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Colony-specific foraging behaviour and co-ordinated divergence of chick development in the wedge-tailed shearwater *Puffinus pacificus*

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ABSTRACT: We examined divergence in foraging, provisioning and chick developmental patterns between wedge-tailed shearwaters *Puffinus pacificus* breeding at a temperate (Lord Howe Island) and sub-tropical (Heron Island) location. We aimed to evaluate the potential for different foraging environments to cause co-ordinated adaptive divergence in these characteristics. Adult foraging and provisioning behaviour differed significantly between locations, reflecting lower near-colony resource availability at Heron Island. Chick developmental patterns also differed significantly between locations. Overall, chicks at Lord Howe Island grew faster and had greater skeletal growth per gram of food delivered. In contrast, chicks at Heron Island exhibited greater body mass gains per gram of food delivered. Based on previously observed physiological or facultative responses to changes in provisioning rates in seabirds and long-term patterns of primary productivity at each location, we propose these developmental differences reflect colony-specific physiological adaptations to differences in long-term provisioning rates. If so, our results suggest co-ordinated environmentally determined divergent coevolution of chick and adult life-history parameters between these 2 locations.

KEY WORDS: Procellariiform · Shearwater · Chick development · Co-ordinated divergence · Foraging behaviour · Adaptation

INTRODUCTION

Increasingly, recent studies of population-specific foraging behaviour suggest that selection on life-history traits associated with foraging in different background environments can lead to local adaptation and promote genetic divergence (Foster 1999, McLaughlin 2001, Remeš & Martin 2002). Despite this, empirical studies examining spatial and temporal variation in foraging behaviour at the population level are rare (Smith & Skúlason 1996, Foster 1999). This is the case in seabirds, where a limited number of comparative studies exist (e.g. Waugh et al. 2000, Hamer et al. 2001, Falk et al. 2002, Tremblay & Cherel 2003). The relative paucity of studies belies the fact that seabirds are good model taxa for examining local adaptive processes. This is because seabird colonies are often located such that individuals from different locations experience substantially different foraging environments, making adaptation to local resource characteristics possible (Congdon et al. 2000, Waugh & Weimerskirch 2003). In addition, many seabirds exhibit philopatry to natal breeding colonies, thus restricting gene flow and further promoting the possibility of local adaptation (Endler 1977, Hendry et al. 2000, Congdon et al. 2000, Coulson 2002).

Where colony-specific resources differ, substantially different foraging strategies may be favoured at each location, each maximising lifetime reproductive output relative to background resource availability (Endler 1977, Suryan et al. 2000, Vos & Hemerik 2002). Entrained by population-specific foraging behaviour, physiological characteristics such as chick developmental patterns may also diverge and become

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population-specific (Arendt 1997). If inter-colony matings then produce chicks with developmental patterns unsuited to either of the foraging environments, character displacement may serve to further promote population differentiation and eventually even speciation (see Endler 1977).

Foraging behaviour in many Procellariiform seabird species varies according to local resource availability (e.g. Granadeiro et al. 1998, Catard et al. 2000, Waugh et al. 2000). When local resources are poor these taxa use a specialised bimodal foraging strategy that alternates multiple short foraging trips (1 to 4 d duration) in near-colony waters for chick provisioning, with longer self-provisioning trips (>5 d duration) to highly productive areas located at-distance from breeding colonies (Weimerskirch 1998, Weimerskirch & Cherel 1998, Congdon et al. in press). However, at colonies where near-colony resources are sufficient, they provision using a unimodal strategy based on local productivity only (Granadeiro et al. 1998, Waugh et al. 2000). The wedge-tailed shearwater *Puffinus pacificus* is one such species. The population at Heron Island, Australia, uses a bimodal strategy (Congdon et al. in press), while the population at Tern Island, Hawaii, uses a unimodal strategy (Baduini 2002). Currently, it is not known if differences between colonies are colony-specific (obligate) or vary according to temporal changes in resource availability (facultative). Nor is it known if chick development at each location reflects differences in provisioning rates associated with these 2 strategies.

We aimed to examine the relationship between chick developmental patterns and adult foraging behaviour for wedge-tailed shearwaters at 2 eastern Australian colonies having predictably different background resource availability; a sub-tropical colony at Heron Island, located on the southern Great Barrier Reef (GBR), and a temperate colony at Lord Howe Island, located in the south-western Pacific Ocean. This was done as an initial step in determining the potential for co-ordinated local adaptation between adult foraging behaviour and chick development to restrict gene flow and promote population divergence in this species.

MATERIALS AND METHODS

This study was conducted at Heron Island (23° 26′ S, 151° 51′ E), in the Capricorn Section of the GBR Marine Park, Australia, and at Lord Howe Island (31° 33′ S, 159° 05′ E), in the south-western Pacific Ocean. Work was carried out during the first month of the chick-rearing period from February to March of 2003 (Heron Island) and 2004 (Lord Howe Island). A total of 20 experimental nests were monitored at each location. At each nest chick skeletal growth measurements (tarsus) were obtained at 4 d intervals using dial callipers (±0.1 mm). Adult provisioning rates and chick mass were monitored at each nest daily. Chicks were weighed twice each day at 09:00 and 16:00 h using an electronic balance (±0.1 g). Meal masses were calculated as the difference between chick mass at 16:00 h and immediately after an adult feed. Banding, handling and trapping protocols were the same as those employed during previous studies of this species (Smithers et al. 2003, Peck et al. 2004).

Primary productivity. To compare background levels of productivity between the 2 locations across multiple years, sea-surface chlorophyll concentrations were obtained from SeaWiFS Local Area Coverage (LAC) ocean colour data (accessed 21 March 2005; http://reason.gsfc.nasa.gov/OPS/Giovanni/ocean.seawifs.shtml) (as per Murtugudde et al. 1999, Weimerskirch et al. 2005). Data consisted of monthly mean chlorophyll concentrations for 50 km^2 of ocean surrounding each island, from 1998 to 2004, at the scale of 0.1°. Chlorophyll data from each island in each year were tested for homogeneity of variance using Levene's *F*-tests. Different levels of variance were consistently observed between locations, but not among years at each location (see 'Results'). As a consequence, between-year comparisons were undertaken separately at each location using monthly samples in a repeated-measures ANOVA, while between-location comparisons were performed using monthly samples in a paired *t*-test that adjusted for unequal variance among samples (Welch's *t*-test).

Foraging behaviour. Foraging behaviour was assessed using the protocols of Peck et al. (2004). To avoid pseudoreplication, mean values for each parent were used as replicates in analyses at each colony. Measures of foraging behaviour obtained per individual included provisioning rate (meals night^{-1}), meal mass (g), meal mass per night (g night^{-1}) and foraging trip length (days). To examine adult foraging efficiency, we calculated the mean proportionate daily mass change per individual using the following equation: proportionate mass change (MC) = (AM – DM)/DM, where AM and DM is arrival mass and departure mass in grams (González-Solís et al. 2000).

Adult foraging patterns were examined using a frequency distribution of the mean time spent (as a proportion of total foraging time) on foraging trips of different lengths for each individual. Kruskal-Wallis ANOVA and post hoc pair-wise Mann-Whitney tests among trip-length categories (with Bonferroni correction) were used to test for bimodality and colony-specific patterns (as per Congdon et al. in press). All proportions were arcsine-transformed prior to analysis.

Chick growth. Mass increase in Procellariiform chicks can be described accurately by the logistic equation: $W = A/1 + e^{-K(T-T_{\mathrm{m}})}$, where W is chick weight at time T, A is the asymptotic value of the curve, and T_{m} is the point of inflection of the age at which the maximum growth rate is achieved (see Ricketts & Prince 1984, Congdon 1990). Data from the first 20 to 30 d post-hatching provide an accurate estimate of growth parameters over the entire pre-fledging period for seabirds having this pattern of development (Congdon 1990). Growth data from individual chicks were fitted to this equation using least-squares regression. To facilitate inter-colony comparisons the asymptotic value (A) for all chicks regardless of colony was standardised to 347.68 g. This is the average mass (±1 SE = 5.14, n = 32) of wedge-tailed shearwaters at fledging across a range of colonies (Pettit et al. 1984, Marchant & Higgins 1990, Carter et al. 1996, D. R. Peck et al. unpubl. data). A standard t-test was used to test for differences in the mean growth rate constant (K) between breeding colonies using chicks as replicates.

The growth of seabird chicks has previously been shown to vary within and among populations in response to spatial and temporal differences in the total quantity of food provided by adults (Cairns 1987, Huin et al. 2000, Tremblay & Cherel 2003). Therefore, to look for underlying differences in developmental rates beyond those attributable to differences in the total quantity of food provided, chick growth at both Heron and Lord Howe Islands was compared relative to per gram of food received by individual chicks. To this end, we conducted an ANCOVA with colony location and chick as factors, meal mass (g night^{-1}) as the covariate, and chick mass change (g d^{-1}) (i.e. the difference between 2 consecutive 16:00 h weightings) as the response variable.

At the beginning of each study period chick ages (based on culmen length) were calculated to be between 1 and 10 d at both locations (Peck et al. 2004, Peck & Congdon in press). Therefore, to account for the potential influence of chick developmental stage on mass changes, the change in mass was standardised relative to total chick mass for each individual at 16:00 h prior to the observed feed for that day (Peck et al. 2004). A similar analysis was used to examine differences in patterns of tarsus growth between the 2 colonies, with the exception that tarsus length was measured at 4 d rather than 1 d intervals.

All statistical analyses were conducted using JMP Ver. 4.0.2 (SAS Institute). The normality of each set of measurements was tested using the Shapiro-Wilk W-test. As appropriate in each case, data were either log or square-root transformed prior to analysis if deviations from normality were detected (Quinn & Keough 2002). Values are given ±1 SE unless otherwise stated.

RESULTS

Primary productivity

Primary productivity as measured by chlorophyll concentration in surrounding waters was not significantly different within the 7 yr period at either location (Fig. 1, Heron, $F_{6,83} = 1.69$, p = 0.13; Lord Howe, $F_{6,83} = 1.88$, p = 0.09). Mean monthly chlorophyll concentration was significantly more variable (Levene's F-test; $F_{1,174} = 57.17$, p = 0.0001) and consistently higher (Welch pairwise t-test; $t_{165} = 4.31$, p = 0.001) at Lord Howe Island (mean = 0.19 mg chlorophyll m^{-3}, ±0.007, n = 84) than at Heron Island (mean = 0.15 mg chlorophyll m^{-3}, ±0.007, n = 84) (Fig. 1).

Foraging behaviour

The majority of adult foraging trips lasted from 1 to 3 d at both study sites. However, mean trip length was significantly longer at Heron Island than at Lord Howe Island (Table 1). At Heron Island, significantly less time was spent on 4 d trips than on either 1 or 2 d trips or trips of >5 d (Fig. 2a, Kruskal–Wallis $\chi^2_{11} = 183.71$, $p < 0.001$). This pattern clearly identifies the use of a bimodal foraging strategy at Heron Island with short trips (ST) ≤4 d and long trips (LT) of ≥5 d. At Lord Howe Island, the proportion of time spent on foraging trips of different length decreased with trip length. Consequently a unimodal foraging strategy was observed (Fig. 2b).

Mean meal mass fed to chicks at Heron Island was not different from that fed at Lord Howe Island

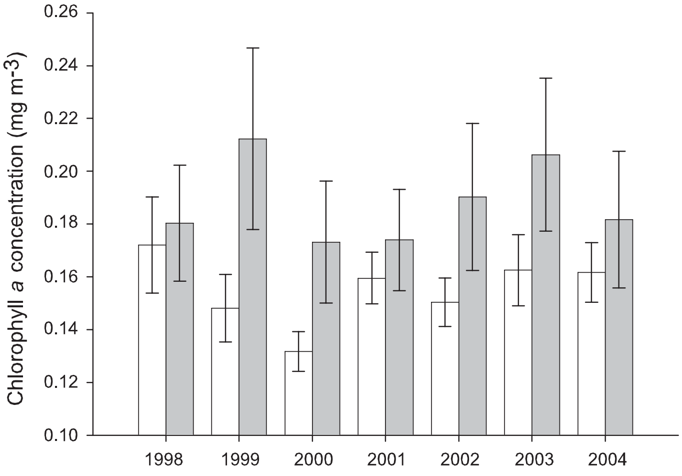

Fig. 1. Variation among years (mean ± SE) in chlorophyll *a* concentration at Heron Island, southern Great Barrier Reef (white bars), and Lord Howe Island, south-west Pacific Ocean (grey bars)

(Table 1). However, the mean meal mass delivered at Heron Island was significantly more variable than that fed at Lord Howe (Levene's *F*-test; $F_{1,78} = 3.68$, $p = 0.05$). After adjusting for unequal variances, mean meal mass delivered at each colony was still not significantly different (Welch *t*-test; $t_{72} = 1.04$, $p = 0.30$).

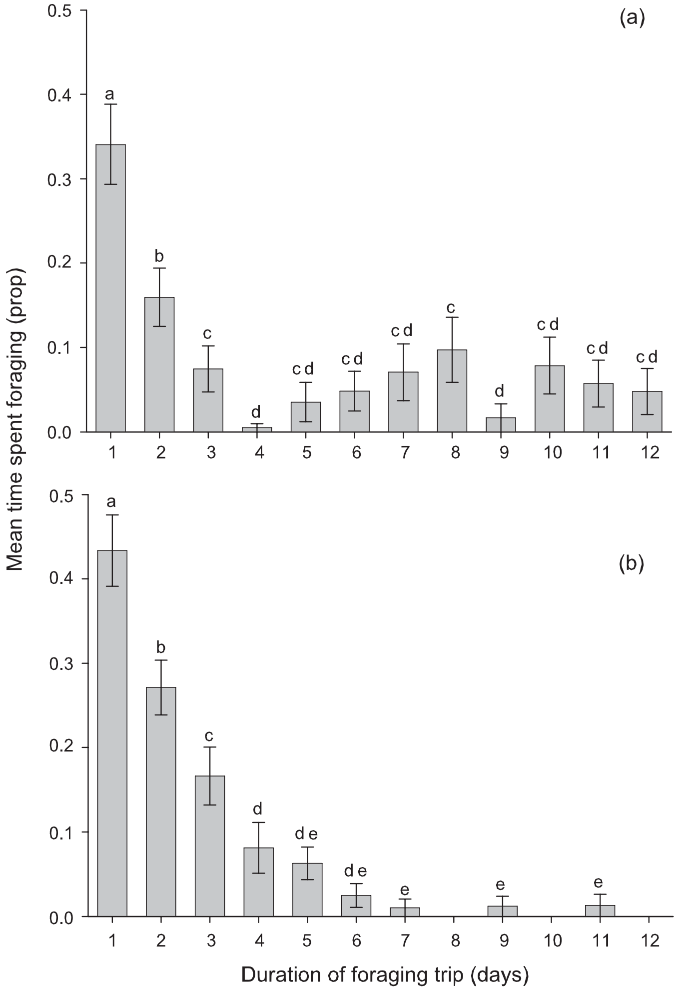

Fig. 2. *Puffinus pacificus*. Mean (±2 SE) proportion of time spent on foraging trips of different lengths by individual adults at (a) Heron Island and (b) Lord Howe Island. Different letters indicate means that are significantly different. prop: proportion

Meal mass delivered to chicks after ST also did not differ significantly between Heron and Lord Howe Islands (Heron mean = 31.99 g, ±2.12, n = 38; Lord Howe mean = 34.48 g, ±1.72, n = 40; $t_{76} = -0.914$, $p = 0.36$). However, chicks at Lord Howe Island were fed on average twice as much per night than those at Heron Island (Table 1). This was because chicks at Lord Howe had a higher probability of being fed by both parents each night (Table 1).

Regardless of foraging trip length, adults at Heron Island and Lord Howe Island gained similar amounts of mass whilst foraging relative to their mass at the beginning of each foraging trip (Table 1). Foraging efficiency of adults at Heron Island was significantly lower during trips of 4 d or less than during foraging trips of 5 d or greater ($t_{23} = 5.70$, $p < 0.001$). In fact, adults at Heron Island gained weight during LT and lost weight during ST (mean foraging efficiency LT = 0.07, ±0.01, n = 24; mean foraging efficiency ST = –0.04, ±0.006, n = 24), while adults at Lord Howe maintained a relatively constant mass during the provisioning period.

Chick growth

Mean values of *K* (the growth rate constant) for mass change were significantly different between the 2 locations. Chicks at Lord Howe Island had a higher mean *K*-value and thus faster growth to fledging mass than those at Heron Island ($K = 0.09 \pm 0.004$ and 0.03 ± 0.02, respectively; $t_{35} = -3.70$, $p < 0.001$).

Change in chick mass at both locations was positively correlated with the amount of food received (Fig. 3a, $F_{1,526} = 90.80$, $p < 0.0001$, adjusted $r^2 = 0.17$). The ANCOVA revealed a significant effect of island/location on mean mass change (Fig. 3a, $F_{1,497} = 7.37$, $p = 0.007$), but no difference among chicks or between the slopes of the regression lines for each island (Fig. 3a, $F_{27,497} = 1.13$, $p = 0.29$ and $F_{1,1} = 1.50$, $p = 0.22$, respectively). Therefore, at Heron Island, chick mass increase for a given amount of food was

Table 1. *Puffinus pacificus.* Foraging and provisioning parameters of wedge-tailed shearwaters breeding at 2 locations in eastern Australian waters (mean ± SE)

	Length of foraging trip (d)	Meal mass (g)	Meal mass (g night^{-1})	Probability of feed (meals night^{-1})	Adult mass change (g g mass^{-1})
Heron Island	2.69 ± 0.22	32.65 ± 1.80	7.40 ± 0.69	0.21 ± 0.01	0.032 ± 0.01
Lord Howe Island	1.75 ± 0.22	35.01 ± 1.34	14.43 ± 1.13	0.37 ± 0.02	0.007 ± 0.02
p	<0.001	0.29	<0.001	<0.001	0.37

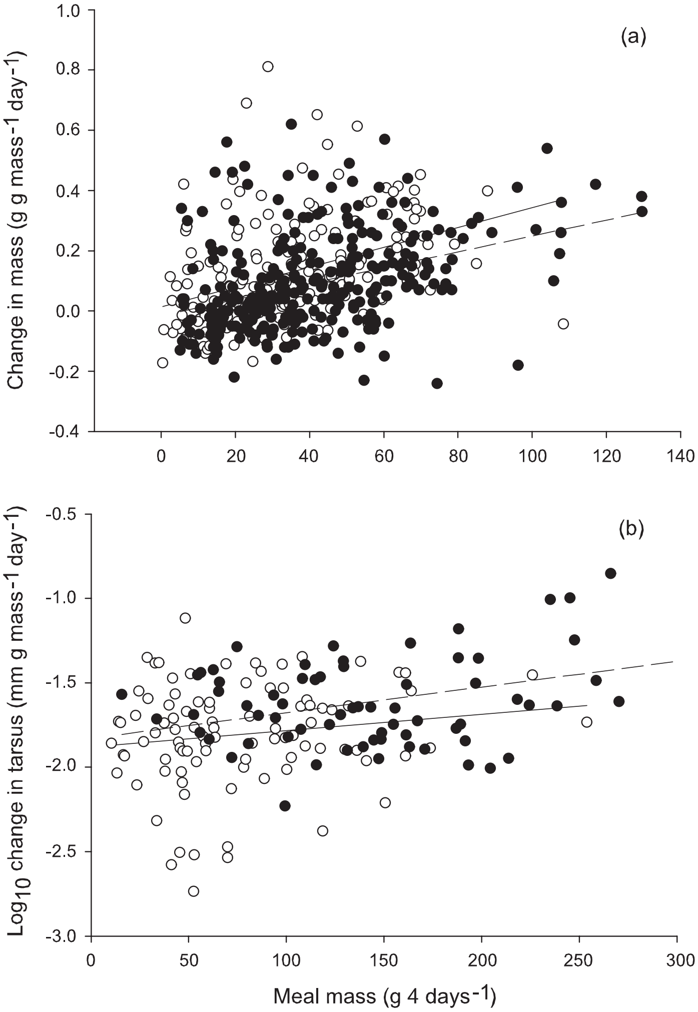

Fig. 3. *Puffinus pacificus.* (a) Relative change in chick mass (g) in relation to meal mass (g) and (b) relative change in chick tarsus (mm) in relation to meal mass (g) from Heron Island (○) and Lord Howe Island (●). Dashed lines represent the regression lines for Lord Howe Island chicks; solid lines those for Heron Island chicks

consistently higher than at Lord Howe Island. Chicks at Heron Island added approximately 0.03 g (per gram of chick) more per gram of food delivered than those at Lord Howe Island (Fig. 3a).

Change in tarsus for chicks at both locations was also positively correlated with the amount of food received (Fig. 3b, $F_{1,165}$ = 25.93, $p < 0.0001$, adjusted r^2 = 0.17). ANCOVA revealed a significant effect of island/location on mean tarsus change (Fig. 3b, $F_{1,137}$ = 4.13, p = 0.04), but no difference among chicks or between the slopes of the regression lines for each island (Fig. 3b, $F_{26,137}$ = 0.69, p = 0.85 and $F_{1,1}$ = 0.14, p = 0.70, respectively). Therefore, at Heron Island tarsus growth for a given amount of food was consistently lower than at Lord Howe Island. At Lord Howe Island chicks required approximately half the amount of food for the equivalent amount of tarsal growth (Fig. 3b).

DISCUSSION

Primary productivity

Oceanographic data suggest a resource-poor foraging environment at Heron Island relative to Lord Howe Island. Mean chlorophyll concentrations at Heron Island were consistently lower than those at Lord Howe Island and were similar to other regions of known low productivity in the tropical Pacific (Murtugudde et al. 1999) and Indian Oceans (Weimerskirch et al. 2005). Moreover, chlorophyll concentrations at both locations remained relatively stable and divergent across the 7 yr period for which data were available (Fig. 1). This suggests that the foraging environments experienced at each location were consistent across the 2 yr of our study and that the colony-specific differences we observed likely reflect general long-term patterns of resource availability at each location.

Divergent foraging strategies

Birds at Lord Howe Island used a unimodal strategy as described previously for wedge-tailed shearwaters in Hawaii (Baduini 2002). Both in Hawaii and elsewhere, unimodal foraging patterns have been attributed to birds provisioning using only near-colony areas of high productivity (e.g. Granadeiro et al. 1998, Baduini 2002). Our results suggest that Lord Howe Island adults may also forage exclusively using productive near-colony locations. This contrasts with the bimodal strategy observed at Heron Island both in 2001 (Congdon et al. in press) and 2003 (present study). Comparisons with other Procellariiforms (Weimerskirch 1998, Weimerskirch & Cherel 1998) imply that at Heron Island wedge-tailed shearwaters adopt a bimodal strategy to supplement food input to chicks beyond levels possible using only resource-poor, near-colony waters.

Therefore, combining results from both productivity and foraging analyses suggests that prey availability at Lord Howe Island differs substantially and consistently from that at Heron Island and that adult foraging strategies at each location are adjusted accordingly. Previously, temporal and spatial variation in food availability or productivity between locations has been shown to drive population-specific foraging behaviour in a number of seabird species (e.g. Hamer et al. 2001, Falk et al. 2002, Tremblay & Cherel 2003). Our results suggest that the same is true for wedge-tailed shearwaters.

Chick growth and local adaptation

Chick physiology and growth at the 2 study locations are significantly divergent in a number of ways. Firstly, overall growth in body weight (as measured by K), was significantly higher at Lord Howe Island than at Heron Island. This was not surprising given that Lord Howe Island chicks were provisioned approximately twice the amount of food per unit time and that seabird growth is sensitive to provisioning rates (Pettit et al. 1984, Cairns 1987). It also reinforces our suggestion that resource availability was lower at Heron Island. By itself, this result implies that overall growth rates at the 2 locations respond to different levels of provisioning by parents (Ricklefs 1973, 1979).

However, when comparing developmental changes per gram of food received, growth patterns for chicks at the 2 locations also differed significantly. Chicks at Heron Island showed substantially less skeletal development per gram of food obtained than those at Lord Howe, but gained significantly larger amounts of body mass, with the pattern reversed at Lord Howe Island. To our knowledge this has not been seen previously in seabirds. Such growth patterns imply that chicks at Heron Island may 'store' mass at the expense of skeletal growth, possibly as an adaptation to lower and less predictable long-term provisioning rates (Hulsman & Smith 1988, Congdon 1990, Schaffner 1990, Hamer et al. 2000). The differences we observed must reflect either physiological or facultative season-specific responses at each colony, or colony-specific adaptations resulting from divergent selection. Based on available evidence, as outlined below, we believe that colony-specific adaptation is more likely.

Firstly, chicks at Heron Island do not show suppressed overall development (per gram of food) with decreased provisioning. This has been the standard within or between season physiological response observed in many Procellariiformes and other seabirds when provisioning rates and/or food availability declines (e.g. Ricklefs et al. 1987, Hamer et al. 1998, Takahashi et al. 1999, Weimerskirch & Lys 2000).

Alternatively, the relative increase in mass gains at Heron Island (per gram of food) may reflect a physiological response to differences in the nutritional content of prey at each location. For example, our results may be explained by higher lipid content in prey at Heron Island compared to Lord Howe Island. Unfortunately, we do not have the data on prey energy content at each colony needed to test this hypothesis directly, but again our results contrast with expectations from the literature. In general, the energy density of foragefishes is positively correlated with lipid content (Van Pelt et al. 1997), implying that high-lipid-content prey is also high-quality prey. In seabirds, high-energy, high-lipid-content diets have been shown to increase body mass gains (Litzow et al. 2002, Dahdul & Horn 2003), fat reserves and rates of wing development, without effecting tarsus or culmen growth (Dahdul & Horn 2003). This suggests that a high-lipid diet at Heron Island could produce the increase in relative mass gain observed at this location, but not the differences in relative tarsus growth between colonies.

Thirdly, our findings do not agree with expectations of the only other previously documented facultative response of seabird chicks to reduced provisioning rates (Congdon 1990). This model suggests that, in pelagic foraging seabirds under low predation pressure, mass should be preferentially maintained at the expense of other types of growth during periods of increased food stress (Congdon 1990, Ashton & Armstrong 2002). Under this model, in similarly adapted populations, we would expect equivalent mass storage at both locations and retarded skeletal growth only at Heron Island. This was not the case.

It is possible that our findings reflect an as yet undocumented facultative response. If so, then chick developmental physiology at each location must be responding to a season-specific assessment of background food availability that has occurred in the very early stages of chick development; well within our 26 d study period. The previously documented variability in day-to-day provisioning rates in both wedge-tailed shearwaters (Baduini 2002, Peck et al. 2004) and other pelagic foraging seabirds (Ricklefs et al. 1985, Congdon 1990, Warham 1990, Catard et al. 2000) makes such a season-specific assessment theoretically difficult in the time available. Therefore, while we cannot discount a facultative mechanism entirely, such a response would highlight a novel and significant physiological ability not previously documented in other taxa.

CONCLUSIONS

In summary, wedge-tailed shearwaters breeding at Heron and at Lord Howe Islands have divergent foraging strategies consistent with a relatively resource-poor, local foraging environment at Heron Island. We see concomitant divergence in chick development at the 2 locations. Per gram of food delivered, chicks at Heron Island exhibit a marked increase in body mass development over skeletal growth, while chicks at Lord Howe Island show the reverse. Based on previously observed facultative responses to changes in food availability, theoretical expectations on the rate at which season-specific assessments of background food availability can occur and an analysis of long-term productivity at both locations, we propose that the growth patterns observed are probably colony-specific physiological adaptations to differences in long-term provisioning rates at each location. If so, our results suggest coevolution of chick and adult life-history parameters across these 2 locations, and thus have important implications for models of population divergence and speciation in seabirds.

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