





Research Article

Pre-Emptive Action as a Measure for Conserving Nomadic Species

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ABSTRACT Nomadic species are globally threatened by anthropogenic habitat change, but management options to address their decline are limited. Their unpredictable settlement patterns pose major challenges for conservation because identifying where to implement action is difficult. We address this challenge by preempting settlement patterns in a nomadic species using data from a long-term study of the critically endangered, cavity-nesting swift parrot (*Lathamus discolor*) and by taking action at the sites identified. We detected flower bud growth (the primary settlement cue) and deployed artificial nests at 3 predicted breeding sites before the birds arrived. At the broad breeding-range scale, swift parrots settled wherever bud abundance was highest, including the study area. Within the study area, artificial nest occupancy was greatest at the site with abundant historical natural nesting sites. At the local scale, we found significant effects of study site and distance to forest edges on nest box occupancy by swift parrots. Despite significant differences in thermal properties between artificial and natural nests, we found no differences in clutch size, brood size, or body condition of swift parrots in each. Monitoring settlement patterns and future food availability of nomadic wildlife can empower conservation managers to make predictions about breeding and target ecologically relevant times and locations when deploying conservation resources. Our study is an example of how conservation challenges posed by nomadic species can be overcome, and demonstrates that with effective monitoring, practical action can be targeted to address acute conservation needs and augment habitat availability. © 2018 The Wildlife Society.

KEY WORDS conservation, endangered species, *Lathamus discolor*, monitoring, nest box, nomadic species, swift parrot, tree cavity, tree hollow.

Nomadic species are of global conservation concern because their movements expose them to different threats in different locations, and these can act cumulatively on their populations (Runge et al. 2014). Unpredictable movements of nomadic wildlife hamper conservation because action at one location may not address problems elsewhere in the range (Runge et al. 2014, 2016). Long-term data are important to understanding variation in settlement patterns of nomadic species (Webb et al. 2017), but such data are scarce (Cottee-Jones et al. 2016), making spatial prioritization of on-ground action difficult (Runge et al. 2016). Many threatened

nomadic species remain poorly studied and are inadequately protected (Cottee-Jones et al. 2016).

Practical actions to address factors limiting animal populations are often constrained by incomplete knowledge and insufficient resources (Walsh et al. 2015, Watson et al. 2017). For example, large-scale threatening processes (e.g., widespread introduced predators) may be difficult to address at ecologically relevant scales or in short time frames. Consequently, small-scale actions that can be achieved with more limited resources may be more attractive as management options (Helmstedt et al. 2014, 2016). If implemented at critical locations, small-scale actions may still benefit a threatened population, despite the persistence of threats elsewhere in the range (Wilson et al. 1998). Such approaches are particularly effective for sedentary or philopatric species, whose predictable behavior facilitates targeted actions at

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critical locations (Angulo et al. 2007, Berkunsky et al. 2014). In contrast, the unpredictable settlement patterns of many nomadic species hinder similar planning because identifying where and when to act is difficult (Runge et al. 2016). If a nomadic population does not settle in areas where conservation action has been implemented, those management efforts may be wasted. As a result, conservation management for nomadic wildlife rarely involves targeted action (Runge et al. 2015). Nevertheless, where the conservation needs of a threatened nomadic species are acute (Heinsohn et al. 2015), actions that offer immediate conservation returns (Sanz-Aguilar et al. 2009, Olah et al. 2014) are important. So too is evaluation of the success or failure of management action via the collection of detailed data on the target species that may be informative about the efficacy of intervention.

We evaluated the feasibility and efficacy of proactive conservation action for the critically endangered nomadic swift parrot (*Lathamus discolor*; Heinsohn et al. 2015). Swift parrot food (i.e., nectar from flowering trees) fluctuates over a large potential breeding range in Tasmania, Australia (Webb et al. 2014). Breeding is limited each year to the subset of the overall breeding range where food and nest sites (i.e., tree cavities) co-occur (Webb et al. 2017). The species breeds in aggregations (Webb et al. 2012) and when food draws the population back to known breeding sites, previously used nest cavities may be reoccupied (Stojanovic et al. 2017). Introduced sugar gliders (*Petaurus breviceps*; Campbell et al. 2018) are the main predator of swift parrot nests (Stojanovic et al. 2014) and offshore islands free from this predator are important swift parrot habitats (Heinsohn et al. 2015). But no permanent swift parrot subpopulations occur on islands (Stojanovic et al. 2018) and island carrying capacity may limit how many individuals can breed in safety at any one time (Webb et al. 2017). For example, only 5% of the available tree cavities in some forests are suitable as nests (Stojanovic et al. 2012). When food availability is low and nest sites are limited, breeding may not occur (Webb et al. 2017). Maximizing breeding opportunities on predator-free islands is critical (Heinsohn et al. 2015), but how to achieve this conservation goal via intervention is unclear.

We examined a proactive, adaptive conservation intervention to compare reproductive parameters between artificial and natural nests. Based on knowledge of swift parrot ecology, we predicted that locally high bud abundance would correspond to occupancy of our study area in the coming breeding season. Based on this prediction, we deployed artificial nests at 3 sites and predicted that occupancy would be highest where the most abundant historical natural nesting sites occurred. We evaluated whether habitat characteristics at broad and fine scales influenced patterns of nest occupancy by swift parrots and tested whether artificial nests provided habitat of comparable quality to natural nests.

STUDY AREA

Our study took place over the spring and summer of September 2016 until January 2017. The potential swift parrot breeding range occurs in the temperate forests of

southeastern Tasmania, Australia. Our study area on north Bruny Island (Fig. 1) is free from sugar gliders (Stojanovic et al. 2014), so nest survival is high (Heinsohn et al. 2015). Mean annual maximum temperature is 16.9°C, minimum temperature is 8.9°C, with 31 mm annual mean rainfall. Spring-summer occurs from September to March and autumn-winter occurs from April to August. We used data on bud abundance from across the breeding range to select a study area (north Bruny Island), and focused on 3 study sites: Roberts Hill, Lodge Hill, and Yellow Bluff (Fig. 1). Between 2009 and the time of the study, swift parrots were recorded repeatedly nesting across the study area whenever flowering conditions were suitable (Roberts Hill: 2011, 2013, 2015; Lodge Hill: 2013, 2015; Yellow Bluff: 2013, 2015; D. Stojanovic, Australian National University, unpublished data). The sites were on private land dominated by patchy blue gum (*Eucalyptus globulus*) and white peppermint (*E. pulchella*) forest with a grassy understory, scattered within a predominantly agricultural matrix between 0 and 150 m in elevation. Although the forest across the study area is similar, within 1 km of the centroid of each site, mature forest cover was greatest at Roberts Hill (86%) compared to Lodge Hill (38%) and Yellow Bluff (48%), corresponding to higher abundance of natural nesting sites at Roberts Hill. We deployed nest boxes over 2.62 km² of forest at Roberts Hill, 0.65 km² at Lodge Hill, and 0.22 km² at Yellow Bluff. Based on Webb et al. (2017), we assumed that our sites were comparable in terms of potential swift parrot settlement given equal food abundance.

METHODS

Settlement Prediction

Swift parrots breed primarily where food (nectar from eucalyptus flowers) is locally abundant relative to elsewhere in their potential breeding range (Stojanovic et al. 2015). Flower bud development occurs over many months in blue gums before blossoms open (Jones et al. 2011), so buds indicate future food availability. We used flower bud abundance to predict where settlement would occur at broad scales over the potential swift parrot breeding range to identify our study area.

As part of annual monitoring (Webb et al. 2017) we quantified abundance of buds on food trees from 1 to 4 (Webb et al. 2014) at 989 monitoring sites across the potential Tasmanian breeding range. In 2015, most of the potential breeding range showed limited bud development, but we detected widespread, abundant young blue gum flower buds across north Bruny Island (M. H. Webb, Australian National University, unpublished data). We predicted that at the breeding range scale, swift parrots would occupy areas with the highest bud scores, including north Bruny Island. Based on this prediction, we deployed artificial nests at the 3 Bruny Island study sites before the 2016 spring breeding season.

We tested our range-wide prediction of occupancy of north Bruny Island based on bud scores using data from annual monitoring in 2016. We followed Webb et al. (2017) and quantified bud abundance across the entire potential swift

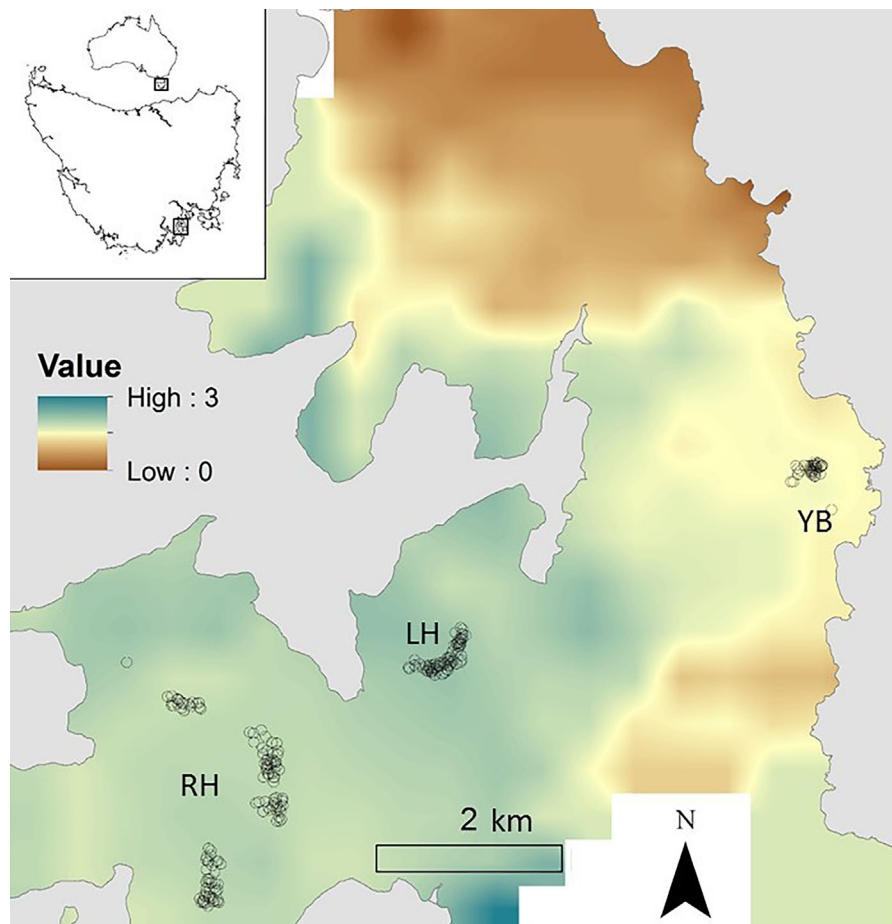


Figure 1. North Bruny Island study area, Tasmania, Australia, showing the location of artificial nest cavities (circles) deployed for swift parrots during the 2016 breeding season, and interpolated bud scores of their primary food source derived from kriging at 3 study sites: Roberts Hill (RH), Lodge Hill (LH), and Yellow Bluff (YB).

parrot breeding range. At the level of our study area, we investigated local-scale variation in bud abundance by interpolating the 2016 flower bud scores in ArcMap 10.2 (Environmental Systems Research Institute, Redlands, CA, USA) using kriging with cell size of 500 m, search radius of 2 km, and a spherical semivariogram model (Webb et al. 2014). We predicted that within north Bruny Island, swift parrots would breed at the site with the most abundant nesting habitat (Roberts Hill).

Habitat Augmentation

We used mean characteristics of natural nest cavities to construct 2 types of artificial nests: boxes and carved cavities. Nest boxes were oriented so that their longest axis was approximately 30° off horizontal. We scarified the floor of boxes to improve grip for the birds and cut small drainage holes into the back bottom corner. We painted boxes white to reduce the risk of thermal stress (Rowland et al. 2017) and used 2.5-cm-thick marine plywood for construction. We created carved cavities using chainsaws to hollow out horizontal branches or vertical stems of double-stemmed trees following Rueegger (2017). We pruned branches and stems to within 1 m of carvings to reduce risk of limb collapse.

Internal dimensions of artificial nests were 45 × 15 × 15 cm, with a 5-cm-diameter entrance hole (Stojanovic et al.

2017). We deployed nest boxes (Roberts Hill, $n = 105$; Lodge Hill, $n = 56$; Yellow Bluff, $n = 21$) and carved cavities (Roberts Hill, $n = 21$; Lodge Hill, $n = 20$; Yellow Bluff, $n = 18$) near known natural nests to increase the likelihood parrots would encounter artificial nests, and to facilitate group nesting (Webb et al. 2012). We selected trees for artificial nest deployment based on structural stability and safety for climbing (i.e., trees that were >40 cm diameter at breast height with a healthy crown). We deployed artificial nests in blue gums and white peppermints, which are dominant in the canopy of the study sites, and >20 m from other artificial or natural nests. We added approximately 3 large handfuls of decomposing wood dust to each artificial nest to mimic the interior of natural cavities. We assigned artificial nest orientation and tree species randomly.

We measured distance to the nearest forest edge of each artificial nest. At Roberts Hill, we also measured distance of nest boxes to known natural swift parrot nest cavities. We calculated distances in meters using ArcMap 10.2 geographic information system software.

Nest Monitoring

From September to January 2016, we confirmed occupancy of artificial nests by climbing trees and found additional swift parrot natural nests following standard search methods

(Stojanovic et al. 2014, 2015). We also checked all known natural swift parrot nest cavities that could be accessed by climbing, and confirmed whether inaccessible nests were active using ground-based observations. We recorded clutch and brood size of all accessible swift parrot nests and handled nestlings once for ringing and to record flattened wing chord (mm) and body mass (g). We checked nests 3 times on average (on discovery, after nestlings were >10 days old for measuring, and post-fledge at 35 days after hatching to check for dead nestlings). Unhatched eggs and dead nestlings are not removed from the nest by adult swift parrots. We determined clutch size by counting eggs or by counting unhatched eggs plus the number of nestlings (live and dead). We recorded brood size as the number of chicks that hatched. We also recorded all other species that occupied artificial nests. To evaluate saturation of the natural cavity resource at Roberts Hill, we randomly selected 50 historical nest trees to check whether swift parrots reoccupied their old nests during the study. We confirmed occupancy by climbing and using observations of parrot behavior.

Thermal Properties

Nestling birds are sensitive to temperature during development (Dawson et al. 2005, Larson et al. 2015) and nest boxes can vary in temperature depending on their design (Griffiths et al. 2017). We deployed temperature loggers (Thermochron i-Buttons, Thermodata, Baulkham Hills, Australia) at a random subset of swift parrot occupied nest boxes ($n = 20$) and natural cavities ($n = 20$) to compare their internal thermal properties. We excluded carved cavities because of low occupancy by swift parrots. Loggers recorded temperatures at 1-minute intervals from midnight on 11 November 2016 until midnight on 16 November 2016. We pinned loggers to the nest wall 15 cm away from the entrance hole to record ambient internal temperature and to avoid fouling of loggers. We conducted the work with approval from the Australian National University Animal Ethics Committee (A2014/26) and the Tasmanian Government (TFA16234).

Analytical Approach

To test our broad-scale prediction that swift parrots would occupy regions within the breeding range with the highest bud scores, we used presence-absence of birds at sites across the breeding range as response variables in generalized linear models, with bud score as a categorical fixed effect and a binomial error distribution.

To test our prediction that within the study area, swift parrots would breed at the site with the most abundant nesting habitat, we assessed spatial patterns in nest box occupancy at local and fine scales. For local-scale analyses, we included data from all 3 study sites and nest boxes and carved cavities. We used presence-absence of swift parrots as the response variable in generalized linear models with binomial distributions and logit link functions. We used backwards selection from a saturated model to fit the following fixed effects: study site (Roberts Hill, Lodge Hill, Yellow Bluff), interpolated flower bud score at each artificial nest, distance of artificial nests to the nearest forest edge, and artificial nest type (carved or box). Because our sample size was small, we

avoided overfitting by limiting the number of covariates in models to 2. For fine-scale analyses, we used only the subset of nest boxes deployed at Roberts Hill (we excluded carved cavities because the sample of swift parrot nests in carved cavities was too small). We used a similar approach as for our local-scale analysis. However, we fitted only 2 fixed effects: distance of nest boxes to forest edges and distance of nest boxes to the nearest known natural swift parrot nest cavity.

For all subsequent analyses, we used data from nest boxes and natural cavities at Roberts Hill. To compare temporal variation in fledge date between nest boxes and natural cavities, we estimated the fledge date of the eldest nestling in nests using wing chord measurements and the formula for swift parrot nestling wing growth, and assumed a 35-day nestling period (Stojanovic et al. 2015). We used fledge date (expressed as Julian day) of the eldest nestling as the response variable in a linear model with nest type (natural or box) as a fixed effect.

To examine the thermal properties of nest boxes and natural cavities occupied by swift parrots, we calculated mean, absolute maximum, and absolute minimum temperature and temperature range (i.e., the difference between max. and min. temperatures) from i-button data. We used these parameters as response variables in linear mixed models, with nest type (natural or box) as the fixed effect and date as a random term.

To investigate whether swift parrot reproductive parameters varied among natural and artificial nests, we fit Poisson distributed generalized linear models with a log link function, using clutch and brood size as response variables and nest type as a fixed effect. To evaluate whether swift parrot nestling quality varied between nest boxes and natural cavities, we used a body condition index to account for age-related variation in body mass (because we measured nestlings at different ages). Body mass is a reasonable predictor of condition in birds (Labocha and Hayes 2012). We calculated our condition index as the difference between measured body mass of a given nestling, and population mean body mass of nestlings at that age. Thus a nestling in average condition would have a body condition index of zero, whereas heavier or lighter than average nestlings would score positive or negative values, respectively. We estimated nestling age on the day it was measured using wing chord as described above. We estimated predicted average body mass for a given age using the logistic growth formula for body mass of nestling swift parrots (Stojanovic et al. 2015). Given the data presented by Stojanovic et al. (2015) were collected over only 3 years, our estimates of body condition index are relative to average nestling mass in the sample of individuals used to create growth models (rather than an absolute measure of individual quality in this study). We fit linear mixed models with body condition as a response variable and nest type as a fixed effect. We included a unique nest identifier as a random term to account for the inclusion of siblings in our sample.

We performed backwards selection using the function stepAIC in MASS (Venables and Ripley 2002) in R (R Development Core Team 2008). We compared competing

Table 1. Summary data on food abundance, distance to a forest edge, and occupancy of the 3 nest types by swift parrots across our 3 study sites on Bruny Island, Tasmania, Australia, during the 2016 spring-summer breeding season.

	Roberts Hill	Lodge Hill	Yellow Bluff
Flower bud score ^a	2.14 ± 0.03	2.33 ± 0.02	1.83 ± 0.03
Edge distance (m) ^b	428 (7–867)	120 (13–231)	43 (2–112)
Nests in natural cavities ^c	39	1	3
Nests in boxes ^c	29	3	0
Nests in carved cavities ^c	1	1	0

^a Mean ± standard deviation.

^b Mean (range).

^c Count of swift parrot nests.

models using Akaike's Information Criterion (AIC); if multiple models were supported (<2 ΔAIC), we selected those with fewer terms. We analyzed thermal data in Genstat (VSN International 2015). We conducted all other analyses in R (R Development Core Team 2008).

RESULTS

Only 86 sites (8%) across the potential Tasmanian breeding range were occupied by swift parrots in 2016. Bud scores were higher at occupied sites ($\bar{x} \pm SD = 2.6 \pm 0.7$) than unoccupied sites (1.0 ± 1.2 ; deviance = 213.35, $\chi^2_3 < 0.001$). Only 5% of monitoring sites were on north Bruny Island, but of the sites occupied by swift parrots, 16% were in our study area. Swift parrots were detected at 49% of sites on north Bruny Island.

We found significant local variation in flower bud scores within north Bruny Island ($F_{2,31} = 4,740$, $P < 0.001$; Table 1). We found 77 swift parrot nests in our study sites, distributed among all 3 nest types and at all 3 sites but most abundantly on Roberts Hill (Table 1). Of the historical natural nest cavities on Roberts Hill, 3 had collapsed and were no longer suitable as nesting sites. Of the remaining 47 historical nests, 83% were re-occupied by swift parrots during the study. Swift parrots occupied 32 nest boxes but only 2 carved cavities. All monitored swift parrot nests produced ≥ 1 fledgling.

For local-scale patterns of artificial nest occupancy (i.e., for both artificial nest types across all 3 sites), the best model of swift parrot occupancy included the variables site and forest edge distance (AIC = 168, the next best model AIC = 171; Table 2). Roberts Hill supported the largest number of swift parrot nests during the study both in natural and artificial nests (Table 1). For all study areas, occupied artificial nests were on average 269 m from a forest edge, whereas unoccupied artificial nests were on average 287 m from a

forest edge. For fine-scale patterns of artificial nest occupancy (i.e., nest boxes deployed at Roberts Hill), the best model included a negative effect of forest edge distance on swift parrots (AIC = 116, the next best model AIC = 121; Table 3). At Roberts Hill, occupied artificial nests were on average 308 m from a forest edge, whereas unoccupied artificial nests were on average 466 m from a forest edge.

At Roberts Hill, swift parrots fledged earlier in natural cavities (mean first fledge date = 4 Dec 2016 ± 22 days, $F_1 = 13.84$, $P < 0.001$) than in boxes (25 Dec 2016 ± 20 days). The mean temperature of nest boxes (12.74°C) was cooler than natural cavities (14.13°C; Wald statistic = 31.05, $df = 1$, $P = 0.001$). Similarly, the mean absolute maximum temperature of nest boxes (15.53°C) was lower than natural cavities (17.59°C; Wald statistic = 13.94, $df = 1$, $P = 0.002$), and the mean absolute minimum temperature of nest boxes (10.94°C) was lower than natural cavities (11.96°C; Wald statistic = 19.98, $df = 1$, $P = 0.005$). We found no difference in temperature range experienced by nest boxes and natural cavities ($P = 0.07$).

Swift parrot mean clutch size was 4.44 ± 0.95 , mean brood size was 4.14 ± 0.88 , and body condition was -3.56 ± 11.28 . Mean clutch size in nest boxes (4.55 ± 0.85) was not different than natural cavities (4.33 ± 1.02 ; $P = 0.38$). Similarly, there was no difference in mean brood size between nest boxes (4.22 ± 0.75) and natural cavities (4.06 ± 0.98 ; $P = 0.51$), or in mean nestling body condition between nest boxes (-3.74 ± 9.51) and natural cavities (-3.73 ± 12.75 ; $P = 0.78$).

DISCUSSION

Our study represents the first documentation of wild swift parrots using artificial nests to breed and it demonstrates the possibility of predicting the settlement patterns of a nomadic species. We show that conservation actions can be targeted across a large potential breeding range. We used abundant bud development to successfully predict that swift parrots would settle on north Bruny Island. At the local level, we successfully predicted that swift parrots would breed at Roberts Hill, where historical nest site availability was greatest. Nearly half of the swift parrot nests detected there occurred in nest boxes. Breeding opportunities for aggregations of swift parrots may be limited by nest site availability (Webb et al. 2017), and suitable nests for swift parrots comprise as little as 5% of the available tree cavity resource across the study area (Stojanovic et al. 2012). Our intervention provided abundant alternative nesting sites despite near saturation of the local natural cavity resource at

Table 2. Parameters of the most parsimonious models for swift parrots occupying artificial nests deployed across the study area on Bruny Island, Tasmania, Australia, 2016, at 3 study sites: Roberts Hill (RH), Yellow Bluff (YB), and Lodge Hill.

Response	Model	Coefficients	Estimate	SE	Z	P
Swift parrot presence-absence	Site+distance to forest edge	Intercept	-2.52	0.53	-4.81	<0.001
		RH	2.52	0.53	3.85	<0.001
		YB	-15.9	1,044	-0.02	0.99
		Distance to forest edge	-0.002	0.0008	-2.70	0.007

Table 3. Model parameters of the most parsimonious models for swift parrot occupancy of nest boxes deployed at Roberts Hill, Tasmania, Australia, 2016.

Response	Model	Coefficients	Estimate	SE	Z	P
Swift parrot presence-absence	Distance to forest edge	Intercept	0.17	0.39	0.43	0.67
		Distance to forest edge	-0.003	0.001	-3.17	0.002

Roberts Hill. Artificial nests provided comparable quality habitat for swift parrots, and we did not find significant differences in clutch size, brood size, or nestling quality between nest boxes and natural cavities, despite differences in fledge date and thermal properties.

Low occupancy of artificial nests away from Roberts Hill highlights the importance of accurately predicting where local settlement will occur before expending resources deploying artificial nests at sites that are not subsequently occupied (we recorded only 49% site occupancy across the study area in our annual monitoring survey). At Lodge Hill and Yellow Bluff (only 2 km and 5 km distant, respectively, from Roberts Hill), we found few natural nests, and occupancy of artificial nests was negligible. Across most of the remainder of the breeding range, swift parrots were absent, and action implemented at sites where bud development was low would have been wasted. Intervention options are limited for nomadic species (Cottee-Jones et al. 2016) and although artificial nests may increase breeding opportunities, this is contingent on their deployment at ecologically relevant locations and times.

Traditional approaches of deploying on-ground work at a logistically convenient location and hoping that nomadic wildlife are eventually attracted to the area are likely to be ineffective (Lindenmayer et al. 2017). As expected, settlement across the breeding range was predicted by bud abundance and at local scales by site (Roberts Hill, where natural nests are abundant). This confirms the results of other work identifying the importance of co-occurrence of food and suitable tree cavities (Stojanovic et al. 2015, Webb et al. 2017). We found a slightly negative effect of forest edge distance on the likelihood that swift parrots would occupy a nest box; further investigation is necessary to determine whether swift parrots prefer to nest close to edges (which we consider unlikely given the distribution of nests elsewhere in the breeding range). Other factors such as conspecific attraction (influenced by high occupancy of natural nest cavities by swift parrots at Roberts Hill during the study) or some other unmeasured forest characteristic (e.g., spatial variation in cavity abundance) may also explain patterns of occurrence we observed, but there are no data available currently to test these possibilities.

Carved cavities were significantly less likely than boxes to be occupied, but it is unclear why this was the case. This information gap must be addressed to evaluate whether carved cavities are an effective habitat augmentation approach. Boxes and carved cavities had the same internal dimensions, so it is unlikely that morphology contributed to this result. Boxes were better sealed than carved cavities (attributable to splitting of seams as green wood dried) making them darker and less drafty and more likely attractive

as nests. Compared to natural cavities, nest boxes were cooler, but this difference did not correspond to differences in swift parrot clutch or brood size or nestling body condition. Our nest boxes differed to those of other similar studies; for example Rowland et al. (2017) used dark green painted, 17-mm-thick walls and Maziarz et al. (2017) used brown painted, 22-mm-thick walls. Colored nest boxes are warmer than white boxes because of their lower solar reflectance and this may be an important consideration where overheating may threaten box occupants (Griffiths et al. 2017).

The challenges posed by nomadic species are an emerging global conservation priority (Cottee-Jones et al. 2016), but few practical approaches have been developed to address them (Runge et al. 2015). Local fluctuation in food abundance causes swift parrots to rarely settle in the same location in successive years (Stojanovic et al. 2015), and this lack of spatial predictability has hindered their conservation (Webb et al. 2017). We show how knowledge of the life history of a nomadic species (range-wide food availability and local breeding habitat occurrence) may be used to inform where and when to implement on-ground work. Predicting where settlement will occur, coupled with detailed knowledge of historical habitat utilization may empower managers to implement on-ground actions to enhance available breeding habitat. However, artificial nests cannot compensate for deforestation (Lindenmayer et al. 2017). We caution that protecting natural nesting habitat is important to addressing the acute conservation needs of swift parrots (Heinsohn et al. 2015). Overcoming the chronic challenges of conserving swift parrots in logged forests has been politically and economically challenging (Webb et al. 2018). In context of ongoing deforestation of critical habitat (Webb et al. 2017), artificial nests may only offer a temporary reprieve from habitat limitation.

MANAGEMENT IMPLICATIONS

We demonstrate that the challenges posed by variable settlement patterns may be overcome using predictions of habitat suitability derived from rigorous, long-term, and landscape-scale population monitoring. Existing techniques may offer conservation benefits to nomadic wildlife, but the way these tools are deployed requires detailed understanding of species ecology, and flexible management strategies. Programs seeking to use nest boxes to maximize breeding opportunities for nomadic wildlife could implement repeated deployment of artificial nests in different locations each year regardless of known historical settlement patterns; permanent deployment of artificial nests at historical nesting sites across the potential range in knowledge that in most years, only a fraction are likely to be occupied; or some combination

of permanent and mobile artificial nests. Based on our results, the location of nest box deployments for swift parrots could be informed at broad spatial scales by flower bud development, and at finer spatial scales by the location of known historical breeding sites. Whether saturation of available natural nests is necessary for occupancy of artificial nests is a question (i.e., whether birds prefer natural nests but will use artificial nests if necessary) that should be addressed with further study because this consideration is important for identifying locations where artificial nests may have a greater impact.

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