Exploiting the richest patch has a fitness pay-off for the migratory swift parrot

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Summary

1. Unlike philopatric migrants, the ecology of nomadic migrants is less well understood. This life-history strategy reflects responses to spatiotemporal variation in resource availability and the need to find resource rich patches to initiate breeding. The fitness consequences of movements between regions of patchily distributed resources can provide insight into ecology of all migrants and their responses to global change.

2. We link broad-scale data on spatiotemporal fluctuation in food availability to data on settlement patterns and fitness outcomes for a nomadic migrant, the endangered swift parrot *Lathamus discolor*. We test several predictions to determine whether facultative movements are adaptive for individual swift parrots in an environment where resources are patchily distributed over time and space.

3. Variation in the availability of swift parrot food resources across our study period was dramatic. As a consequence, swift parrots moved to breed wherever food was most abundant and did not resettle nesting regions in successive years when food availability declined. By moving, swift parrots exploited a variable food resource and reproduced successfully.

4. Exploiting the richest patches allowed swift parrots to maintain stable fitness outcomes between discrete breeding events at different locations. Unlike sedentary species that often produce few or lower quality offspring when food is scarce, nomadic migration buffered swift parrots against extreme environmental variation.

5. We provide the first detailed evidence that facultative movements and nomadic migration are adaptive for individuals in unpredictable environments. Our data support the widely held assumption that nomadic migration allows animals to escape resource limitation.

Key-words: breeding, *Eucalyptus*, facultative migration, flower, individual fitness, *Lathamus discolor*, migration, mobile species, nestling growth, sugar glider

Introduction

Migratory birds are a major focus of international conservation and research, and the factors that regulate their populations are well known in some biomes (Newton 2004; Faaborg *et al.* 2010). The best-understood migratory species are obligate migrants (i.e. consistent timing, direction and distance of migration) because they typically exhibit strong site fidelity and can be studied over time in the same locations. In contrast, the settlement patterns of so-called nomadic migrants (Dingle 2014) and the fitness consequences for migrants that exploit temporally variable and spatially heterogeneous resources are poorly understood (Newton 2008, 2012; Jahn *et al.* 2010).

Less mobile species, or those committed behaviourally to only one breeding site or migration strategy, must make the best of local conditions when food is scarce (Winkler *et al.* 2014). The best evidence for the effects of food availability on individual fitness comes from nest box studies or species with strong breeding site fidelity. These studies indicate that reproductive success is strongly correlated with local variation in food availability. For instance, birds can breed when conditions are good (Nagy & Holmes 2005; Perfito *et al.* 2007) or not breed when conditions are bad (Powlesland *et al.* 1992; Whitehead *et al.* 2012). Similarly, individuals adjust the number of eggs they lay (Bryant 1975; Hogstedt 1980; Verboven,

Tinbergen & Verhulst 2001) or how many chicks they rear (Legge 2002; Kloskowski 2003) depending on food availability. Nestlings are particularly vulnerable because they are entirely dependent on local habitat quality, which determines the amount of food available to them (Terauds & Gales 2006; Catlin, Felio & Fraser 2013) or their parents (Saunders 1986; Renton 2002).

Some species move long distances to exploit the richest patches of food availability (hereafter 'rich patch'; Cornelius *et al.* 2013). For instance, common crossbills *Loxia curvirostra* can travel over 3000 km between successive breeding areas when attracted by masting tree seed crops (Newton 2006b). Further, common redpoll *Carduelis flammea* opportunistically take advantage of rich patches (Hochachka *et al.* 1999), and curtail their migration to rear successive broods in different patches of seeding trees along the course of their migratory path (Newton 2008). There is a growing body of evidence from ringing and telemetry studies to show that individual movements of migrant bird species between rich patches may be common (Fuller, Holt & Schueck 2003; Berthold, Kaatz & Querner 2004; Newton 2006a; Roshier, Doerr & Doerr 2008; Fox *et al.* 2009; Linden *et al.* 2011).

Finding food has profound implications for the evolution of movement strategies in birds (Bell 2011), but there are to date insufficient data to test hypotheses on movement strategies in nomadic migrants. To demonstrate that moving between rich patches is an adaptive life-history trait, there must be a fitness pay-off for individuals that move (i.e. they should produce more or better quality offspring than if they had not moved). However, the reproductive biology of such species is difficult to study because of their low breeding site fidelity. As a result, knowledge has mostly been accumulated through 'scraps of information' (for a detailed summary, see Newton 2008). Studies of nomadic migrants are constrained by the challenge of locating nesting birds between breeding events separated over space and time (Newton 2006a). Consequently, the best available data to test hypotheses regarding such species comes from indirect evidence such as behavioural cues (Marquiss & Rae 1994), flock age-ratios, moult patterns (Newton 1999), individual physiology (Hahn 1998; Cornelius *et al.* 2013), sedentary subpopulations (Dixon & Haffield 2013) or captive birds (Benkman 1993).

In this paper, we present novel data on the reproductive performance of a nomadic migrant that moves to different regions each year to breed. We also use models from a related study (Webb *et al.* 2014) on highly variable settlement patterns and food availability across the entire potential breeding range of the endangered *Lathamus discolor* (swift parrot). By concurrently monitoring swift parrot breeding as they settled at different sites over multiple seasons, we investigated whether they reduced variation in their reproductive success by exploiting the richest patches of food availability. If this occurred, we predicted that (i) nest cavities would not be reused in successive years when food availability was low and (ii) birds would prefer to breed in rich patches. If rich patches are consistently located by swift parrots, then we further predict that (iii) reproductive investment (clutch size) and breeding success (number of fledglings) would be maintained at high levels and (iv) nestling quality, as indicated by their growth, would also remain high. We interpret our results in the context of whether nomadic migration is adaptive for individuals dependent on patchily distributed resources and discuss the implications of our data for the evolution and conservation of migratory species.

Materials and methods

STUDY SPECIES AND SYSTEM

The swift parrot is a small (60–80 g), endangered Austral migrant (i.e. its entire migration is undertaken within the southern hemisphere), whose main food is the nectar from patchily distributed ephemeral flowering of *Eucalyptus* spp. Nectar in eucalypt woodlands is produced synchronously in waves of flowering that move through various woodland types over weeks and months in patterns that differ year-to-year (Keatley, Hudson & Fletcher 2004). As a result of the local variation in flower (i.e. food) availability, swift parrots undertake a nomadic migration across both their wintering (continental Australia) and breeding range (Tasmania, an island; Saunders & Heinsohn 2008). If food is available, some individuals may not migrate in some years and winter in Tasmania (M. J. Westgate unpublished data), but typically the population undertakes a sea crossing to move between their wintering and breeding sites. At broad spatial scales, the specific location of swift parrot breeding aggregations across Tasmania varies annually in response to the spatial configuration of food (Webb *et al.* 2014; Fig. 1). Nectar and pollen from the flowers of *E. globulus* (blue gum) and *E. ovata* (black gum) are the main food source for breeding swift parrots. At fine spatial scales, habitat availability for breeding swift parrots is constrained by the availability of suitable tree cavities for nesting (Stojanovic *et al.* 2012). These are found in mature trees (Webb, Holdsworth & Webb 2012) and can be very uncommon (Stojanovic *et al.* 2014a). Potential breeding habitat is confined to a relatively small geographic area so, unlike many nomadic migrants, it is logistically feasible to annually survey the entire breeding range of swift parrots for both flower abundance and parrot breeding. Recent work has shown that swift parrots suffer severe predation on mainland Tasmania from *Petaurus breviceps* (sugar gliders), which dramatically reduce fecundity and increase mortality (Stojanovic *et al.* 2014b). Sugar gliders, a small, volant marsupial, are widely considered to have been introduced to Tasmania from continental Australia (Gunn 1851; Lindenmayer 2002; Hui 2006). Sugar glider predation intensifies when landscape scale cover of mature forest around swift parrot nests is low (Stojanovic *et al.* 2014b). Anthropogenic degradation of Tasmanian forests by habitat loss and sugar glider introduction results in swift parrots sometimes being attracted by high food availability to breed in places where sugar gliders occur, with negative fitness consequences. However, in this study, our focus is whether facultative movements between rich patches are adaptive, so our analysis excludes the negative effects of sugar gliders (which are presented in detail by Stojanovic *et al.* 2014b).
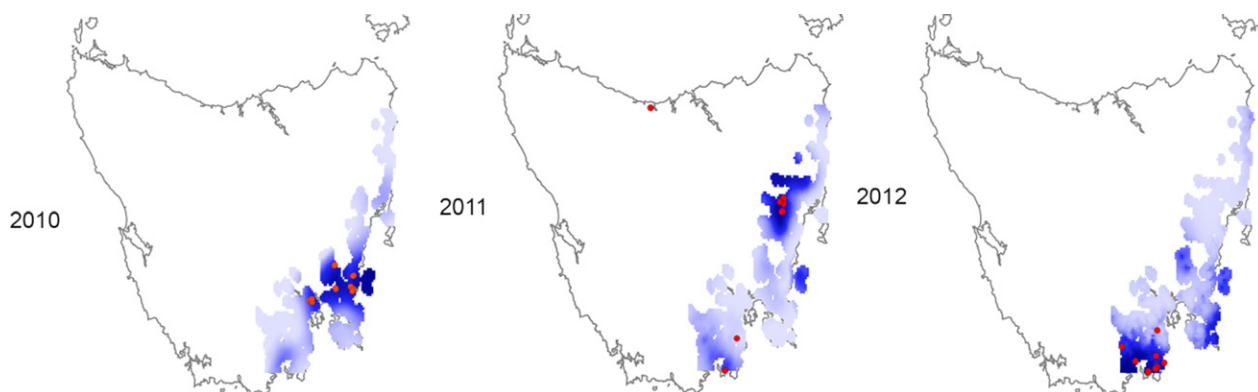
Fig. 1. Interpolated occupancy of swift parrots across their entire breeding range during the study period (adapted from Webb *et al.* 2014). Blue shading represents interpolated swift parrot occupancy, and red points indicate the location of nests found in that year.

FOOD AVAILABILITY AND PARROT OCCUPANCY

Webb *et al.* (2014) monitored swift parrot occurrence and tree flowering across the entire breeding range each October. For details, see Webb *et al.* (2014), but briefly, a flowering score was assigned to each site, where 0 = no flowering (1% of crown flowering), 1 = light (<10% of crown), 2 = moderate (10–40% of crown), 3 = heavy (40–70% of crown) and 4 = very heavy (>70% of crown). The score for each site was determined by the most heavily flowering blue or black gum. Swift parrot presence/absence data were collected during repeated visits. These data were used to construct annual occupancy models for the breeding range (Fig. 1; Webb *et al.* 2014). Site-level flowering intensity and swift parrot occupancy estimates were interpolated across Tasmania using kriging with 0·02° pixel size (1·6 km), 50 neighbours and neighbour search radius of 0·05° for each year between 2009 and 2012 (Webb *et al.* 2014).

NEST MONITORING AND NESTLING GROWTH

Nests were found (for search method see Stojanovic *et al.* 2012) where aggregations of swift parrots were identified by Webb *et al.* (2014) after the entire potential breeding range was surveyed. Here, we present data collected over three consecutive summer breeding seasons (2010/2011, 2011/2012 and 2012/2013). Not all nests could be monitored (due either to inaccessibility or predation), but whenever possible, nests were monitored using the method described by Stojanovic *et al.* (2014b). All known nests were checked annually, and monitored nests were used only once by swift parrots during the study period. Here, we present data for 53 nests where both reproductive investment (clutch size) and fecundity (number of fledglings) were known. Swift parrots nest relatively close together (Webb, Holdsworth & Webb 2012), so nests within 10 km of one another were grouped into regions (Fig. 2). These were usually separated by at least 40 km, except for region six (Bruny Island), which was separated by a 17-km sea barrier from the nearest region on mainland Tasmania.

Nests were monitored from the time of discovery until they either succeeded (i.e. produced at least one fledgling) or failed (for details of the nest monitoring approach, see Stojanovic *et al.* 2014b). We recorded clutch size by climbing nesting trees and visually inspecting nest cavities. Approximately every third day we collected data on growth using seven morphological variables
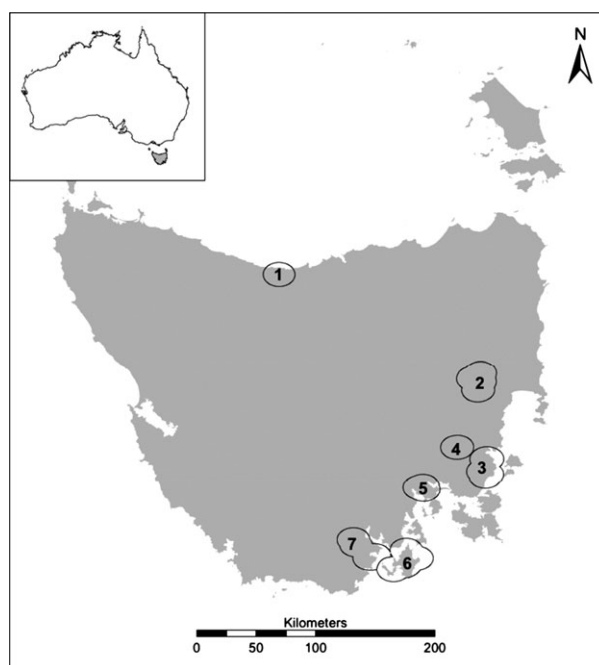

Fig. 2. The study area showing each region where swift parrot nests were monitored. Each region was only used once by swift parrots over the 3 years of the study, except for region six, where three nests were found in 2011, and 14 nests were found in 2012. The regions were as follows: (1) Devonport, (2) the Eastern Tiers, (3) Wielangta, (4) Buckland, (5) the Meehan Range, (6) Bruny Island and (7) the Southern Forests.

for each nestling: the length of the head bill (±1 mm), culmen (±1 mm), flattened wing chord (±1 mm), radius (±1 mm), tarsus (±1 mm), tail (±1 mm) and body mass (±0·1 g).

ANALYTICAL APPROACH

Our four predictions were tested using a range of modelling techniques with three breeding fitness and three chick growth parameters. All nests in study Region one (Fig. 2) failed due to sugar glider predation, and no nestlings were monitored there (Stojanovic *et al.* 2014b). However, clutch sizes were ascertained prior to failure for these nests allowing this region to be included in

some of the models. Furthermore, due to severe habitat loss at Region one due to agriculture, logging and urban development, flower surveys could only be undertaken at a very small sample of sites.

We tested our first prediction (that nest cavities would not be reused in successive years when food availability was low) by comparing nearby food availability at nest cavities with two consecutive years of data ($n = 38$). We used a paired *t*-test to compare food availability (i.e. interpolated flowering intensity scores) in the year when swift parrots nested, to the subsequent year when they did not. We also investigated whether there were landscape level differences in occupancy patterns using models published by Webb *et al.* (2014; Fig. 1) by comparing interpolated swift parrot occupancy at monitored nests in each region (when they were used for breeding) against occupancy over the rest of the breeding range.

To test prediction two, that swift parrots would breed in the richest patches, we first looked at food availability at active nests and compared this to background food availability across the whole breeding range. We then fitted linear models in R (R Development Core Team 2008) with interpolated flowering intensity at active nests as the response variable and breeding region as a fixed effect explanatory variable. This allowed us to examine food availability in different regions and test for differences among regions.

To test prediction three, that reproductive investment and success would be maintained at high levels, we fitted a suite of models using clutch size, number of fledglings and breeding success (i.e. proportion of eggs that become fledglings) as response variables, with region and flowering intensity as (fixed effect) explanatory variables. We also included the interaction terms between region and flower in these fixed effect models. Further models were fitted to account for the potential effects of spatial-autocorrelation in the data and heterogeneous patterns of sugar glider predation. These included generalized additive models (GAM) using a smoothed location covariates (implemented in R package mgcv: Wood 2006); generalized linear mixed models (GLMM) where each nest was included as a random effect (implemented using R package MCMCglmm: Hadfield 2010) and spatial simultaneous autoregressive models (SAR) using a spatial autocovariate (implemented using R package spdep: Bivand *et al.* 2013).

We tested prediction four, that nestling quality would remain high, by analysing morphological data from known age nestlings ($n = 58$) in a three-step process:

1 We pooled data for all nestlings of known age to create global models for each of the seven morphological variables, using the logistic function

$$Y = \frac{a}{(1 + e^{(b-x).k})}$$

where a = asymptote, b = inflection point, k = slope, y = the morphological variable (e.g. wing length) and x = time (days).

2 Using the global values of a, b and k from step one as a starting point for comparison, we fitted logistic functions to the morphological variables of each individual nestling. Thus, for each nestling there were seven sets of coefficients (a, b and k), corresponding to each morphological variable (wing length etc.).

3 We used the coefficients from each nestling as response variables in linear mixed models to investigate how interpolated flower intensity influenced nestling growth. To account for relatedness of siblings and unmeasured variation between regions, we used nest ID as a random effect term and region, flowering intensity and an interaction term as the fixed effects in each model. To reduce the potential for error or unrepresentative trends, we excluded nestlings with less than four measurements. We also excluded nestlings when the standard errors of a, b or k in their models were more than twice the value of the coefficients. To test for systematic bias in our data sampling, we used the same approach outlined in step three to model the standard errors of the coefficients for all seven morphological variables of each nestling. Morphological data from 46 nestling swift parrots were used in our analysis of nestling growth, but for some morphological parameters, fewer chicks were included because we could not estimate the coefficients of a logistic curve in some cases. The smallest sample of nestlings used was for the tarsus models ($n = 31$). The mean number of measurements per nestling in our sample was seven (range 4–10). We did not test for a difference in nestling growth between regions because sample sizes for some regions were too small and there was no significant difference in the availability of food between regions (prediction two).

The analysis of nestling growth parameters was undertaken using the 'nlme' and 'lme4' package in R (Bates *et al.* 2013; Pinheiro *et al.* 2013).

Results

We found support for prediction one because swift parrots only nested in cavities when food was locally abundant, and not when food was scarce in the subsequent year ($t = 11.15$. d.f. = 37, $P < 0.001$). Region six was the only region where nests were recorded in the same cavity in 2 successive years. We found three nests there in 2011 when food was scarce (mean interpolated flower intensity = 0.23 ± 0.04, corresponding to the lowest flowering intensity at an active nest recorded in this study) and 13 nests in 2012 when food was abundant (mean flower = 1.45 ± 0.07). Swift parrot occupancy in the landscape around active nests was significantly higher (0·695) than background occupancy across the remainder of the breeding range (0·18; pooled data for all years, $t = -16.4$, $P < 0.0001$; Fig. 3).

We found support for prediction two because mean flowering intensity at active nests (1·5) was significantly higher than mean flowering intensity across the remainder of the potential but unused breeding range (0·73; pooled data for all years, $t = 11.4$, $P < 0.0001$, Fig. 4). Although flowering intensity was consistently higher at active nests, there was some evidence of differences between regions. In particular, compared to the other regions flowering intensity at Region one was significantly higher ($t = 6.3$, $P < 0.0001$), as was flowering intensity at Region four and to a lesser extent, Region three ($P = 0.048$ and $P = 0.02$, respectively). As noted above, the fragmented nature of forest in Region one meant that flowering intensity there was less representative of flowering occurring in

Fig. 3. Interpolated swift parrot occupancy around active nests compared to background occupancy across the remainder of the breeding range. Swift parrot occupancy at study regions was significantly higher than elsewhere. The *x*-axis refers to region names from Fig. 2, and occupancy data were adapted from Webb *et al.* (2014). Data for the 3-year study period are presented as means, but the values for nesting sites represent only the year when monitored nests were active.
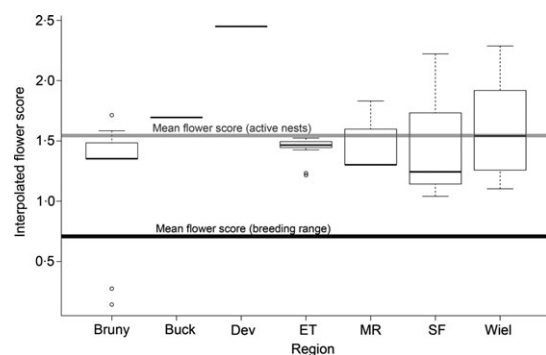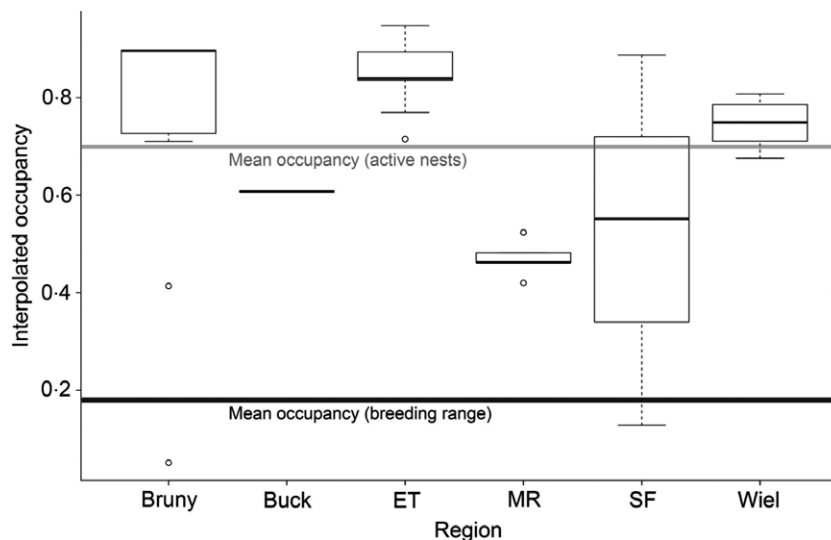

Fig. 4. Interpolated flowering intensity around active swift parrot nests, compared to background food availability across the remainder of the breeding range. Wherever swift parrots nested, food was significantly more abundant than background food availability across the whole breeding range ($t = 11.4$, $P < 0.00001$). The *x*-axis refers to region names from Fig. 2, and flower intensity data were adapted from Webb *et al.* (2014). Data for the 3-year study period are presented as means, but the values for nesting sites represent only the year when monitored nests were active.

the broader landscape. When we fitted the models without the Region one data, no significant differences were found across the six regions ($F = 1.5$, $P = 0.2$, ns, Fig. 4).

The consistency that we found in fitness-related life-history parameters provided strong support for prediction three. Swift parrot nests ($n = 58$) produced a mean of 3.6 eggs (± 0.2 SE), 2.5 (± 0.2 SE) fledglings, and overall breeding success (% of eggs that fledged chicks) was 67.2% (± 5.6 SE). Excluding the 12 nests that failed (10 of 12 attributable to sugar glider predation), successful swift parrot nests had mean clutch sizes of 3.8 eggs (± 0.2 SE) and produced 3.2 fledglings (± 0.2 SE), equating to breeding success of 86.9% (± 3.0 SE). If we first consider the models that did not include a spatial term, reproductive investment (eggs) was not significantly influenced by year, food availability or region (Table S1a, Supporting information). In contrast, the best (simple) linear model for

number of fledglings raised included both region and flower, while the best model for breeding success only included region (Table S1b). The presence of region in the best models for chicks and breeding success was largely driven by the low breeding success in regions one and two, caused by sugar glider predation. When the models were fitted without these data, region was not found to have a significant influence on breeding success.

Of the models with the spatially explicit terms, the GAMs performed better than the simpler models. For reproductive investment (eggs) and breeding success, the best model contained only the smoothed spatial term (eggs: $F = 4.6$, $P = 0.01$, success: $F = 3.58$, $P < 0.0001$), indicating that clutch size and breeding success were independent of year, flowering intensity or region, thereby providing support for prediction three (Table S1a,c). For number of fledglings, the best model included the spatial term and flower ($F = 14.0$, $P < 0.0001$), again reflecting the importance of food availability on the ability of swift parrots to raise multiple chicks (Table S1b).

The global models for swift parrot nestling growth fitted logistic curves well (Fig. 5), and data from these models provided strong support for prediction 4. To test this prediction, we created 42 models using the equation coefficients and the standard error of individual nestling growth curves. We only found one significant effect of flower intensity, for the inflexion point of head-bill length (predictor value = -4.1 ± 1.7 SE, $t = -2.5$, $P = 0.03$). The remaining 41 models indicated no significant effects of flowering intensity ($0.055 \leq P \leq 0.97$) confirming that nestling swift parrots were of comparable quality irrespective of where they were reared.

Discussion

We provide strong evidence to support the widely held assumption that nomadic migration is adaptive for animals in dynamic environments where resources are
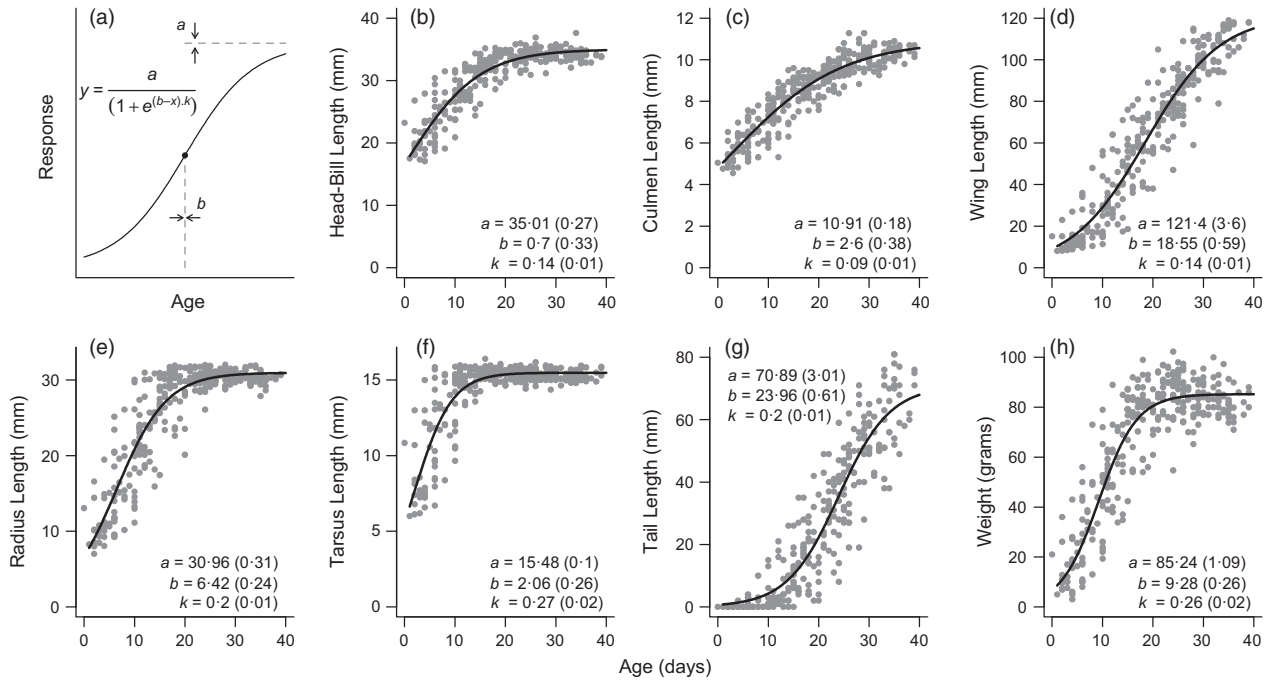
Fig. 5. Global models for the growth of nestling swift parrots. The growth of all morphological variables fitted logistic curves well, explained by the formula in the first panel. The coefficients of the formula are as follows: a = asymptote, b = inflexion point and, k = slope of the line. The points show raw data from all nestlings, and the lines show the global models of best fit for the data. The values of the coefficients for the growth equation of each trait are presented in the panels with standard errors in parentheses. The panels each refer to a different morphological variable, shown with units on the y-axis, plotted against nestling age (days) on the x-axis. Hatch day is when the x value is equal to zero.

patchily distributed in time and space. The availability of food for swift parrots was highly variable over our study period. In response to broad-scale patterns of tree flowering, the swift parrot population exhibited low breeding site philopatry and moved to different locations separated sometimes by hundreds of kilometres to exploit the richest patches of food available for nesting each year (Fig. 1). We found no difference in the availability of food among sites where we monitored swift parrot nests, but at those sites, food was significantly more abundant than elsewhere over the potential breeding range. However, in successive years, nests were not reused when local food abundance declined (a similar pattern was found by Webb, Holdsworth & Webb 2012). Despite dramatic spatiotemporal fluctuations in food availability across their breeding range, swift parrots maintained their reproductive output by exploiting the richest patches of food available. By moving, adult swift parrots produced nestlings of comparable number and quality irrespective of the particular location where they bred. When the effects of site-specific introduced sugar glider predation (Stojanovic *et al.* 2014b) are controlled for (see below), swift parrot reproductive investment and success fluctuates less in response to extrinsic factors than species that breed in the same place in successive years despite annual variability in local food supply (Bryant 1975; McCarty & Winkler 1999; Renton 2002).

Overall, with just one exception outlined below, our results provide evidence that breeding in a rich patch may optimize reproductive success when food availability is variable (Newton 2008). Nestling quality has been linked to subsequent survival and reproductive performance (Morrison *et al.* 2009; Hegyi *et al.* 2011), and by moving to the richest patch, swift parrots nesting in different locations were generally able to rear a comparable number of nestlings to a similarly high quality. This is the first direct empirical evidence that facultative movements enable animals to maintain consistently high reproductive success by locating and exploiting the richest available patches over time and space.

Despite an extensive modelling effort, we were mostly unable to find any significant differences in the number or development of swift parrot nestlings in this study. The exception was one significant effect of flower intensity on nestling development and related to a small sample of nestlings ($n = 7$) reared under poor flowering conditions in Region six during 2011. Relative to nestlings reared in rich patches, these seven nestlings reached their inflexion point more slowly for head-bill length. However, we view these significant results with caution because of the small sample of birds reared under poor flowering conditions. It is possible that the weak trends detected here are indicative of effects that might emerge with a larger sample of nestlings from a broader range of flowering conditions.

Although we provide evidence to show that nomadic migration is adaptive for swift parrots, Stojanovic *et al.* (2014b) show that in a degraded landscapes, anthropogenic habitat change can seriously impact the reproductive success of this species. The effects of sugar glider predation on productivity and fitness of swift parrots resulted from heterogeneous patterns of predation intensity. As resources fluctuate in their availability and distribution, swift parrots may be attracted into or away from areas where they are at high risk of predation. This phenomenon warrants urgent research to clarify the fitness and conservation consequences of variable and patchy food availability and predation pressure on swift parrots.

Migration systems where some breeding site philopatry is maintained year-to-year are the principal source of theoretical, experimental and field data available to understand the evolution of migration (Alerstam 1990; Greenberg & Marra 2002; Berthold, Gwinner & Sonnenschein 2003; Newton 2008). But migratory strategies are diverse, and understanding nomadic migrants is becoming increasingly important as a means to understand the consequences of global environmental change (Knudsen *et al.* 2011). Global warming has important phenological impacts on species (Cotton 2003; Gordo & Sanz 2010; Jones & Cresswell 2010; Forrest 2015), and understanding how species might cope with an increasingly variable and changing climate is a priority area of research (Visser & Both 2005; Charmantier *et al.* 2008). This study is a step towards understanding the ecology of animals that can survive in variable environments and provides rare baseline evidence to support the direct link between landscape level variation in food availability and individual fitness.

Acknowledgements

Data accessibility

Nestling growth data and R code to construct growth curves are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.23h73 (Stojanovic *et al.* 2015).

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Supporting Information

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

Table S1. Saturated and best models (with and without spatial covariate; SpaCov) found to explain variance in breeding fitness parameters: (a) number of eggs, (b) number of fledglings and (c) breeding success. Shading indicates the best models (dark shading indicates the best simple models without a spatial covariate, lighter shading indicates the best models that included the spatial covariate).