

# Parental care does not compensate for the effects of bad years on reproductive success of a vagile bird

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## Keywords

resource variation; migratory species; breeding success; body condition; Life History theory; swift parrot; *Lathamus discolor*; parental care.

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## Abstract

Life history theory predicts that long-lived animals trade off the costs of reproduction against individual survival. If the costs of reproduction are too high, animals should prioritize their own survival. During bad times, mobile animals may be able to compensate for local food shortages by travelling further to provision their offspring. But, whether inherent mobility alleviates individual fitness costs of this parental strategy is not known. We studied parental investment and breeding success of long-lived, nomadic, migratory swift parrots *Lathamus discolor* over two successive years at the same site where food abundance went from locally low to high. We hypothesize that in a bad year, swift parrots should adjust their parental strategy by foregoing breeding altogether, producing smaller clutches/broods or reducing provisioning investment. Fewer swift parrots bred locally when food was scarce. In the bad year, clutch and brood sizes were smaller and nestlings were >20 g lighter (approximately 28% of mean body mass) than in the good year. Compared with the good year, fathers spent longer foraging, less time at the nest and travelled further during provisioning trips in the bad year. Although limited to only 2 years, our results suggest that mobile species may attempt to mitigate the effects of a bad year on their reproductive success by rearing fewer offspring and investing more in provisioning behaviour, but this strategy may not necessarily compensate for environmental conditions.

## Introduction

Life history theory is an essential framework for understanding trade-offs between individual survival and reproductive success (Williams, 1966; Stearns, 1992). It predicts that animals must balance finite resources against reproductive effort, and that long-lived species should invest in self-maintenance (i.e. survival), not reproduction, when faced with limited resources (Erikstad *et al.*, 1998; Hamel *et al.*, 2010). Consequently, parental investment varies as a result of these trade-offs (Monaghan *et al.*, 1989; Weimerskirch, Prince & Zimmermann, 2000), and this is especially so for animals that obtain resources for rearing offspring from within locally variable environments (Meijer & Drent, 1999; Mullers & Tinbergen, 2009). If food is abundant locally, then parental strategies might involve reduced foraging effort, or producing more/better-quality offspring (Naef-Daenzer & Keller, 1999; Wilkin, King & Sheldon, 2009). Mobile species that can easily travel long distances, may be capable of exploiting distant resources over large areas while provisioning (Phillips *et al.*, 2007). If searching for food is less costly for mobile animals, parents could adjust provisioning behaviour to match local resource

abundance and regulate their reproductive success (Hipfner, Gaston & Smith, 2006). However, if the costs of provisioning are too high, even mobile species may be unable to avoid negative impacts on reproductive success in bad times (Weimerskirch, Prince & Zimmermann, 2000; Catry *et al.*, 2013).

In variable environments, where food availability and abundance are unpredictable over space and time, life history theory predicts that when resources are scarce, reproductive investment might be reduced by laying fewer or smaller eggs (Ruuskanen *et al.*, 2016). Alternatively, a bet-hedging strategy might be used, where irrespective of environmental conditions surplus eggs are laid, but some fail to produce fledglings in bad times (Mullers & Tinbergen, 2009). By reducing brood sizes in bad years, bet-hedging ensures that at least one healthy nestling survives. Although long-lived animals are likely to favour individual survival in bad times, other life history traits may provide important nuance to this general theory. For example, mobile species may be able to overcome the challenges posed by breeding in suboptimal conditions. Although long-lived sedentary species may invest less in reproduction during bad times, mobile animals may compensate by changing their parenting strategies (e.g. moving longer distances to

find resources) at relatively low cost to their own survival. Understanding the interactions between resource limitation and mobility in bad times may provide an important nuance to life history theory in increasingly unpredictable environments.

In this study, we consider the case of a long-lived (generation time 4–6 years, Heinsohn *et al.*, 2015), income breeding, altricial migratory nomad, the swift parrot *Lathamus discolor*. This species is critically endangered, and survives as a single panmictic population (Stojanovic *et al.*, 2018b) of potentially fewer than 300 individuals (Olah *et al.*, 2020). Swift parrots settle wherever their primary food source (nectar from blue gum *Eucalyptus globulus* and black gum *E. ovata*) is most abundant within a large potential breeding range but nesting opportunities are limited by the configuration of food relative to nesting habitat (i.e. mature forest with cavity-bearing trees) (Webb *et al.*, 2014; Webb *et al.*, 2017). Whether flowering occurs near or far from mature, cavity-bearing forest may have important consequences for the cost of nestling provisioning in swift parrots (Webb *et al.*, 2017). Furthermore, nectar volume and concentration can vary among individual *Eucalyptus* trees (Law & Chidel, 2008; Law & Chidel, 2009), so that food resource quality may be heterogeneous even within an area of flowering forest. On average, swift parrot nestlings experience low variation in their body condition before fledging irrespective of where nesting occurs because they breed where food is abundant and close to suitable nesting sites (Stojanovic *et al.*, 2015). In years with high food abundance (good years), swift parrots can rear up to five healthy offspring (Stojanovic *et al.*, 2018a), but how years with scarce food (bad years) change these reproductive parameters is unknown. It is likely that in bad years, the 'least bad' site may be the only option available for settlement (Webb *et al.*, 2017). These traits of swift parrots (long-lived, mobile, dependent on unpredictable food, relatively large broods) provide a good opportunity to test whether predictions from life history theory are true for mobile species, assuming the cost of longer provisioning trips is lower than for sedentary species. If the ability of swift parrots to fly long distances means that they invest more in reproductive success in bad times, the theory that reproductive and parental investment is reduced during bad times might apply better to less mobile species.

We studied breeding success and provisioning effort of swift parrots over two successive years at a site where food abundance went from locally low to high. Based on predictions from life history theory, we hypothesized that in a bad year, swift parrots should adjust their parental strategies by one of the following mechanisms: (1) foregoing breeding altogether, (2) lowering their reproductive output (smaller clutches, brood reduction) or (3) rearing normal-sized broods but increasing the number, distance or duration of provisioning trips. We expected that when food was scarce, fewer swift parrots would breed, and if they attempted to nest, provisioning trips would be more frequent/longer, but nest productivity would be low. If more investment in provisioning by parents compensates for bad local conditions, we expect that nestlings reared in the bad year should be of similar body condition to those in the good year. We test these predictions using data on clutch and brood size, nestling condition and telemetry of provisioning swift parrot fathers.

## Materials and methods

### Study area and species

The study took place in a 12 km<sup>2</sup> area of north Bruny Island (Lat: 43°9', Long: 147°18'), Tasmania, Australia between September and January of 2015 and 2016. Bruny Island is an important breeding area for swift parrots because it is free of an introduced predator that can severely reduce their nest survival on mainland Tasmania (Stojanovic *et al.*, 2014). The study area receives an average of 396–587 mm of rainfall per year, and maximum mean temperature over the study was 23.6°C. Weather conditions were similar in both years of the study. The study site is a dry, grassy forest with blue gum and white peppermint *E. pulchella* as the dominant canopy species. Within 5 km of the study area, only 48% of the land area is forested, with the remainder comprising cleared agricultural land and scattered rural dwellings. The site is an important swift parrot breeding area, and nesting cavities have been recorded throughout the study site since 2005 and 83% of these nests were reoccupied in 2016 (Stojanovic *et al.*, 2018a). In addition, we deployed artificial nests at the site (Stojanovic *et al.*, 2019; Stojanovic *et al.*, 2020b). Swift parrots are social and nests at the study site were clustered within relatively small areas (some trees had two nests). Swift parrots (when not subject to predation) have a mean clutch size of 3.8 eggs which in turn produce a mean of 3.2 fledglings per nest (Stojanovic *et al.*, 2015). The nestling period is 60 days from the laying of the first egg to the first fledging, and at our island study area, survival of nests is very high (Stojanovic *et al.*, 2014). Swift parrot mothers undertake all incubation (approximately 25 days) and brooding of nestlings and are fed by their mate (fathers do not brood or incubate), but brooding ceases when the eldest chick is about a fortnight old (Stojanovic, D., unpublished data). After this point, mothers contribute to nestling provisioning for about a week, but fathers assume most (and sometimes all) provisioning responsibilities in the last week before fledging (Stojanovic, D., unpublished data). In total, the nestling period is approximately 35 days. Swift parrots engage in extra-pair paternity (Heinsohn *et al.*, 2019), but there is no evidence to suggest that extra-pair fathers provision their offspring.

### Food abundance

We quantified food abundance in 2015 and 2016. When food was abundant, we considered it a good year, and when it was scarce, we considered it bad. Although other unmeasured factors may also affect swift parrots each year, but for the purposes of our question we consider food abundance was a suitable metric for understanding parental strategies and investment. Quantification of food abundance in 2016 is described in detail elsewhere (Stojanovic *et al.*, 2018a), but briefly, at 989 sites across the study area (and the broader Tasmanian range of the swift parrot), we undertook surveys of flower bud abundance, and categorized sites on a scale of 0 to 4, where 0 = no buds, 1 = light (<25% of the tree crown budded), 2 = moderate (25–50% of the crown budded), 3 = heavy

(50–75% of the crown budded) and 4 = very heavy bud cover (>75% of the crown budded). We then interpolated these bud scores over the study area following the method described by (Webb *et al.*, 2017) to provide an estimated bud abundance at nearby unsurveyed areas. We identified the availability of future flowering both within the study area and more broadly across the entire potential breeding distribution of the species using these interpolated bud counts. The resulting estimates of food abundance were coarse and are indicative of large-scale patterns of food abundance. There was a mast flowering event in 2016 and most trees on the study site flowered, producing very high food abundance throughout the area over the duration of the breeding season.

In 2015, flowering by *E. globulus* was minimal (scattered flowering of <50 trees at low elevations in agricultural fields). Because of this stark contrast in food availability between years, the broad-scale resolution of food abundance estimates we used in 2016 would likely have missed the scattered individual flowering trees in 2015 because many occurred away from established monitoring sites. To improve the accuracy of our estimate of this low food abundance, we quantified food abundance in 2015 by using extensive on-ground searches to identify scattered flowering trees and record their phenology early (late November/early December 2015) and late (January 2016) in the 2015 breeding season. We used data from GPS-tracked provisioning male swift parrots to estimate an ecologically relevant spatial scale at which to survey food availability. Based on the telemetry results (Table 1), we used a 5 km radius around the study site because this captured the movements of all of the tracked individuals in 2015, with the exception of one bird. Within 5 km of the study site, we recorded tree flowering intensity at: (1) 100 randomly distributed survey points within contiguous forest patches, (2) incidental tree flowering during swift parrot nest searches and (3) all individual relict trees in fields and forest fragments. We scored flowering intensity using the same approach used for interpolating bud counts in 2016 (above). *Eucalyptus spp.* have variable flowering duration (Davis, Major

& Taylor, 2015), so we recorded the GPS coordinates of each flowering tree to reassess flowering intensity at the same trees late in the season. We also scored flowering intensity at new flowering trees located during late season visits. We compared flowering scores for all individual trees in the early and late 2015 season with a paired *t*-test.

## Parrot reproductive parameters

In 2015 and 2016, we estimated the abundance of breeding swift parrots by systematically surveying 47 known historical nests in natural tree cavities from the ground by looking for parrot nesting behaviour. We climbed 92 confirmed active nests (including 30 artificial nests) during the incubation and nestling phases. We recorded clutch size, the number of nestlings that survived to fledge and the fledging date of the first hatched nestling. All nestlings detected were weighed and measured (wing chord to the nearest mm, mass to 0.1 g), and nests were climbed within a week of fledging to detect nestling mortality (nestlings that survive to this stage very rarely die before fledging, Stojanovic, D., unpublished data). We measured nestlings when they were all at least 10 days old and handled them only once (thus providing only a snapshot of body condition on the day we handled them). We avoided measuring nestlings which had wing chords >100 mm because from this age onward, they are capable of fledging. We estimated the age and hatch order of nestlings using their wing chord and models of nestling growth (Stojanovic *et al.*, 2015). Only 72 nestlings fledged in 2015, compared to 217 fledglings in 2016, and we collected morphological data from all of them.

## Parrot movements

In the fortnight before fledging, swift parrot mothers usually stop provisioning their broods, leaving fathers to provision until fledging. Thus, we focussed on fathers to exploit the widest possible time window for telemetry during the late

**Table 1** Summary of tracking data from individual swift parrots captured in 2015 and 2016. 'No. of fixes' shows the total number of valid GPS locations collected for each bird

ID	Year	Tracking period (days)	No. of fixes	% Expected fixes	Mean speed (km/hr)	Cumulative distance (km)	Max displacement (km)
Tag05	2015	0.2	82	41.9	0.49	3.46	3.8
Tag07	2015	0.8	370	39	0.32	11.18	3.06
Tag08	2015	2.2	187	58.9	0.29	49.4	3.17
Tag09	2015	1.9	36	12.6	0.14	1.79	3.96
Tag10	2015	0.8	439	45.1	0.06	2.58	1.36
Tag14	2015	1.9	177	62.8	0.21	35.71	2.23
Tag30	2015	1.8	141	54.9	0.32	41.87	9.67
Tag80	2016	1.9	161	57.5	0.1	15.74	2.09
Tag81	2016	0.8	17	14.2	0.12	0.37	0.75
Tag90	2016	1.2	100	56.2	0.09	7.93	0.96
Mean		1.35		44.31	0.21	17.00	3.11
SD		0.67		18.04	0.14	18.36	2.57

'% Expected Fixes' reflects the proportion of the total expected GPS locations, based on the programmed fix rate, which were actually achieved by the logger. 'Mean Speed' is calculated as distance moved per hour, averaged over the entire tracking period. 'Cumulative Distance' shows the total distance moved over the entire tracking period. 'Maximum Displacement' is the furthest distance moved from the nest.

nestling period. We tracked seven swift parrots in 2015 and three in 2016. We targeted male swift parrots when broods were 15–25 days old, which was the same period during which we measured nestlings. Males were captured at their nests, and we attached 1.8 g GIPSY4 GPS loggers (Technosmart, Guidonia, Italy) to their back feathers. Loggers were secured using three strips of Tesa® marine cloth tape (Tesa SE, Hamburg, Germany). Total package mass was <2 g, which was <5% of body mass for all the captured birds. We deployed loggers for up to 4 days before we recaptured birds and removed loggers to download the data. We lost four loggers when swift parrots plucked the feathers securing the logger. The first logger deployed was set to a schedule of one GPS fix (estimated accuracy <10 m) every three seconds as a trial, and thereafter, all loggers were set to operate between 0500 h and 2100 h (first and last light respectively) with one fix every 10 min. Based on evidence from motion-activated cameras, swift parrots provision their nests roughly every 3 h. Provisioning fathers are near their nests for about 20 min, including about 15 min of vigilance before entering the nest, and about 5 min to feed (DS unpublished data). Thus, it is unlikely that the fix schedule we used would underestimate the number of times a father returned to the nest.

A range of movement metrics was chosen to describe foraging behaviour and quantify paternal effort. We quantified distance between successive GPS fixes, distance flown from the nest and time spent foraging at a given site as measures of provisioning effort. We used the time taken for a father to revisit a given foraging site as an indication of the quality and abundance of food at a given site. We calculated the time a father spent at the nest and time between nest visits as a measure of investment in parental care.

We chose a radius of 30 m to represent a single foraging site (approximately the crown diameter of a tree where foraging might occur) and to account for potential error in the GPS data. To identify foraging sites, we excluded GPS data from a 30 m radius around the nest site of each bird (although parrots will forage within the nest tree, most of the at-nest behaviour of fathers is provisioning related, DS unpublished data). We drew a circle of radius 30 m around each GPS location and calculated the time spent inside that circle, the number of times that circle was visited and the time between visits to that circle. Brief excursions from a circle were ignored (e.g. a bird taking flight, circling and landing in the same tree). We derived the cumulative distance travelled and maximum displacement of each provisioning male parrot from GPS data, and calculated the per day values for cumulative distance and displacement. Step length for each bird was calculated from the distance moved between successive fixes. We calculated the mean value of step length for each year for all birds for each year. We calculated the straight-line distance to the nest for each GPS fix for each bird (excluding a 30 m radius around the nest).

### Analytical approach

We carried out all analyses in R (R Development Core Team, 2020), with data visualization using *ggplot* (Wickham, 2016), generalized linear mixed models implemented using the *lmer*

function in package *lme4* (Bates *et al.*, 2015). We estimated modelled means and confidence intervals using the *emmeans* function in package *emmeans* (Lenth, 2021). We used the function *check\_distribution* in the package *performance* (Lüdtke *et al.*, 2020) to determine the model family that best fit the response variables. We provide code and summarized data as R Markdown script in Appendix S1.

### Reproductive success

We looked for an effect of year on clutch size, brood size and fledging date. A normal distribution was the best fit for these three response variables, so we fitted linear models and compared the effects of year to a null model with a Chi-square test.

We then estimated the body condition of nestlings. First, wing length was used to estimate nestling age based on growth models; then, we calculated a body condition index as the difference between the nestling's body mass and mean population body mass of nestlings for that age (Stojanovic *et al.*, 2015). A nestling with a body condition index value of zero is at average mass expected for that age, whereas positive and negative values reflect respectively heavier and lighter nestlings than average. This approach is useful for evaluating the quality of nestlings relative to intrinsic/extrinsic variables that might influence individuals and enables utilization of snapshot data by providing a way of estimating nestling age and correcting for it when assessing body mass (Stojanovic *et al.*, 2015; Stojanovic *et al.*, 2020a). We used the nestling body condition index as the response variable in generalized linear mixed models with a normal error distribution and fitted the following fixed effects: (1) sex, (2) hatch order, (3) brood size, (4) fledge date, (5) year and (6) year × hatch order. We fitted a saturated model and then used automated backward selection to derive the most parsimonious model. We included nest ID as a random term to account for the inclusion of siblings in the data.

### Spatial analysis

To compare these movement metrics across years, we used a series of generalized linear mixed models, with each movement metric as a response, year as a fixed effect and controlling for individual variation by including bird ID as a random effect. The distributions of values of movement metrics used as responses in these models were skewed towards lower values. In order to meet the assumption of normality, each response variable was log transformed before analysis. We compared models to a null using a Chi-square test.

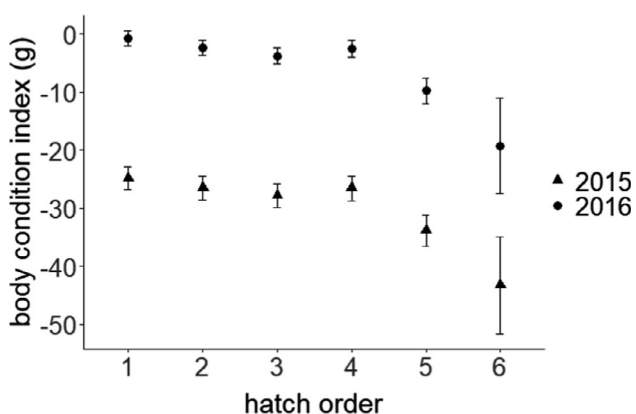
We used the maximum and mean body condition of each brood of a father tracked in 2015 ( $n = 7$  broods) as response variables in linear models where we fitted the cumulative distance travelled and maximum displacement of each provisioning male parrots as fixed effects. We note that both the response and predictor variables in this analysis are snapshots (i.e. body condition on the day chicks were measured; provisioning behaviour on the day the father was tracked) but consider them useful indices for comparing these traits but caution they are not absolute measures. Our sample of tracked parrots in 2016 ( $n = 3$ ) was too small to use for this analysis.

## Results

**Food availability in 2015** – We recorded 339 trees in flower early in the 2015 breeding season, but this declined to only 37 trees still flowering late in the season. Only blue gums flowered and most abundantly in fragmented forest, or scattered throughout contiguous forest. Only 3.8% ( $n = 13$ ) of trees flowered continuously throughout the season, and 24 trees began flowering late in the season. This represented a significant reduction in individual tree flowering intensity from mean score of 1.58 early in the season to 0.04 late in the season ( $t = 39.476$ ,  $d.f. = 337$ ,  $P < 0.0001$ ). This contrasted strongly to the extremely abundant tree flowering across the study area in 2016, when a mast flowering occurred in blue gums (see Fig. 1 in Stojanovic *et al.*, 2019). So many blue gums flowered over the study area in 2016 that food resources did not diminish as the breeding season progressed. This was because even though early flowering trees finished flowering at sea level approximately mid-season, this lost food source was replaced by the emergence of late flowering trees on higher slopes of the study area in the mid to late breeding season. Furthermore, most low elevation nests had fledged before the end of flowering in those areas during 2016 (see below).

### Parrot reproductive parameters

Of the known historical natural tree cavity nests we checked, 25 (53%) in 2015 and 39 in 2016 (83%) were reoccupied. There was a significant difference in the mean clutch size between the two years ( $d.f. = 1$ ,  $F = 12.685$ ,  $P < 0.001$ ), with a mean of 3.64 eggs (lci: 3.28, uci: 3.99) laid in 2015, compared to 4.37 eggs (lci: 4.16, uci: 4.59) in 2016. There was also a significant difference in the mean brood size between the two years ( $d.f. = 1$ ,  $F = 8.74$ ,  $P = 0.004$ ), with a mean of 3.08 nestlings (lci: 2.60, uci: 3.56) per brood in 2015,



**Figure 1** Estimated means from the best model of the swift parrot nestling body condition index (BCI) showing the effects of hatch order and year of birth. Whiskers show standard errors. The population mean of swift parrot nestlings is represented by a body condition index of zero. A negative value for body condition indicate individuals lighter than the population mean, whereas positive values are heavier than the mean.

compared to 3.91 nestlings (lci: 3.62, uci: 4.20) in 2016. We also found a significant difference in the mean fledge date between the two years ( $d.f. = 1$ ,  $F = 7.87$ ,  $P = 0.006$ ). The mean fledging date in 2015 was 30/12/15 ( $\pm 4.7$  days se), compared to 14/12/16 ( $\pm 3.1$  days se) in 2016. The most parsimonious model of nestling body condition included additive effects of hatch order ( $d.f. = 5$ ,  $F = 4.69$ ,  $P = 0.0004$ ) and year ( $d.f. = 1$ ,  $F = 125.02$ ,  $P < 0.0001$ ). Based on this model, nestling condition declined with later hatch orders and was lower in 2015 than in 2016 (modelled estimates of means and standard errors presented in Fig. 1).

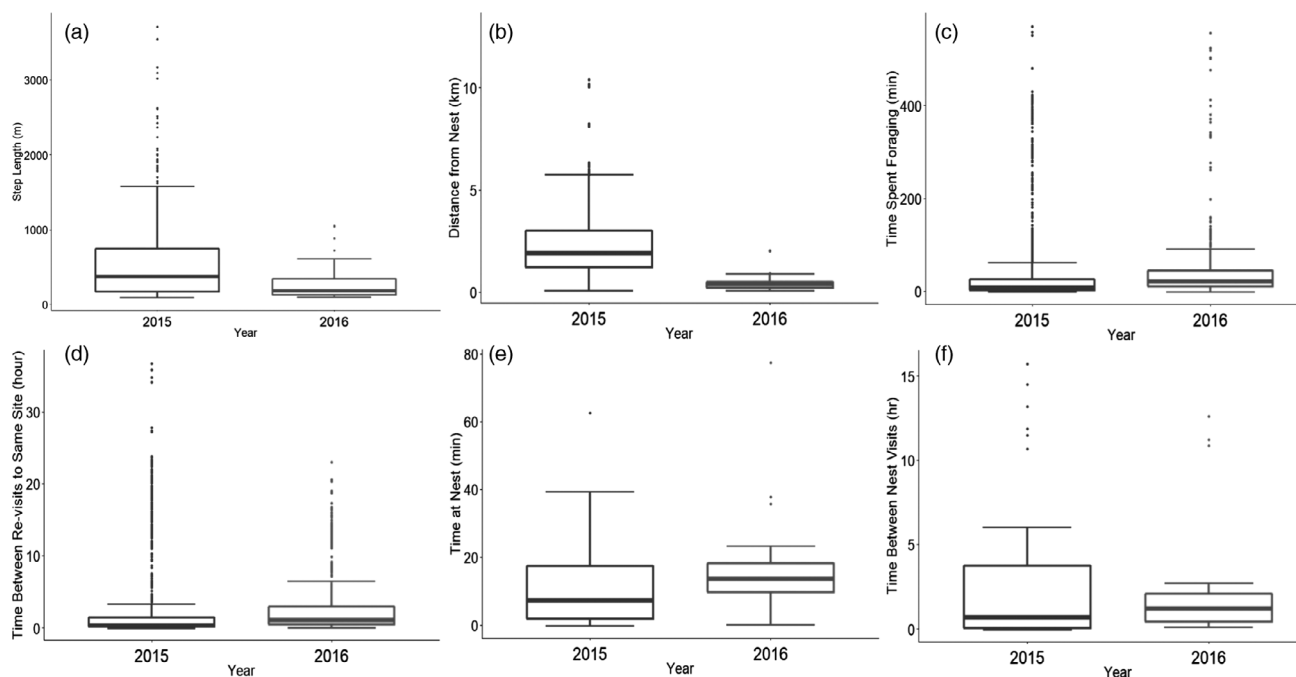
### Parrot movements

We tracked the ten swift parrot fathers for mean 1.35 days. Loggers produced a data set totalling 2725 GPS relocations (2403 from 2015 and 322 from 2016). For a detailed summary of logger performance see Table 1. On average birds moved a maximum of 3.11 km from their initial location with an average speed of 0.21 km/h (Table 1). We found no significant differences in time between revisits to the same site during provisioning ( $d.f. = 4$ ,  $F = 0.92$ ,  $P = 0.3$ ), the interval between nest visits ( $d.f. = 4$ ,  $F = 0.59$ ,  $P = 0.45$ ) and step length ( $d.f. = 4$ ,  $F = 0.07$ ,  $P = 0.79$ ) between the good and bad year. But we did find significant differences in the time spent foraging ( $d.f. = 4$ ,  $F = 8.49$ ,  $P = 0.001$ ), time spent at the nest ( $d.f. = 4$ ,  $F = 3.66$ ,  $P = 0.04$ ) and the distance from the nest of provisioning trips ( $d.f. = 4$ ,  $F = 33.03$ ,  $P = 0.001$ ) between the good and bad year. The effect sizes for the models with significant effects are presented in Fig. 2. We illustrate the differences in provisioning behaviour of swift parrot fathers in each year of the study in Fig. 3 by presenting the number of revisits to a foraging tree relative to the position of nests for all fathers that we tracked.

Mean body condition of the broods being provisioned by males tracked in 2015 was 26 g below average and was independent of the distance travelled to forage each day ( $d.f. = 1$ ,  $F = 0.22$ ,  $P = 0.7$ ) or their maximum displacement distance ( $d.f. = 1$ ,  $F = 0.61$ ,  $P = 0.4$ ). Likewise, the body condition of the highest quality nestling in the broods of the 2015 tracked males was -21 g (i.e. compared to the average mass of nestlings for a given age, 2015 was 21 g underweight, which is approximately 28% of normal nestling body mass). The highest quality nestling body condition was independent of the distance fathers travelled to forage each day ( $d.f. = 1$ ,  $F = 0.73$ ,  $P = 0.4$ ) or their maximum displacement distance ( $d.f. = 1$ ,  $F = 0.49$ ,  $P = 0.5$ ). In an extreme case, one father (Tag 30) flew >9 km over water to forage on the Tasmanian mainland after flowering ceased at the island study site late in the 2015 breeding season, but three of his four nestlings died despite this extreme provisioning behaviour (Table 1).

## Discussion

Based on life history theory, long-lived animals should invest more in self-maintenance than reproduction when times are bad (Erikstad *et al.*, 1998; Hamel *et al.*, 2010). We show that swift parrots adjusted their parental strategies in the bad year.

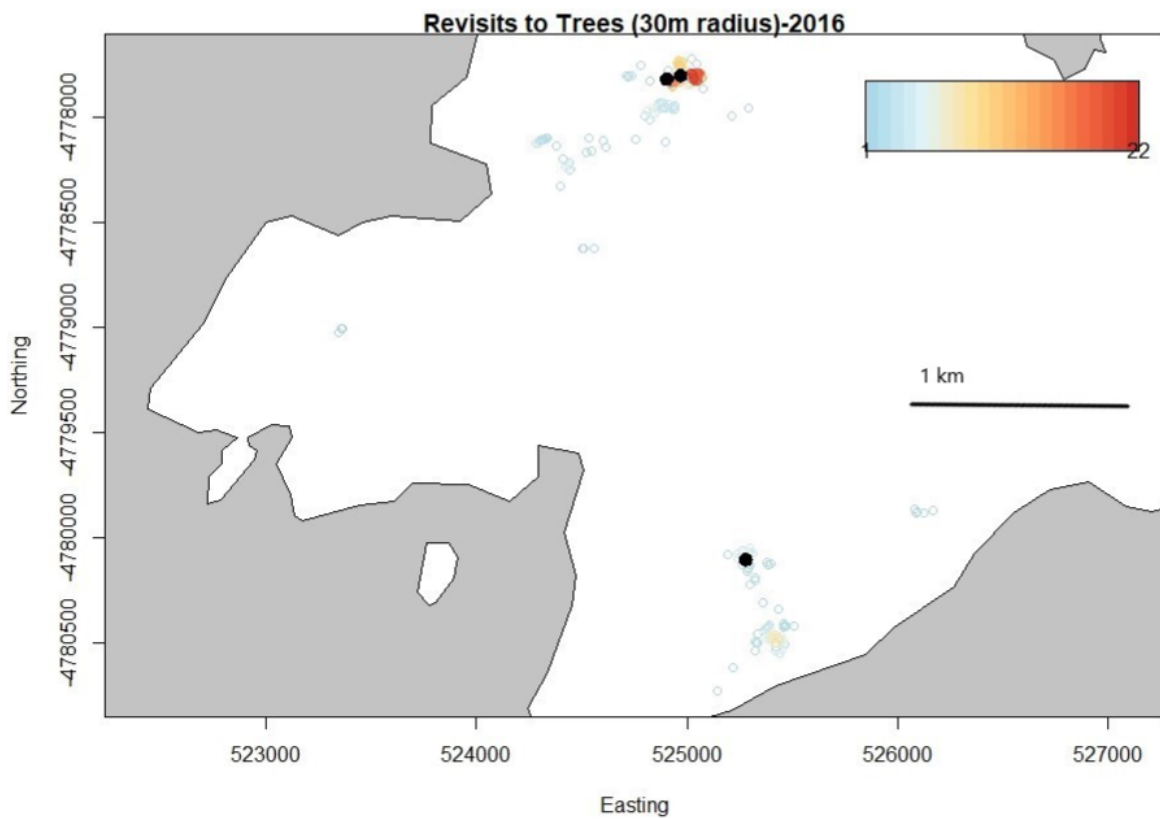
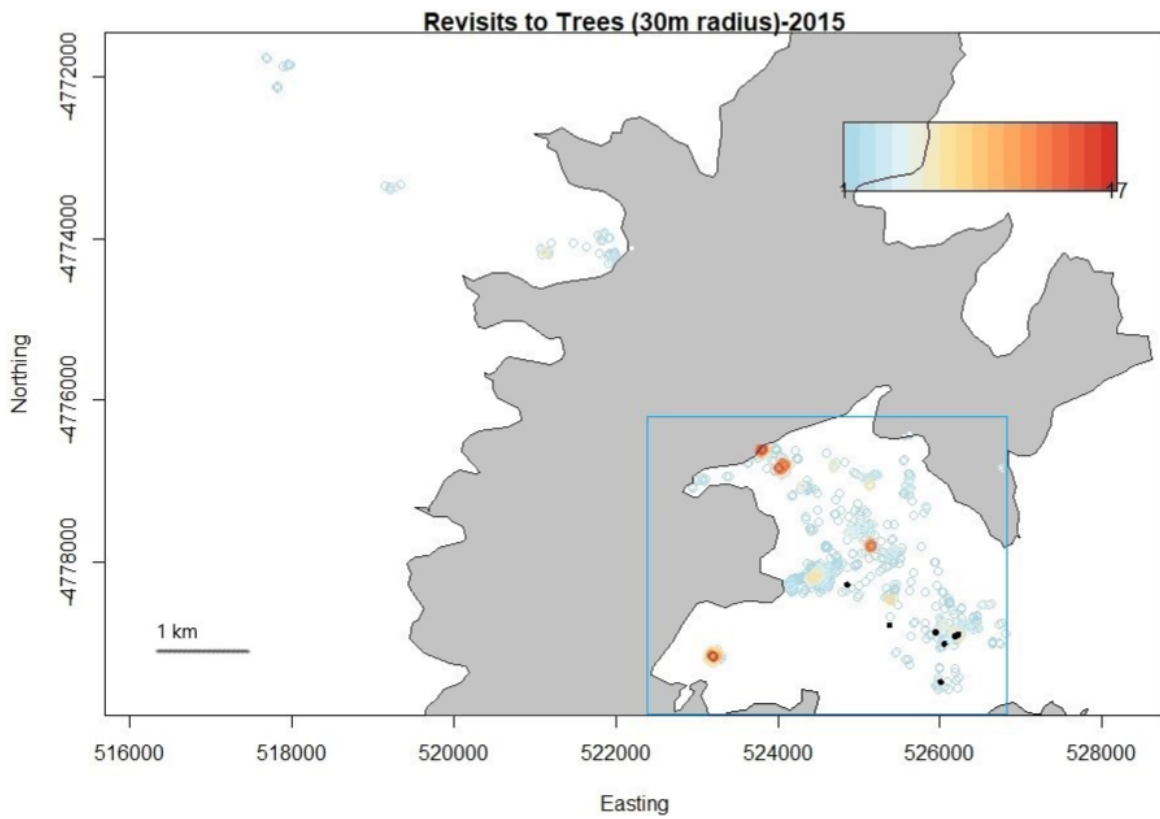


**Figure 2** Boxplots comparing movement characteristics and revisitation rates of tracked parrots across two study years when food was scarce (2015) and abundant (2016). The thick line indicates the median, whiskers represent 1.5 x the inter-quartile range and dots represent outliers. (a) Step length (distance in metres between successive GPS fixes) compared across years. Birds tracked in 2016 moved significantly smaller distances between fixes. (b) Distance between all GPS locations and the nest for each bird compared across 2015 and 2016. GPS locations of birds in 2015 were significantly further from their nests than those for birds in 2016. (c) Time spent inside a 30m radius (i.e. within the crown of a given tree) at any given foraging site. Birds in 2015 spent significantly less time in foraging trees than in 2016. (d) Comparison of time between revisits to a given foraging site across 2015 and 2016. Most sites were never revisited and in 2015 birds revisited fewer sites than those in 2016. In 2016, birds took significantly longer to revisit a given site than those in 2015. (e) Comparison of time spent at the nest between 2015 and 2016. Birds in 2016 spent significantly more time at the nest than those in 2015. (f) Comparison of time between nest visits across both years. There were no significant differences in time between visits across years.

Fewer swift parrots settled at the study site to breed when food was locally scarce (which fits expectations from life history theory and our knowledge of swift parrot ecology). Those parrots that did settle bred later in the season and produced smaller clutches and broods. Fathers also invested more effort provisioning their smaller broods in the bad year, flying further and faster, visiting more unique locations, spending less time foraging at a given site and less time at their nests than birds in the good year. Although our sample of tracked fathers was small, these data are unsurprising given the limited food availability in 2015 compared with 2016. These results also reinforce the suggestions of our previous work that the local configuration of food availability relative to nesting sites is critical for breeding swift parrots (Webb *et al.*, 2017).

Population-level data on nestling body condition provide further support for the impact of low food abundance on the life history of swift parrots – chicks born in the bad year were underweight compared to nestlings born in the good year. During the good year, our small sample of fathers foraged within an area of about 1 km around their nests, which was much smaller than the foraging radius of fathers in the bad year. This is evidence that despite their capacity to undertake long distance movements, swift parrot fathers attempt to minimize the length of provisioning trips. A limitation of our study is that it only contrasts one good and one bad year and a small sample of tracked fathers. Although this is a limited contrast, the differences we found in reproductive parameters were large, and the study was controlled for spatial location (and thus the

**Figure 3** Foraging locations visited by swift parrots provisioning their offspring when food was scarce (2015) and abundant (2016). Circles represent a 30m radius around each GPS location, and the scale bar shows 1 km. Circles are coloured by the number of unique visits by swift parrot fathers to that site. From blue (1 visit) to red (maximum 17 visits in 2015 and maximum 22 visits in 2016). Nest trees are indicated by black points, and the sea is indicated by grey fill. The study area is indicated by the blue outline in the map for 2015. The map for 2016 is zoomed into this study area and so is at a smaller scale. In 2015, a swift parrot flew over water from Bruny Island back to the Tasmanian mainland to provision his brood.



characteristics of the local food environment with regard to the abundance and spatial configuration of local blue gums). Ideally, a larger sample of bad years and locations would be compared to confirm our observations.

Conditions experienced during early life can create carry-over effects on later life stages (Harrison *et al.*, 2011). Underweight nestlings can suffer fitness consequences especially when undertaking risky life history stages like migration (Mitchell *et al.*, 2011). This can result in lower post-fledging survival than their heavier siblings, or reduced lifetime reproductive success (Saino *et al.*, 2018). If carry-over effects exist in swift parrots, the population-level nestling body condition data we present, combined with the smaller sample of telemetry data, suggest that attempting to breed when local conditions are bad is likely to be maladaptive in this species. Tracking swift parrots is highly labour intensive, but our study offers clues about how their parental strategies of are risky in bad times even with reduced clutch/brood sizes, and that these risks do not necessarily pay off in terms of offspring quality. More broadly, our results have implications for modelling population viability. Islands like our study site are an important refuge for swift parrots from their main predator (Stojanovic *et al.*, 2014), the introduced sugar glider *Petaurus breviceps* (Campbell *et al.*, 2018). However, our results suggest that islands do not always support optimal nesting conditions, but these conditions do not necessarily prevent attempted breeding. Existing models of population viability for swift parrots assume that islands are consistently high-quality habitats for swift parrots (Heinsohn *et al.*, 2015; Heinsohn *et al.*, 2019), and our results do not support this assumption.

Our results highlight gaps in our knowledge about the drivers of tree flowering phenology. Many trees that flowered in farmland sites in 2015 did not flower again in 2016 (when the forest trees masted). Future research should focus on understanding what drives tree flowering and swift parrot foraging behaviour to inform habitat restoration for swift parrots, which are at risk from severe deforestation of their nesting habitat in Tasmania (Webb, Stojanovic & Heinsohn, 2019). Individual flowering trees may be disproportionately important to breeding swift parrots in years when food is scarce (or, for example, if flowering phenology is mismatched with nest initiation). In the bad year, we found that only a few scattered trees flowered in the early breeding season, and within 2 months, tree flowering was mostly finished. This contrasted dramatically with the good year when most food trees at the study site flowered heavily for the entire duration of the breeding season (Stojanovic *et al.*, 2018a), providing a stable food resource throughout the nestling provisioning period and for weeks after fledging. Male parrots breeding in the bad year travelled further to forage at the few available flowering trees than those that bred in the good year. Late in the bad breeding season, total food availability declined to less than 40 trees, which suggests that phenological mismatch between food availability and nestling quality may be an important component of fitness in swift parrots. Areas with low tree cover may exacerbate the risk of phenological mismatch because fewer trees are available to provide a food source over the long nesting period.

Constrained by the need to maintain their own body condition, even mobile animals are vulnerable when environmental

conditions are poor across large areas (Weimerskirch, Prince & Zimmermann, 2000). It is conceivable that the parental strategies we observed during the bad year (i.e. reduced number of offspring, longer provisioning trips) could pay off for mobile species if sufficient food is available at distant but still accessible sites. However, our study suggests that spatial or phenological mismatches between nesting and food resources may incur a penalty for offspring due to low individual quality and potential future carry-over effects despite the compensatory provisioning behaviour of their parents. If this is the case, then it may be more adaptive for mobile species to forego breeding altogether when local food conditions are poor. Our results highlight the need to consider the dispersal abilities of animals in context of life history theory because vagile species may take greater risks to reproduce than sedentary species.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Analysis of swift parrot reproductive success, nestling body condition.