

An Empirical and Mechanistic Explanation of Abundance-Occupancy Relationships for a Critically Endangered Nomadic Migrant

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ABSTRACT: The positive abundance-occupancy relationship (AOR) is a pervasive pattern in macroecology. Similarly, the association between occupancy (or probability of occurrence) and abundance is also usually assumed to be positive and in most cases constant. Examples of AORs for nomadic species with variable distributions are extremely rare. Here we examined temporal and spatial trends in the AOR over 7 years for a critically endangered nomadic migrant that relies on dynamic pulses in food availability to breed. We predicted a negative temporal relationship, where local mean abundances increase when the number of occupied sites decreases, and a positive relationship between local abundances and the probability of occurrence. We also predicted that these patterns are largely attributable to spatiotemporal variation in food abundance. The temporal AOR was significantly negative, and annual food availability was significantly positively correlated with the number of occupied sites but negatively correlated with abundance. Thus, as food availability decreased, local densities of birds increased, and vice versa. The abundance–probability of occurrence relationship was positive and nonlinear but varied between years due to differing degrees of spatial aggregation caused by changing food availability. Importantly, high abundance (or occupancy) did not necessarily equate to high-quality habitat and may be indicative of resource bottlenecks or exposure to other processes affecting vital rates. Our results provide a rare empirical example that highlights the complexity of AORs for species that target aggregated food resources in dynamic environments.

Keywords: distribution-abundance, range-abundance, density-occupancy, nomad, mobile species, swift parrot.

Introduction

A well-documented pattern in ecology, both within and among species, is that species occupying more sites or with

larger geographic distributions are generally more locally abundant, resulting in a positive abundance-occupancy relationship (AOR; Brown 1984; Gaston and Lawton 1990; Borregaard and Rahbek 2010). This implies that if the local abundance of a species is reduced (e.g., by degradation of habitat), then the number of sites it occupies will also be reduced (Gaston and Curnutt 1998). The AOR has been studied for a diverse range of taxa (e.g., Gaston et al. 1998; Conrad et al. 2001; Kotze et al. 2003; Blackburn et al. 2006; Webb et al. 2007; Buckley et al. 2010; Verberk et al. 2010; Faulks et al. 2015) and has numerous implications for population monitoring and management (Gaston 1999), biological invasions (Kulhanek et al. 2011), pest management (Wilson and Room 1983), and setting harvest limits (Gaston et al. 2000; Buckley et al. 2017). Furthermore, species that occur at low abundance tend to be narrowly distributed and so face “double jeopardy,” whereby extinction risk increases due to the chance of local stochastic events affecting entire populations (Gaston 1998).

Nomadic migrants undergo large-scale irregular movement patterns, exhibiting variation in their geographic ranges over time (Newton 2006). Their movement strategies have typically evolved to enable them to better track and exploit rich patches of sporadic and often spatially aggregated food. A major research challenge is to study them at ecologically relevant spatial and temporal scales (Dingle 2008), and robust empirical data on their movements are rare (Runge et al. 2014, 2015b). Hence, few studies on these species have examined trends in intraspecific AORs or predictions of spatial and temporal patterns in the probability of occupancy and abundance (Howard et al. 2014; Kalle et al. 2018). However, the variation in range dynamics and density of nomads mean that they provide excellent opportunities for exploring the causal mechanisms driving the relationships outlined above (Gaston et al. 1998; Freckleton et al. 2005; Webb et al. 2012).

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Developing a better understanding of AORs for nomads may be informative for understanding ecological mechanisms driving their movements and interpreting predictions from dynamic species distribution models (SDMs; Maclean et al. 2011; Steenweg et al. 2018). Indeed, understanding these relationships will also provide insights into the range dynamics of other species that target spatially aggregated food sources (e.g., Kalle et al. 2018). Most SDMs utilize presence-only or presence-absence data and environmental variables to predict the probability of a site being occupied (or habitat suitability and other suitable indices; Phillips et al. 2006; Howard et al. 2014). Interpretation of SDMs heavily relies on the assumption of a positive relationship between the probability of a site being occupied and local abundance at that site (e.g., Maclean et al. 2011; Collier et al. 2012; Carrascal et al. 2015; Weber et al. 2016). This also usually implies a direct (and linear) relationship between habitat quality and a species' abundance (e.g., Freckleton et al. 2005; Mosser et al. 2009; Buckley et al. 2010). To date, the relationship between abundance and occupancy in SDMs has generally been considered separately from traditional AORs, and potential relationships between the two areas of study have rarely been examined (but see Steenweg et al. 2018). Furthermore, the AOR literature has been "fractured by the use of different terminology" (Borregaard and Rahbek 2010).

In the AOR literature, temporal trends (i.e., temporal AORs) have received less attention than interspecific or spatial forms of AOR (Webb et al. 2007; Borregaard and Rahbek 2010). Similar to many studies utilizing SDMs, most AOR studies assume that relationships remain constant over relatively short time frames (e.g., Maclean et al. 2011; Gutiérrez et al. 2013). Several hypotheses have been proposed to explain the existence and nature of AORs, which can be divided into three categories (Faulks et al. 2015): (1) niche breadth in relation to abiotic and/or biotic factors (Brown 1984; Holt et al. 1997; Freckleton et al. 2006), (2) population dynamics mediated by dispersal and colonization (Freckleton et al. 2005; Werner et al. 2014), and (3) sampling artifacts resulting from range position and the resolution of sampling (Gaston et al. 2000; He and Gaston 2000; Wilson 2011). Importantly, these mechanisms are not mutually exclusive (Faulks et al. 2015), and a common thread connecting these hypotheses, explicitly or implicitly, is the degree of spatial aggregation at multiple spatial scales (Storch et al. 2008). Despite this well-established theory, there are few detailed empirical and mechanistic examples of intraspecific AORs that account for both time and space (Borregaard and Rahbek 2010; Faulks et al. 2015; but see Werner et al. 2014 for an example). This is especially so for rare or declining species that may not follow the positive abundance-occupancy paradigm (e.g., Freckleton et al. 2005; Webb et al. 2007).

Here we address these questions using long-term data to provide a rare empirical explanation of the AOR for a crit-

ically endangered nomadic migrant (the swift parrot *Lathamus discolor*) and how this relates to predictions from dynamic SDMs over time. Like many nomads, the species exploits dynamic and spatially aggregated pulses in food when breeding and also requires tree cavities for nesting. This results in dramatic changes in the location and availability of habitat from one year to the next (Webb et al. 2017). Variation in the species' range provides ideal opportunities to test assumptions about the relationship between abundance and "occupancy" for both AORs and SDMs.

Patterns of food availability in dynamic systems are often spatially autocorrelated, causing species to undergo dynamic changes in spatial aggregation (Webb et al. 2014; Kalle et al. 2018). For example, when resources are spatially widespread and dispersal and colonization ability allow (Buckley and Freckleton 2010), populations may expand their geographic range to exploit current conditions, resulting in decreased spatial aggregation (fig. 1). Likewise, when resources are scarce, high densities (or aggregations) of individuals may form (fig. 1). Beyond some threshold, populations may experience resource bottlenecks whereby individuals may use low-quality

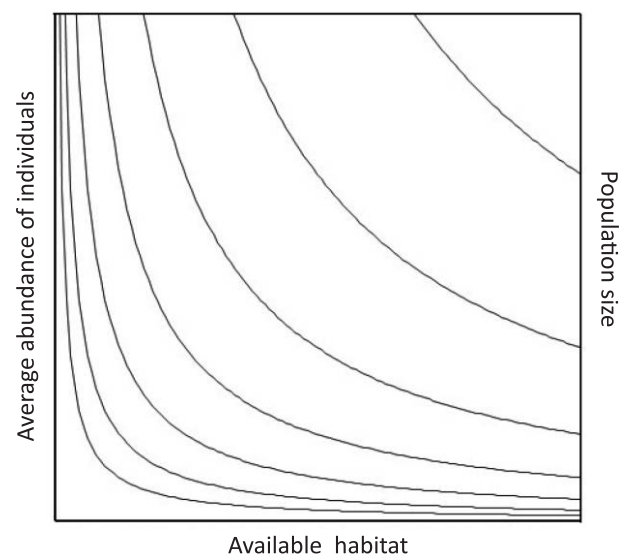


Figure 1: Schematic outline of how changes in available habitat (i.e., number of occupied sites) may affect the average abundance of individuals of a nomadic species in a dynamic environment. Assuming the number of occupied sites increases with available habitat (X-axis), the density of individuals (left-hand Y-axis) will increase with population size (right-hand Y-axis) as available habitat decreases and vice versa. Each curve is generated on the basis that as the area of available habitat is halved, the average density of individuals doubles for a given population size (i.e., each curve). Because changes in available habitat can vary over short time-scales (e.g., interyear), so too can the number of occupied sites (or range size) and average abundance of individuals. Thus, for a relatively stable population, the temporal abundance-occupancy relationship is likely to be negative. Importantly, beyond some threshold resource limitation may occur as habitat availability decreases and density increases.

habitats that would not be occupied under better conditions (Manning et al. 2007; Werner et al. 2014). These patterns are not restricted to nomads; other species that rely on spatially dynamic food sources or have different movement strategies, such as altitudinal or partial migrants, also show variation in range dynamics (Boyle 2008; Sekercioglu 2010; Barçante et al. 2017; Bastille-Rousseau et al. 2017). Understanding these relationships for nomads might also provide insights into the range dynamics of these other species.

The effect of food limitation may be further compounded if other resources are limited. For example, food is often the driver of animal movements, but if other required resources (e.g., nesting sites) are limited where food is abundant, this may have overall consequences for habitat quality or carrying capacity. In turn, this may result in changes in a species' distribution and density (fig. 1). Similarly, where nest sites are abundant, food limitation may constrain a species' distribution or carrying capacity. Understanding how the relationship between dispersal ability and the abundance of resources in time and space affects the relationship between abundance and occupancy may provide critical information to evaluate changes in carrying capacity and vital rates over time.

For highly mobile species such as nomads, assuming that local densities are a direct function of habitat suitability, resource availability, or range size (e.g., Brown et al. 1984; Holt et al. 1997) may be misleading and conflate the underlying ecological processes causing observed patterns (Boyle 2011). Similarly, the effects of dispersal ability and habitat patchiness on the AOR that apply to less mobile species (Freckleton et al. 2005) are likely to be much weaker, or absent for nomads.

We hypothesize that for species that depend on dynamic and aggregated food sources, such as the swift parrot, the temporal AOR and the relationship between abundance and the probability of occupancy are likely to be linked but variable in time and space due to changes in food availability. Using 7 years of data collected from a population monitoring study, we test the predictions that (1) the temporal AOR is likely to be negative, with local abundances decreasing in response to increasing food resources, and (2) the relationship between abundance and the probability of occupancy should be positive but increase in strength with decreasing food availability. Our study provides novel empirical insights into the causal mechanisms of the relationship between abundance and occupancy in dynamic systems for both traditional AOR studies and studies using SDMs to predict animal occurrence and abundance from presence-absence data.

Material and Methods

Empirical Data and Study Species

The swift parrot breeds only in Tasmania, Australia (Webb et al. 2017). During breeding, the species depends on the

flowering dynamics of two eucalypt tree species for food (Webb et al. 2014). Underlying this spatiotemporal variation in flowering is a high level of fragmentation in the density and distribution of food trees due to both natural and anthropogenic processes (app. A; apps. A–C are available online). This also results in significant temporal variation in the availability and co-occurrence of foraging habitat and nesting habitat (Webb et al. 2017).

Swift parrot presence-absence data were collected during the early breeding season (i.e., October) when the species has settled to nest, allowing their breeding distribution to be measured in that year (Webb et al. 2017). Between 2009 and 2015, several hundred fixed sites were surveyed (mean number of sites surveyed each year: 942; SD: 105) across their breeding range (approximately 10,000 km²). A site was defined as a 200-m radius around a fixed point and was surveyed using repeated site visits (two to five visits per site). Variation in the number of site visits was due to access to remote or private land sites and deliberately focusing more effort in regions where birds were present to better estimate detectability at a site (given presence; see Specht et al. 2017). Counts of swift parrots were conducted at the same time (and spatial scale); here we use the maximum count from each site for each year as a measure of site abundance. Flowering of food trees was also recorded during bird surveys to provide a measure of food abundance. Flowering was scored on a scale of 0–4, where 0 = none, 1 = light, 2 = moderate, 3 = heavy, and 4 = very heavy flowering. Each site was assigned the flower score of the heaviest flowering tree (for further details, see Webb et al. 2014).

To examine both the temporal and the spatial AORs, we used the maximum count data from each site and annual site occupancy model predictions from Webb et al. (2014, 2017), with additional data from 2015. Occupancy models are now one of the most commonly utilized approaches to model a species' distribution when presence and absence data are available. These models provide predictions of the probability of a site being occupied in each year (e.g., Collier et al. 2012). The zero-inflated binomial occupancy models (from Webb et al. 2014, 2017) use swift parrot presence-absence data as the response variable and account for imperfect detection, food availability, and spatial autocorrelation through the inclusion of a spatially explicit covariate. Models were implemented in a generalized additive model (GAM) framework in R package *mgcv* (Wood 2004) utilizing the expectation-maximization algorithm (Webb et al. 2014), as opposed to a traditional generalized linear model structure. This approach allows space to be viewed as continuous (through the use of a bivariate spatial term) with the advantage of simple model selection procedures (Webb et al. 2014).

The spatial scale of aggregated flowering events is generally much larger than the scale of the sites surveyed (0.125 km²), and swift parrots can forage several kilometers from their nest

(Webb et al. 2014). Therefore, we also examined the relationship between site occupancy and abundance at a broader ecologically relevant scale that accounted for the bird's mobility and use of the landscape ($\sim 80 \text{ km}^2$; see below).

*Prediction 1: Negative Temporal AOR
and Food Availability*

We predicted that a negative temporal AOR exists for the swift parrot population, which can be attributed to a decrease in local abundances in response to increasing spatial extent of food resources or vice versa. To examine this, we tested for a correlation between local mean abundance and the number and proportion of occupied sites in each year of the study using Pearson's product-moment correlation. Local mean abundance was the mean count at all sites where the species was detected, a commonly used abundance metric to investigate AORs (Webb et al. 2012). The proportion of occupied sites was calculated by dividing the number of sites where the species was detected by the total number of surveyed sites. We then tested for a relationship between the proportion of occupied sites and the proportion of sites with high densities of birds, following Conrad et al. (2001). Here the term "high density" refers to unusually large aggregations of birds at a single site. In this context, high-density sites were defined as those where over 10 birds were recorded, noting that 10 birds exceeds the highest local mean abundance estimate over the 7 years (table 1). We then summed the number of birds counted at high-density sites and calculated the proportional contribution of these sites to the total count of birds each year. Again, using Pearson's product-moment correlation we tested the significance of the relationship between the annual proportion of occupied sites and the annual value of this metric.

To examine whether the temporal AOR was influenced by food availability in each year, we used the proportion

of sites with a flower score equaling or exceeding 2 (i.e., at least moderate flowering) as an index of food abundance (hereafter, "flowering sites"). We used a flower score of 2 or greater because the mean flower score of occupied sites over the 7 years was 2.15 (SD: 0.37). Using the same test as above, we tested for a correlation between our index of food availability and the proportion of occupied sites, local mean abundance, and metrics derived from high-density sites. All analyses were implemented in R (R Development Core Team 2016).

*Prediction 2: Positive Relationship between Abundance
and the Probability of Occupancy*

We predicted that a positive relationship would exist between abundance and occupancy probabilities at both the site and the landscape scales but that the strength of the relationship would increase with decreasing availability of food.

Site Scale. At the site scale we used GAMs in R package mgcv (Wood 2004). We fitted models with $\text{ABUNDANCE}_{\text{site}}$ (maximum count at each site) as the response variable, site-level $\text{OCCUPANCY}_{\text{site}}$ estimates (Webb et al. 2014, 2017) as a continuous predictor variable (grouped by YEAR), and YEAR as a factor (which we considered a surrogate for annual variation in food availability). The inclusion of $\text{OCCUPANCY}_{\text{site}}$ as a smoothed term in models accounted for potential non-linear relationships (hence the use of a GAM framework), and we used a negative binomial distribution to account for overdispersion in the data (Wood 2004).

Landscape Scale. To examine the relationship at the landscape scale we interpolated annual occupancy model predictions ($\text{OCCUPANCY}_{\text{land}}$) using kriging with a cell size of 2.25 km^2 , a search radius of 5 km, and a spherical semivariogram model (using ArcMap 10.2 sensu Webb et al. 2014).

Table 1: Summary of swift parrot occurrence, abundance, and food availability over 7 years

	2009	2010	2011	2012	2013	2014	2015
Occupied sites	66	151	127	151	156	87	136
Total sites surveyed	755	834	996	989	982	1,045	990
Proportion of sites occupied	.087	.181	.127	.153	.159	.083	.138
Total count	526	619	693	665	556	602	688
Local mean abundance	7.8 (1.1)	4.3 (.3)	5.5 (.7)	4.4 (.4)	3.6 (.3)	6.8 (1.2)	5.1 (.5)
No. high-density sites	20	12	16	13	11	16	22
Proportion of occupied sites with high density	.303	.079	.126	.086	.071	.184	.162
Total count from high-density sites	382	192	346	224	174	401	350
Proportion of total count recorded at high-density sites	.726	.310	.499	.337	.313	.666	.509
Proportion of sites with a flower score ≥ 2 (flowering sites)	.139	.393	.150	.233	.309	.110	.178

Note: Standard errors for local mean abundance are in parentheses. High-density sites were those with >10 individuals recorded. All sites were assigned a flower score from 0 to 4 (see "Methods").

Using the same kriging method we then interpolated observed maximum swift parrot abundances from each site ($ABUNDANCE_{land}$) for each year, resulting in an annual mean of 4,517 ($SD \pm 424$) comparable cells for each of the 7 years. We used the same model structure for the site-scale analyses, fitting negative binomial GAMs with $ABUNDANCE_{land}$ from each cell as the response variable. Again, YEAR was included as a factor, and a smoothed $OCCUPANCY_{land}$ term (grouped by YEAR) was used to account for nonlinear relationships.

For both the site-scale and the landscape-scale analyses, all three combinations of the two covariates were fitted: (i) $ABUNDANCE \sim YEAR$, (ii) $ABUNDANCE \sim OCCUPANCY$ (grouped by YEAR), and (iii) $ABUNDANCE \sim OCCUPANCY$ (grouped by YEAR) + YEAR. In models with the occupancy term, a smoothed function was included to account for nonlinear relationships. Akaike information criterion (AIC) scores were used to rank the best models (i.e., >2 AIC points; table B1; tables B1, B2, C1 are available online).

Results

Prediction 1: Negative Temporal AOR and Food Availability

Local mean abundance was significantly and negatively correlated with the proportion of sites occupied (Pearson's $r = -0.92$, $P < .01$; table 1), supporting the existence of a negative temporal AOR (fig. 2A). The proportion of occupied sites was significantly and negatively correlated with the proportion of high-density sites (Pearson's $r = -0.85$, $P = .016$) and the proportional contribution of counts from high-density sites to the total count of birds each year (Pearson's $r = -0.96$, $P < .01$; fig. 2B).

The proportion of flowering sites (table 1) was significantly positively correlated with the proportion of occupied sites each year (Pearson's $r = 0.90$, $P < .01$) but negatively correlated with local mean abundance (Pearson's $r = -0.77$, $P < .05$). Flowering sites were significantly negatively correlated with the proportional contribution of counts from high-density sites to the total count (Pearson's $r = -0.85$, $P = .015$) but not with the proportion of sites defined as high density (Pearson's $r = -0.70$, $P = .082$).

Prediction 2: Positive Relationship between Abundance and the Probability of Occupancy

At both spatial scales the best models (based on AIC scores) included the smoothed $OCCUPANCY$ covariate (grouped by YEAR) and YEAR as a factor (table B1). The relationship between abundance and occupancy probabilities was positive but nonlinear and varied in strength and shape between years at both the site and the landscape scales (figs. 3, 4; table B2).

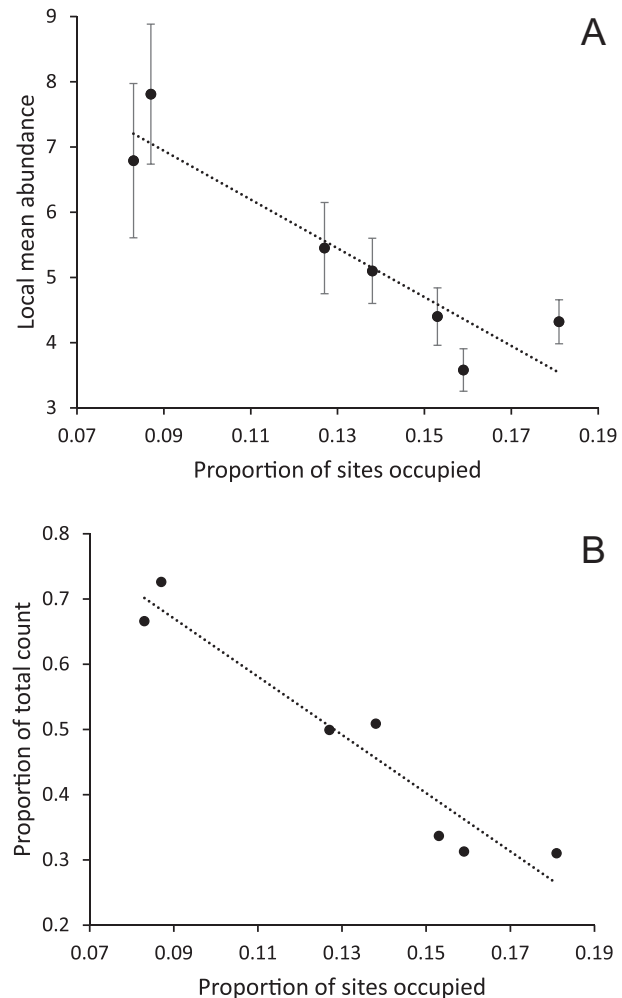


Figure 2: Proportion of occupied sites plotted against mean swift parrot abundance (A) and proportional contribution of counts from high-density sites to the total count of birds each year (B); error bars represent standard errors; the dotted line represents the linear trend line.

At the site scale, in 2010, 2012, and 2013 abundance increased gradually with occupancy probabilities (fig. 3). These years also had the highest proportion of flowering sites (table 1). A slightly stronger relationship was observed in 2009 and 2015 with a corresponding increase in the proportion of flowering sites compared to the years above. The strongest relationship was observed in 2014, particularly at higher occupancy values (fig. 3), and had the lowest proportion of flowering sites (table 1). The initial increase, then asymptote observed in 2011, with little increase in abundances beyond occupancy of 0.4 and then another increase again at high occupancy (0.9), is more difficult to interpret. However, this is likely due to key flowering sites being located in a region where most food (and birds) occurred in naturally spatially segregated patches of *Eucalyptus ovata* trees with very little food between sites.

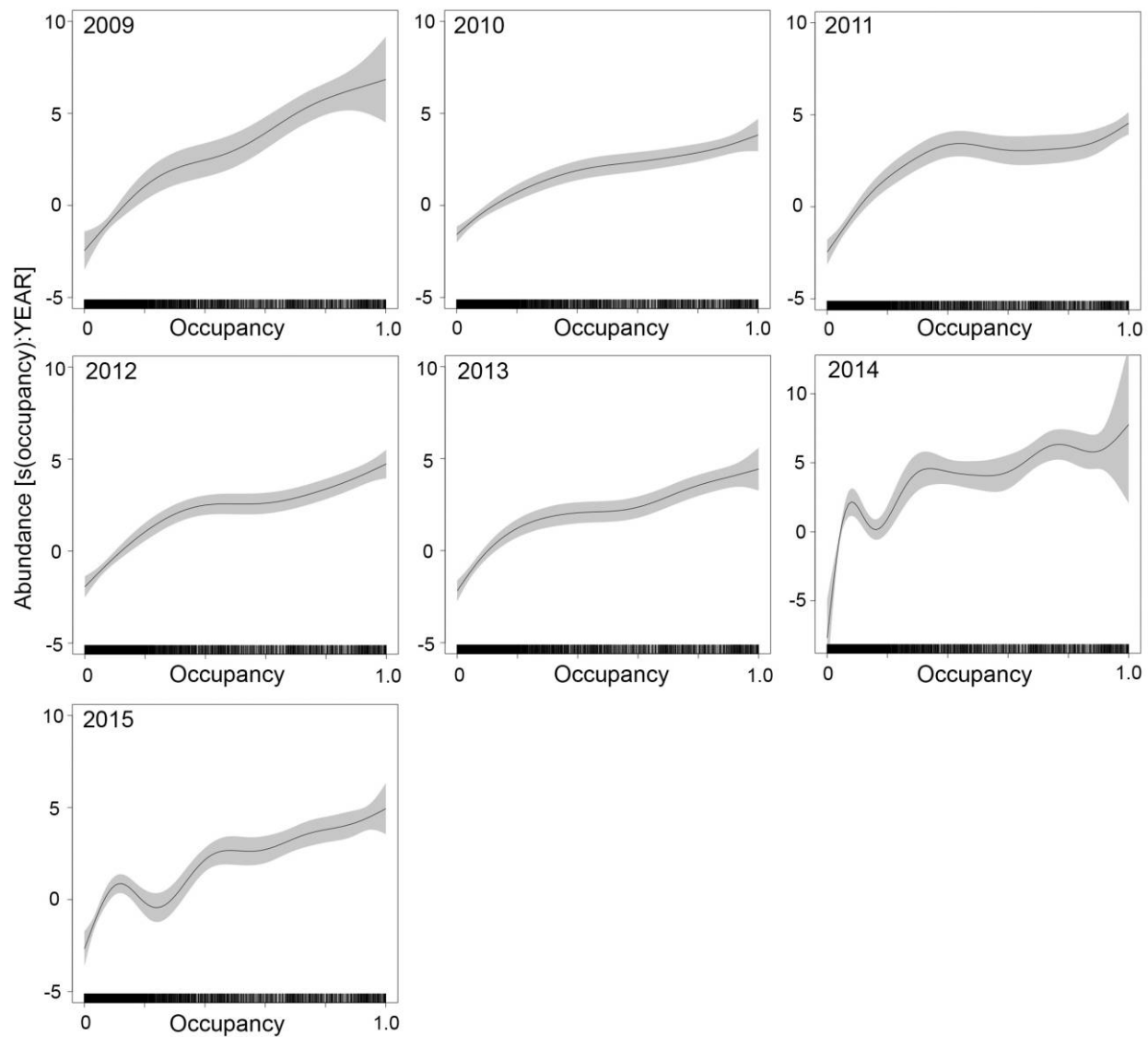


Figure 3: Relationship between swift parrot abundance (log scale) and occupancy at the site scale for each year based on the best model ($ABUNDANCE_{site} \sim s(OCCUPANCY_{site})_{grouped\ by\ YEAR} + YEAR$). Shaded areas = 95% confidence interval. Note different scales on the Y-axis.

Differences among years were even more pronounced at the landscape scale, especially at high occupancy values, with steep positive trends in 2011 and 2014 (e.g., 0.8–1.0; fig. 4). The strength of the positive relationship was again more moderate in 2010, 2012, 2013, and 2015, suggesting that at the landscape scale food was more abundant compared to other years. The clear differences in the shape and strength of the relationships in 2009, 2011, and 2014 corresponded to years with the lowest proportions of flowering sites and occupied sites as well as a higher proportion of the total count attributable to high-density sites (table 1; fig. 2B).

Data are deposited in the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.1g511q5> (Webb et al. 2019).

Discussion

Our findings provide a rare example of spatial and temporal variation in the relationship between abundance and occupancy for a highly mobile nomadic migrant, underpinned by a clear ecological mechanism (i.e., food). Our predictions of a negative temporal AOR and a positive relationship between abundance and occupancy probabilities were both sup-

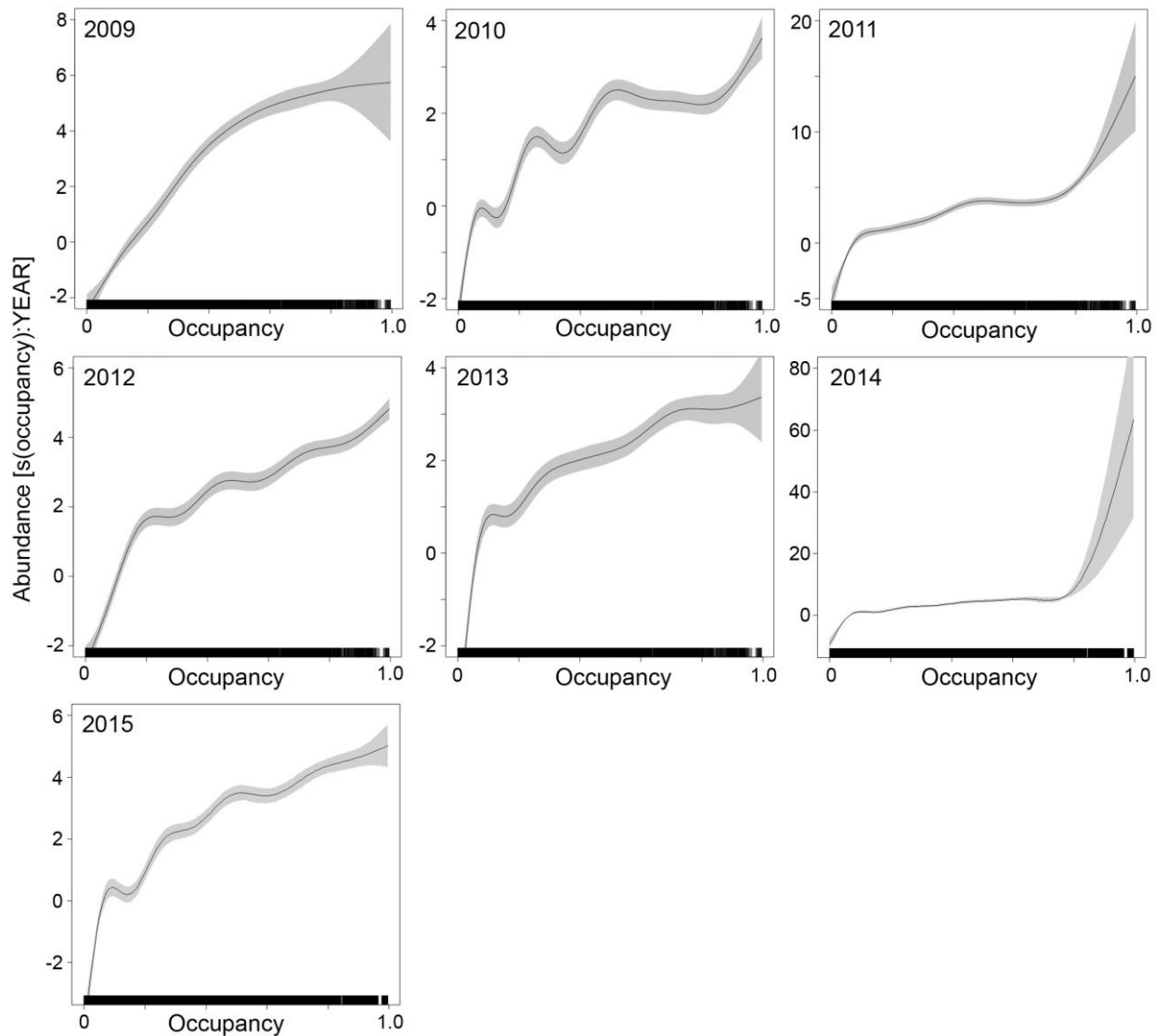


Figure 4: Relationship between swift parrot abundance (log scale) and occupancy at the landscape scale for each year based on the best model ($ABUNDANCE_{land} \sim s(OCCUPANCY_{land}, \text{grouped by YEAR}) + YEAR$). Shaded areas = 95% confidence interval. Note different scales on the Y-axis.

ported by the data. These findings provide strong evidence that these processes are primarily influenced by varying degrees of spatial aggregation (Freckleton et al. 2006; Storch et al. 2008; Webb et al. 2012) caused by dynamic and spatially aggregated patterns in food availability (for annual flowering conditions and food tree mapping, see app. A). Our results provide (i) empirical support for previous hypotheses on the causal mechanisms of AORs and (ii) improved understanding of the ecological consequences of these relationships for species relying on dynamic systems. In this context, our findings are likely to be relevant to both nomadic and nonnomadic species that rely on aggregated

but variable food sources, such as nectarivores (Woinarski et al. 2000; Crates et al. 2017), frugivores (Boyle 2010, 2011; Kalle et al. 2018), arid zone species (Runge et al. 2015a), or species exhibiting variable intraspecific movement strategies (Norbu et al. 2017; Silva et al. 2017).

The temporal AOR shows that as the proportion of occupied sites decreases, local mean abundance increases, with a corresponding increase in variation around the mean (fig. 2A). In consequence, a greater proportion of the total count is attributable to high-density sites (fig. 2B) with a higher degree of aggregation. Spatially, this manifested as an increase in the strength of the relationship between abundance and oc-

cupancy probabilities in years with fewer occupied sites (figs. 3, 4). These changes were most pronounced at the more ecologically relevant landscape scale, particularly in poorer flowering years (e.g., 2009, 2011, and 2014; fig. 4). Notably, these years also corresponded to the lowest predictions of foraging habitat area by Webb et al. (2017), which are more indicative of food availability over an entire breeding season (app. C).

The location and degree of aggregation of a species may make it more or less susceptible to non-habitat-related threats (Buckley et al. 2017), resource bottlenecks (Runge et al. 2014), and habitat loss (Webb et al. 2017). This has interesting implications in the context of double jeopardy (Gaston 1998). That is, rather than abundance decreasing with fewer occupied sites (or range size), it increased. For the swift parrot, this may also increase the proportion of the population being exposed (or not) to spatially explicit threatening processes (e.g., predation; Heinsohn et al. 2015).

While high mobility may help nomads cope with changing environments (Kalle et al. 2018), resource availability across their entire potential range needs to be considered (fig. 1). For example, in this study small spatially aggregated patches of food in 2014 (see app. A) coupled with other spatially segregated sites with food resulted in a dramatic reduction in the availability of nesting habitat (Webb et al. 2017). Under these conditions, habitat limitation may decouple the association between abundance and occupancy probabilities and habitat quality, whereby carrying capacity may be reached or exceeded. This may force remaining individuals into less suitable locations (e.g., isolated occurrences of food unsuitable for breeding) or where intraspecific competition is greater (Silva et al. 2017).

The scarcity of food in some years was reflected in the landscape-scale analyses by plateaus in the abundance and occupancy probabilities at midrange occupancy values and the steep increases at high occupancy values (>0.8 ; e.g., 2011 and 2014; fig. 4). By contrast, in years when food was more abundant (e.g., 2010, 2012, 2013, and 2015; apps. A, C), smaller increases in abundance were predicted across a broad range of occupancy values. Thus, more widespread food results in less spatial aggregation and an overall weaker relationship between abundance and the probability of occupancy. For the process proposed in figure 1 to apply, nomads (or other mobile species) must be effective at tracking shifts in resource availability. This is a common yet poorly understood trait of many nomads (Kalle et al. 2018) but is clearly demonstrated by the variation of the swift parrot's range dynamics (Webb et al. 2014, 2017).

Because the relationship in this study varied between years, was scale dependent, and was generally nonlinear, our results suggest that for nomadic species, incorporating abundance data into dynamic distribution models will be crucial to evaluating changes in carrying capacity (Hobbs and Hanley 1990;

McLeod 1997; Howard et al. 2014), exposure to other threats (McLoughlin et al. 2010), and ultimately vital rates of the population (Heinsohn et al. 2015).

Our results also have important implications for evaluating the relative availability of required habitats for mobile species (e.g., food and nesting sites), which can vary markedly between years (Webb et al. 2017). While food is often the primary driver of the relationship between occupancy and abundance, it is also possible for other required habitats to be limiting in a given year, with overall consequences for the area of available habitat and density of individuals (fig. 1).

In the context of previous hypotheses regarding the mechanisms driving AORs and associated relationships, the causal mechanisms of the processes in this study are most likely a combination of (1) resource use and availability (Brown 1984; Hanski et al. 1993), (2) habitat dispersal (Venier and Fahrig 1996; Freckleton et al. 2005), and (3) density-dependent habitat selection (O'Connor 1987; Wheatley et al. 2002; see also table 1 in Borregaard and Rahbek 2010). When flowering trees were more abundant and widespread, the population dispersed and occupied more sites (i.e., mechanisms 1 and 2). When the distribution of food contracted to smaller areas, so did the swift parrot population. If this results in high individual density and food or nest site limitation (fig. 1), intra- and possibly interspecific competition may force birds into less suitable habitats (i.e., mechanisms 1 and 3; McLoughlin et al. 2010; Silva et al. 2017). The relative importance of each mechanism likely depends on the spatial configuration and availability of food (table 1; app. A), and each is critical to understanding how population dynamics scale temporally and spatially.

The scale at which sampling occurs (i.e., sampling unit) and the spatial extent of sampling can have profound effects on the results of abundance-occupancy studies (He and Gaston 2000); however, such effects have rarely been quantified (Steenweg et al. 2018). While we expect that future empirical work may find comparable patterns for other species that track resources in space and time, sampling at the appropriate scale(s) for target species will be crucial. Because similar patterns for other animals may occur at finer or larger scales (including degrees of aggregation) than those explored in this study (Bradbury et al. 1986; Gaston et al. 1998; Blackburn et al. 2006), future studies need to carefully consider the spatial and temporal scale of sampling in the context of the species range dynamics. For example, if sampling is undertaken at finer resolutions than this study and a species tracks spatially variable and aggregated resources at a similar scale, comparable patterns may be observed (e.g., Guillaumet et al. 2017; 'iwi, *Drepanis coccinea*). For aggregating species with dynamic ranges, we suggest that sampling intensively (to capture aggregations; Crates et al. 2017) and extensively (to sample a species' entire potential range; Vaughan and Ormerod 2003) is critical to generate meaningful data (Webb et al. 2014). Im-

portantly, this may also require more flexibility than traditional sampling designs to allow the spatial structure (or aggregations) in populations (and the resources they rely on) to be captured, rather than explicitly attempting to eliminate spatial autocorrelation and attain independence between sites (Legendre 1993; Hawkins 2012).

By incorporating and contrasting information on AORs and occupancy models for a highly mobile nomad, we take a step toward better identifying fluctuations in carrying capacity, priority sites, and resource bottlenecks (e.g., Veloz et al. 2015; Runge et al. 2016) and interpreting dynamic SDMs (Kalle et al. 2018). Furthermore, we show that understanding the causal mechanisms of AORs for nomads, and how they change over time, may provide an empirical means to understand changes in population size and range dynamics (Steenweg et al. 2018).

We suggest that our results have broad applicability to understanding occupancy and underlying AORs for other species that rely on resources that vary in location and abundance (e.g., frugivores [Kalle et al. 2018]; nectarivores [Crates et al. 2017]; arid zone species [Runge et al. 2015a]; marine species [Buckley et al. 2017]). Our empirical insights highlight how species that have variable resource-driven distributions and/or degrees of spatial aggregation can affect AORs. Furthermore, the mobility of such species means that the potential limiting effects of dispersal and colonization (Freckleton et al. 2005) on the AOR may be negated. Hence, high abundances can potentially occur at locations where habitat quality is high or low depending on overall resource availability across their potential range. Therefore, high densities of individuals do not necessarily always equate to high-quality habitat (Van Horne 1983; Mosser et al. 2009; Thuiller et al. 2014), and such aggregations may be an indication of resource limitation. As recently suggested by Steenweg et al. (2018), empirically integrating these two common areas of research (i.e., SDMs and AORs) and examining multiple spatial scales has allowed us to provide new insights into the ecology of mobile species and highlighted the potential benefits of adopting this approach in future studies.

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Nearly fledged swift parrot (*Lathamus discolor*) chicks. Photo credit: Henry Cook.