tas.gov.au)). 2015. © State of Tasmania. (accessed 1 September 2015)

Newton I. 2006. Advances in the study of irruptive migration. *Ardea* **94**:433-460.

Newton I. 2012. Obligate and facultative migration in birds: ecological aspects. *Journal of Ornithology* **153**:S171-S180.

This article is protected by copyright. All rights reserved.

Olsson O, Bolen A. 2014. A model for habitat selection and species distribution derived from central place foraging theory. *Oecologia* **175**:537-548.

Phillips S, Anderson R, Schapire R. 2006. Maximum entropy modelling of species geographic distributions. *Ecological Modelling* **190**:231–259.

Pulliam HR. 2000. On relationship between niche and distribution. *Ecology Letters* **3**:349-361.

Runge C A, Martin TG, Possingham HP, Willis SG, Fuller RA. 2014. Conserving mobile species. *Frontiers in Ecology and the Environment* **12**:395-402.

Runge CA, Watson JEM, Butchart SHM, Hanson JO, Possingham HP, Fuller RA. 2015a. Protected areas and global conservation of migratory birds. *Science* **350**:1255-1258.

Runge CA, Tulloch A, Hammill E, Possingham HP, Fuller RA. 2015b. Geographic range size and extinction risk assessment in nomadic species. *Conservation Biology* **29**:865-876.

Runge CA, Tulloch AIT, Possingham HP, Tulloch V, Fuller RA. 2016. Incorporating dynamic distributions into spatial prioritization. *Diversity & Distributions* **22**:332-343.

Stojanovic D, Webb MH, Roshier D, Saunders D, Heinsohn R. 2012. Ground-based survey methods both overestimate and underestimate the abundance of suitable tree-cavities for the endangered Swift Parrot. *Emu* **112**:350-356.

This article is protected by copyright. All rights reserved.

Stojanovic D, Webb M, Alderman R, Porfirio LL, Heinsohn R. 2014a. Discovery of a novel predator reveals extreme but highly variable mortality for an endangered migratory bird. *Diversity and Distributions* **20**:1200-1207.

Stojanovic D, Koch AJ, Webb M, Cunningham R, Roshier D, Heinsohn R. 2014b. Validation of a landscape-scale planning tool for cavity-dependent wildlife. *Austral Ecology* **39**:579-586

Stojanovic D, Terauds A, Westgate MJ, Webb MH, Roshier DA, Heinsohn R. 2015. Exploiting the richest patch has a fitness payoff for the migratory swift parrot. *Journal of Animal Ecology* **84**:1194-1201.

Stone M. 1998. Forest-type mapping by photo interpretation: a multi-purpose base for Tasmania's forest management. *Tasforests* **10**:15-32.

Tulloch AIT, Sutcliffe P, Naujokaitis-Lewis I, Tingley R, Brotons L, Ferraz KMPMB, Possingham H, Guisan A, Rhodes JR. 2016. Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. *Biological Conservation*, **199**:157-171.

Vanreusel W, Maes D, van Dyck H. 2007. Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. *Conservation Biology* **21**:201-212.

Webb MH, Holdsworth, MC, Webb J. 2012. Nesting requirements of the endangered Swift Parrot (*Lathamus discolor*). *Emu* **112**:181-188.

Webb MH, Wotherspoon S, Stojanovic D, Heinsohn R, Cunningham R, Bell P, Terauds A. 2014. Location matters: using spatially explicit occupancy models to predict the distribution of the

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highly mobile, endangered swift parrot. *Biological Conservation* **176**:99-108.

Woinarski JCZ, Whitehead PJ, Bowman DMJS, Russell-Smith J. 1992. Conservation of Mobile Species in a Variable Environment: The Problem of Reserve Design in the Northern Territory, Australia. *Global Ecology and Biogeography Letters* **2**:1-10.

Woinarski JCZ, Connors GC, Don F. 2000. Thinking honeyeater: nectar maps for the Northern Territory, Australia. *Pacific Conservation Biology* **6**:61-80.

Xu T, Hutchinson M. 2011. ANUCLIM version 6.1 user guide. The Australian National University, Fenner School of Environment and Society, Canberra.

Table 1. ANCOVA results testing for the effect of modeling approach and year on estimates of occupied habitat (model = habitat suitability model versus occupancy model).

Measure of habitat	Variable	<i>F</i> -value	<i>p</i> -value
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

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Table 2. Nesting occupancy ( $\Psi_n$ ) and detectability ( $p_n$ ) rates in surveyed nesting habitat.

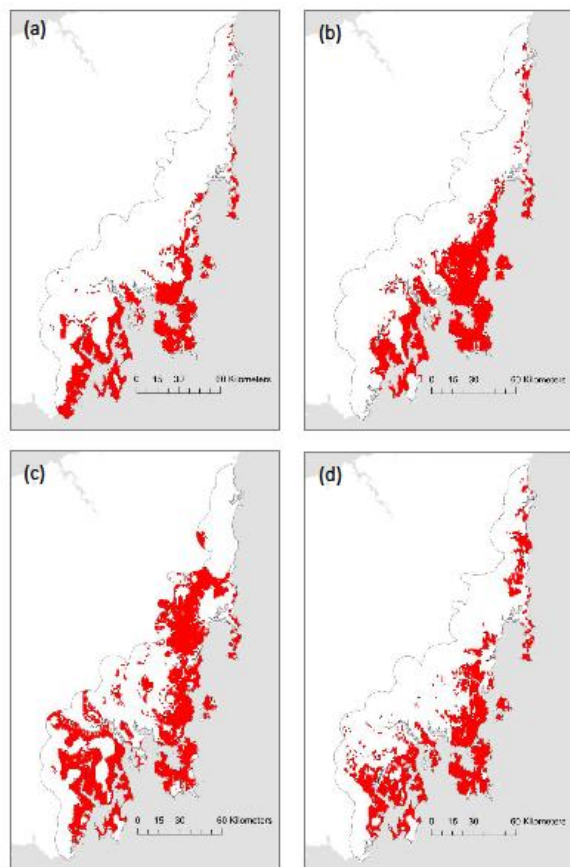
Parameter	Year					
	2009	2010	2011	2012	2013	2014
Naïve $\Psi_n$	0.66	0.66	0.51	0.59	0.65	0.29
$\Psi_n$	0.74	0.83	0.69	0.94	0.74	*
SE	0.07	0.05	0.06	0.07	0.05	*
$p_n$	0.4	0.57	0.55	0.49	0.57	0.35
SE	0.03	0.03	0.04	0.03	0.03	0.04

Naïve  $\Psi_n$  = observed occupancy

\* could not be estimated due to poor model fit

## Figure legends

Figure 1. Habitat suitability models (using Maxent) from 2009-2012 (left to right a, b, c and d) using equal sensitivity and specificity threshold. Threshold values for each year were 0.1557, 0.2070, 0.2481, 0.1670, respectively. Grey line is the swift parrot breeding range (Natural Values Atlas 2015).



**Figure 1**

Figure 2. Swift parrot occupancy models from 2009-2014 (left to right a, b, c, d, e, f). NESTING HABITAT (red), FORAGING HABITAT (blue). Threshold values for each year were 0.3637, 0.3904, 0.4305, 0.3932, 0.3635, 0.2926, respectively.

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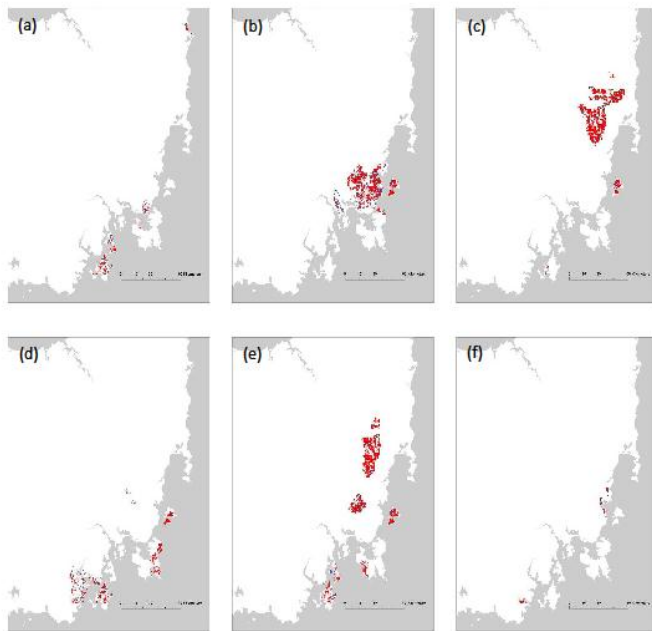


Figure 3. Annual estimates of occupied habitat from habitat suitability models (dashed lines) and occupancy models (solid lines) in the swift parrot breeding range over 6 years: + TOTAL AREA, ◇ FOREST, Δ NESTING HABITAT, □ ADJUSTED NESTING HABITAT, ○ FORAGING HABITAT, - Total functional habitat area; Y axis is on the logarithmic scale.

