

Divergence in chick developmental patterns among wedge-tailed shearwater populations

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ABSTRACT: Mechanisms of population divergence in seabirds are poorly understood. We evaluated whether divergent patterns of chick development among wedge-tailed shearwater *Puffinus pacificus* populations are facultative responses to short-term fluctuations in food availability, or fixed colony-specific phenomena potentially associated with differences in local resource availability. Supplementary feeding at Heron Island increased food intake to levels equal to, or greater than, those observed at Lord Howe Island. In supplemented chicks, mass accumulation per gram of food received was inversely related to current body stores, up to a maximum storage level set by body size. Significantly, maximum storage was lower for Heron Island than for Lord Howe Island chicks at equivalent body size. In contrast, relative allocation to skeletal growth did not differ between supplemented and control chicks, was not influenced by body condition and did not increase to levels observed at Lord Howe Island. Overall, the present study showed that supplemented chicks were unable to use short-term increases in food availability to increase relative mass stores or rates of skeletal development, implying that both life-history parameters have some colony-specific components that are divergent between the locations of this study. Our findings add weight to previous studies suggesting that phenotypic plasticity and/or genetic drift due to philopatry cannot fully explain patterns of morphological, behavioural and physiological divergence among these 2 shearwater colonies.

KEY WORDS: Colony-specific development · Chick growth · Local adaptation · *Puffinus pacificus* · Supplementary feeding

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INTRODUCTION

Breeding seabirds are restricted in the resources they can access by both the need to central place forage and the patchy distribution of prey in the marine environment (Lack 1968, Ashmole 1971). Location-specific climate and oceanic variation, both within and among breeding seasons, further influence patterns of local resource availability (Smithers et al. 2003, Devney et al. 2010). As a result, food availability can vary considerably among breeding colonies throughout a species range (Weimerskirch et al. 2005a), particularly among colonies in different habitats. For example, colonies in more temperate zones are often proximal to highly productive waters which

provide reliable access to food (Brown 1979). By contrast, seabirds breeding in tropical systems with typically more oligotrophic waters face lower and more patchily distributed resources (Longhurst & Pauly 1987).

Such constraints significantly influence a range of seabird life-history characteristics. Intra-specific variation linked to colony location and/or variation in background resource availability has been observed in breeding phenology (Le Corre 2001), foraging strategies (Weimerskirch et al. 1994, Baduini & Hyrenbach 2003), provisioning rates, chick growth and ultimately chick survival (Ricklefs 1968, Monaghan et al. 1989, Piatt et al. 2007). Whether among-colony variation represents short-term facultative

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responses to constantly varying conditions or colony-specific adaptive responses to different background resource availability is generally unknown.

Changes in breeding phenology and adult foraging strategies at individual colonies relative to resource availability suggest that variation in these characteristics is likely facultative (Granadeiro et al. 1998, Weimerskirch et al. 2005b). Less is known about whether chick developmental patterns are also this flexible. Differing developmental responses to variation in food supply have been seen in food manipulation experiments in seabirds. Some species display a facultative ability to adjust to changes in food intake by varying allocation to a range of growth parameters (Congdon 1990, Kitaysky 1999), while others demonstrate little ability to adapt to food reductions (Devney et al. 2010). Comparisons among foraging guilds demonstrate the potential for seabird developmental patterns to be evolved responses to variation in resource availability. For example, developmental patterns in chicks of offshore and pelagic foraging species, which experience consistently low food resources and/or high variability in food availability, characteristically prioritise the accumulation of mass and body maintenance at the expense of growth in other characteristics (Ricklefs & White 1981, Schaffner 1990). This preferential maintenance of body reserves is thought to provide a buffer against periods of sparse and inconsistent food availability (Lack 1968, Ashmole 1971). In contrast, inshore foraging taxa show preferential growth of various skeletal parameters (Benowitz-Fredericks et al. 2006, Sears & Hatch 2008, allowing them to fledge more rapidly, and thus avoid higher predation pressure (Ricklefs 1968).

Wedge-tailed shearwaters *Puffinus pacificus* breeding at Heron Island on the Australian Great Barrier Reef (GBR) experience consistently lower food availability than conspecifics breeding at Lord Howe Island (Peck & Congdon 2005). As a consequence, the Heron and Lord Howe Island shearwater populations display divergent patterns of adult foraging behaviour, chick provisioning and chick development (Peck & Congdon 2005). Lord Howe Island chicks are provided with larger meals and are almost twice as likely to be fed each night. Consequently, they grow faster in all characteristics. Further, relative to Heron Island chicks, Lord Howe Island chicks allocate more of each gram of food received to skeletal growth and less to fat or body stores (Peck & Congdon 2005). Conversely, Heron Island chicks allocate more of each gram of food received to mass accumulation at the expense of

skeletal development. This pattern of allocation presumably provides a buffer against their more unpredictable provisioning regime (Peck & Congdon 2005). Currently, it is not known if these differences in chick development are a facultative response to differences in food availability, or a fixed colony-specific pattern of development potentially linked to long-term patterns of resource availability, and so maintained by natural selection.

We aimed to examine resource allocation and relative growth responses of wedge-tailed shearwater chicks to rapid changes in food supply brought about by artificial food supplementation. That is, can chicks facultatively adjust the proportion of food allocated to different components of growth, or do relative allocations to different components of growth remain fixed and unchanging? We particularly wanted to determine if, for a given amount of food, the relative allocation of resources deviates from patterns previously observed at Heron Island and how these patterns compared with those observed on Lord Howe Island when chicks received equivalent or greater amounts of food.

The degree to which these developmental responses are plastic directly influences the ability of chicks to cope with short-term, climate or non-climate related increases or decreases in food availability. As wedge-tailed shearwaters are sensitive to changes in background resource availability related to climate variation (Smithers et al. 2003, Peck et al. 2004), such information is critical to understanding the potential impacts of human-induced climate variation on the population viability of this species.

MATERIALS AND METHODS

Study species and data collection

We studied wedge-tailed shearwaters at Heron Island (23° 26' S, 151° 51' E), in the Capricorn Bunker Group of islands in the GBR Marine Park, Australia, over the first 6 wk of the chick-rearing period in February/March 2010. Adults forage at sea during daylight hours and return to the colony at night to provision chicks, usually with a single meal shortly after returning to the nest. Protocols for banding, handling, aging chicks and trapping followed those used in previous studies of this species (Congdon et al. 2005, Peck & Congdon 2005). Data were obtained from a total of 10 experimental and 9 control nests all of which were monitored each night between 19:00 and 05:00 h for adult arrival and

chick feeding. After adults had finished feeding chicks, both adults and chicks were weighed. Chicks were also weighed daily between 16:00 and 17:30 h, shortly before dark. All weights were obtained using an electronic balance (± 0.1 g). Adult meal mass for each feeding episode was calculated as the difference between the chick mass immediately after a nocturnal feed and the precedent mass weight at $\sim 16:00$ h. Tarsus measurements of chicks were obtained at each nest every 3 d using dial calipers (± 0.1 mm). This interval was chosen to allow sufficient time between measurements for growth to exceed any potential measurement error. Tarsus length was measured as a proxy for skeletal development in chicks to facilitate direct comparison of our results with those of the previous study by Peck & Congdon (2005), which compared chick growth under natural conditions on both Heron and Lord Howe ($31^{\circ} 33' \text{ S}$, $159^{\circ} 05' \text{ E}$) Islands. Adult morphometrics were also obtained for each adult once, at the end of a long-trip cycle and subsequent to chick feeding, when adults were most likely to be in best physical condition (see Congdon et al. 2005).

Chick supplementary feeding

Little published information is available on the diet of wedge-tailed shearwaters upon which to base the choice of supplementary food. However, in a controlled feeding experiment on common murrets *Uria aalga*, Benowitz-Fredericks et al. (2006) found that when using high energy content food sources, overall food intake influenced growth and development more than diet composition. Therefore, we considered the total mass of high quality supplementary meals to be the most important consideration when developing an effective supplementation protocol. Pilchards *Sardinops sagax* spp., of the order Clupeiformes, are 'oily' fish rich in nutrients, with high energy content relative to other potential shearwater prey (Mullers et al. 2009). Therefore, we selected the Australian pilchard *S. sagax neopilchardus* as the supplementary food source to be used in our experiments. Clupeiformes are a common component of shearwater diets in other areas (e.g. Jackson 1988, Catry et al. 2009) and this particular species is a commonly available bait fish in East and South-eastern Australian waters. As a source of supplementation we assumed that this fish species would provide meals of at least equivalent energy return to those naturally fed to chicks at both Heron and Lord Howe Islands.

Supplementary meals averaging 31.6 g d^{-1} were fed to each experimental chick regardless of whether they had been fed the previous night by an adult. This meal size was based on previously observed average meal sizes on Heron and Lord Howe Islands (32 to 35 g, see Table 1) (Peck & Congdon 2005) and was chosen to ensure that supplemented chicks would get a significantly greater amount of food than controls without exceeding the maximum average amount a chick may receive naturally on any given night at Lord Howe Island due to feeding by 2 parents. Thawed *Sardinops sagax neopilchardus* were cut into small, digestible size pieces and hand fed to experimental chicks between 08:30 and 10:00 h daily. This timing was chosen to maximise chick hunger levels both at the time of supplementation and at the time of adult feeding. No meals were regurgitated during the course of supplementation. Chicks at the control nests were also handled and weighed during the same hours of the morning to mitigate any potential confounding effect of handling during the supplementary feeding process. To determine whether supplementation effectively increased average meal masses to levels required (i.e. exceed those observed in control nest and on Lord Howe Island), we compared total meal masses for control and supplemented chicks with Mann-Whitney *U*-tests. These tests were also used to determine whether meal masses provided by adults at supplementary nests differed to those at control nests. This test was undertaken because adults of some Procellariiform species are known to reduce meal sizes in response to improved chick condition (Granadeiro et al. 2000), a behaviour that could potentially confound our experimental design. Finally, we compared average meal sizes at Heron Island to those published for Lord Howe Island (Peck & Congdon 2005).

Chick growth rates

To obtain accurate estimates of growth and development, data gathered over the 5 to 42 d post-hatching period were used in analyses. We employed a Mann-Whitney *U*-test to determine if overall growth rates in supplemented chicks equated to levels previously observed on Lord Howe Island (Peck & Congdon 2005). Growth in Procellariiform chicks can be described by:

$$W = A/1 + e^{-k(T-T_m)} \quad (1)$$

where W is chick weight at time T , A is the asymptotic value of the curve, and T_m is the time at the point

of inflection of the curve at which the maximum growth rate, k , is achieved (Ricketts & Prince 1984, Peck & Congdon 2005). Growth data (mass and tarsus change) from each chick were fitted to this equation using non-linear least-squares regression. The k -values generated from each curve were then used as replicates in further analyses. To allow accurate comparisons of k between experimental treatments all chick growth curves were fitted to a specific pre-determined A -value. A for mass (440 g) was estimated from average maximum chick weight prior to fledging and A for tarsus (48.6 mm) was estimated from average tarsus lengths of Heron Island adults during the 2010 breeding season. t -tests analysed differences in the mean growth rate constants (k) for mass and tarsus between our supplemented and control nests using chicks as replicates (Peck & Congdon 2005).

Monitoring chick development for a longer period than the previous study (Peck & Congdon 2005) necessitated our using larger A -values for the growth rate curves in our analyses. This meant that k -values for the 2 studies were not strictly comparable. Therefore, to confirm that differences in the A -values used did not significantly affect our results, we reduced our data set to the same number of data points per chick as used by Peck & Congdon (2005), i.e. the first 20 d of the study period, and generated curves to their A -values. The resulting k -values and relative differences between treatment types and locations were not significantly different to those already presented.

Adult behavioural responses

Adult seabirds are known to respond to supplementation experiments by reducing provisioning rates to chicks (e.g. Hamer et al. 1998, Harding et al. 2002). As a consequence, supplementation may be ineffective—supplemented chicks may not receive more food than the control group, thereby confounding the experimental design. To assess adult behavioural responses to food supplementation of chicks, we compared meal masses from the entire season (maximum 35 d) between our control and supplemented nests with a Mann-Whitney U test.

Food allocation

To investigate fundamental differences in chick development patterns beyond those which could be

attributed to an absolute increase in food availability, we compared chick growth between supplemental and control nests relative to grams of food received by individual chicks. In these analyses, changes in chick mass were standardised relative to each chick's weight taken at 16:00 h. This allowed direct comparison of our results with those of Peck & Congdon (2005). Generalised linear model (GLM) analysis of covariance (ANCOVA) with a gamma distribution and log-link function was used to test if the regression slopes or intercepts for these relationships between meal mass and weight change differed significantly between treatment groups. This analysis was most appropriate as the data we obtained consistently conformed to non-normal right skewed distributions. Treatment groups (supplemented or control) and individual chicks nested within treatment groups were used as factors in all ANCOVAs. Chick mass change ($\text{g g mass}^{-1} \text{ d}^{-1}$) and change in tarsal length ($\text{mm g mass}^{-1} \text{ 3 d}^{-1}$) were the response variables, and meal mass (g d^{-1} for mass and g 3 d^{-1} for tarsal length) (including both daily supplementary feeds and nocturnal adult feeds where applicable) was the covariate in each analysis respectively. As we were particularly interested in chick growth responses to food received, only days when meal masses were greater than zero (i.e. only days on which control chicks fed) were included in the analyses. The initial analyses assume full assimilation of both natural and supplementary meals prior to chick weighing at 16:00 h. However, because mass loss rates in seabird chicks are non-linear (Ricketts & Prince 1984) and supplemented chicks had considerably shorter digestion times as a result of supplementation occurring in the morning, we also repeated these analyses after adjusting supplementary chick weights for an estimate of gut content remaining from supplementary meals. Using chick weights obtained every 2 h post feeding we estimated that on average 30% of a meal could remain in the gut of a supplementary chick after 8 h; i.e. the time between supplementation and weighing at 16:00 h (B. C. Congdon unpubl data). These 2 analyses combined give an upper and lower level for the magnitude of the effect of supplementation on chick mass at weighing. Finally, to compare food allocation between Heron Island supplemented chicks and Lord Howe Island chicks we tested for differences in average meal masses between the 2 locations using an independent sample t -test. Using ANCOVA we compared relative mass allocation per gram of food received with meal mass (g d^{-1}) using the data from Peck & Congdon (2005).

Chick condition and provisioning

The results from our analyses above and the results presented by Peck & Congdon (2005) both suggested that chick condition might influence the relative allocation of food to different growth parameters. To test for these potential effects we performed a series of analyses examining the influence of chick condition on these parameters.

We developed an index of chick body condition using the residuals from the linear relationship between chick weight and tarsus length (Cezilly et al. 1995, Congdon et al. 2005). An individual chick's deviation from this general relationship indicates whether it is above or below average body weight for its size; i.e. in relatively good or poor condition. We tested for differences in the means of these residuals between treatment groups using an independent samples *t*-test. Further ANCOVAs including condition as a covariate examined the influence of body condition on weight gain and tarsal growth in the 3 d subsequent to condition indexing. Results led to further examination of the influence of both condition and original tarsus length on tarsal growth using stepwise multiple regressions on both control and supplemented chicks separately.

Statistical analyses

All growth rate analyses were conducted using SigmaPlot Ver. 11 (Systat Software Institute). Food allocation and chick condition analyses were conducted using SPSS Ver. 19. Data were tested for normality and transformed where necessary using either log or +1 square root transformations. Means are presented as ± 1 standard error unless otherwise stated.

RESULTS

Meal sizes and feeding rates

We used the mean adult meal masses and the probability of being fed each night to calculate approximate amount of food per night received by chicks over the season (Table 1). These values were much higher than those observed in the study by Peck & Congdon (2005) (Table 1). Both supplemented and control chicks had the same chance of being fed by a parent each night ($t_{17} = -0.0565$, $p = 0.579$).

Chick growth rates

Supplemented chicks received significantly larger meals (median = 58.3 g total meal mass including parental and supplemental feeds; $n = 253$) than controls (median = 48.60 g; $n = 159$) over the study period (Mann-Whitney: $U = 16225$; $p = 0.001$). Consequently, supplemented chicks grew faster than control chicks. For example, the mean growth rate constant (k) for body mass increase was significantly greater for supplemented chicks ($k = 0.097 \pm 0.006$) than for controls ($k = 0.059 \pm 0.008$), ($t_{17} = -3.726$; $p < 0.01$). The k -values for Heron Island supplemented chicks were also similar to those previously observed for chicks on Lord Howe Island ($k = 0.09 \pm 0.004$, Table 1) (Peck & Congdon 2005). Further, both supplemented and control chicks in the present study received considerably more food than did Heron Island chicks during the study by Peck & Congdon (2005). Hence, they also showed considerably higher growth rates than those recorded previously ($k = 0.03 \pm 0.02$, Table 1). Mean growth rate constants (k) for tarsus were also significantly higher in supplemented chicks ($k = 0.069 \pm 0.0027$) than in controls ($k = 0.059 \pm 0.0029$) ($t_{17} = -2.609$; $p < 0.05$).

Table 1. *Puffinus pacificus*. Provisioning parameters (mean \pm SE) of wedge-tailed shearwaters from the present study, compared directly with those obtained by Peck & Congdon (2005). Mean meal masses exclude supplementary meals; 2010 nightly meals are calculated by multiplying meal mass by probability of feed

	Mean adult meal mass (g)	Adult meal mass (g night ⁻¹)	Probability of feed (night ⁻¹)	Growth rate constant for mass (k)
Lord Howe Island (Peck & Congdon 2005)	35.01 \pm 1.34	14.43 \pm 1.13	0.37 \pm 0.02	0.09 \pm 0.004
Heron Island (Peck & Congdon 2005)	32.65 \pm 1.80	7.40 \pm 0.69	0.21 \pm 0.01	0.03 \pm 0.02
Heron Island (2010)				
Supplemented	39.30 \pm 1.87	21.02	0.535 \pm 0.046	0.097 \pm 0.006
Control	46.85 \pm 1.64	26.80	0.572 \pm 0.045	0.059 \pm 0.008

Adult behavioural responses

Average meal masses received from parents by supplemented chicks, excluding supplementary additions (median 41.55 g, $n = 170$), were significantly less than those received by controls (median 49.45 g, $n = 160$) (Mann-Whitney: $U = 10839.50$, $p = 0.001$) (Table 1). This means that supplementation effectively added an average of 23.6 g d^{-1} to the food intake of supplemented chicks but the exact amount these chicks received daily varied according to adult provisioning. Nevertheless, this result confirms that adult shearwaters did not confound the supplementation with an equivalent reduction in meal masses.

Food allocation

While differences in the absolute amount of food received by chicks in each treatment resulted in different absolute growth rates, we wanted to determine whether supplementation also changed the proportion of food allocated to different components of growth. Chick mass change was positively correlated with quantity of food received (meal mass) for both supplemented and control chicks (Fig. 1a, ANCOVA: Wald $\chi^2_{1,368} = 131.267$, $p < 0.0001$). However, the interaction between treatment and meal mass in this analysis was also significant (Fig. 1a, Wald $\chi^2_{1,368} = 6.833$, $p < 0.01$), indicating that supplemented chicks ($r^2 = 0.204$) put increasingly less of each gram of food received into mass accumulation compared to controls ($r^2 = 0.310$) as meal size increased. There was no difference among chicks (nested within supplemented or control categories; ANCOVA: Wald $\chi^2_{17,368} = 18.566$, $p = 0.354$), nor any interaction between chicks and meal masses (ANCOVA: Wald $\chi^2_{17,368} = 11.011$, $p = 0.856$).

To account for the possibility that some portion of the supplementary meal could have remained as gut content at the time measurements were taken, we repeated this analysis after adjusting chick mass change for the average potential amount of residual supplementary food that could have been present. The results of this second analysis did not differ from those already presented; i.e. chick mass change was positively correlated with quantity of food received (meal mass) for both supplemented and control chicks (Wald $\chi^2_{1,368} = 136.557$, $p < 0.0001$). Supplemented chicks ($r^2 = 0.218$) put increasingly less of each gram of food received into mass accumulation than controls ($r^2 = 0.314$) with increasing meal size (Wald $\chi^2_{1,368} = 6.368$, $p < 0.05$). Similarly, there were no differences

among chicks (nested within supplemented or control categories; ANCOVA: Wald $\chi^2_{17,368} = 14.731$, $p = 0.615$), nor any interaction between chicks and meal masses (ANCOVA: Wald $\chi^2_{17,368} = 19.573$, $p = 0.297$).

We also directly compared changes in chick growth per gram of food received between Lord Howe Island chicks and the Heron Island supplemented chicks. Heron Island supplemented chicks received larger average meals than chicks at Lord Howe Island ($t_{545} = -7.691$, $p < 0.0001$), and as a consequence were in the same (but not better) physical condition (Fig. 2, $\chi^2_{1,544} = 117.459$, $p < 0.0001$). In addition, an interaction between location and meal mass in the ANCOVA showed that Heron Island supplemented chicks ($r^2 = 0.15$) allocated significantly less food (per gram received) to mass stores than chicks on Lord Howe Island ($r^2 = 0.21$) (Fig. 2, Wald $\chi^2_{1,544} = 6.521$, $p < 0.05$).

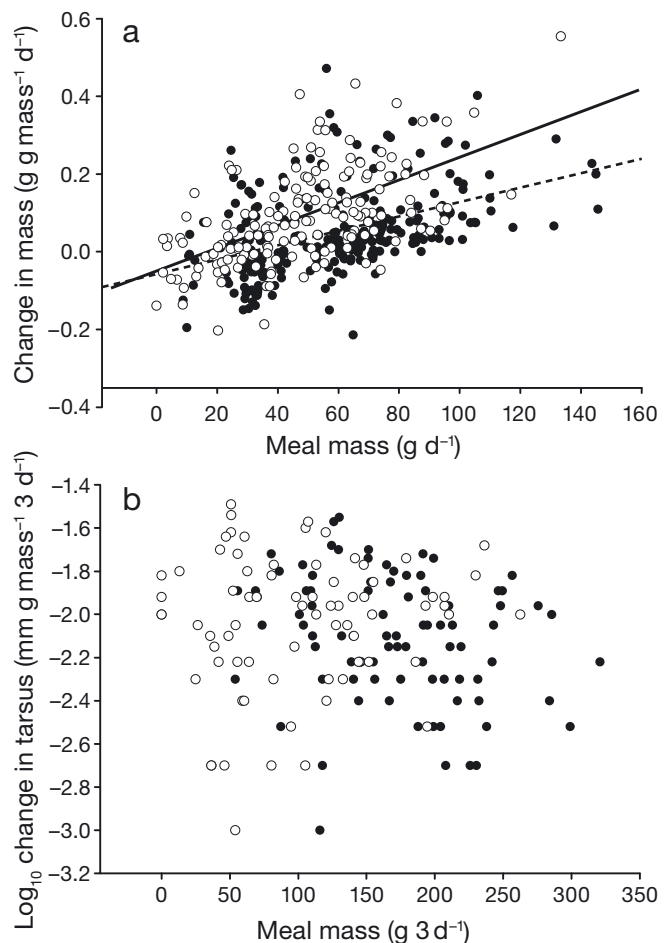


Fig. 1. *Puffinus pacificus*. (a) Relative change in chick mass in relation to meal mass and (b) tarsal length in relation to meal mass. Control chicks are represented by (o) and solid regression line, supplemented chicks by (●) and dashed regression line

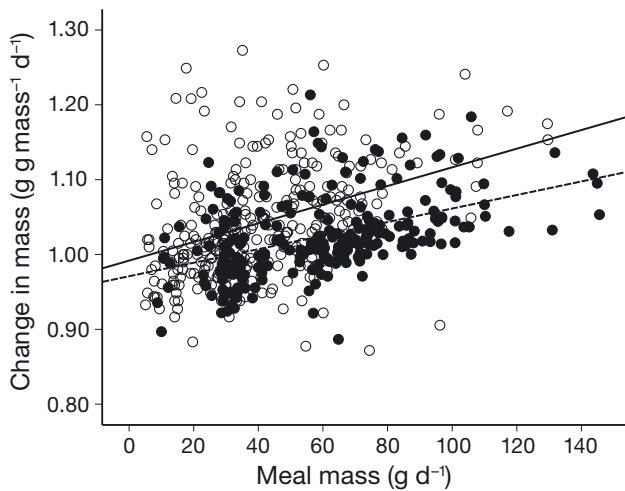


Fig. 2. *Puffinus pacificus*. Inter-island comparison of relative change in chick mass in relation to meal mass. Heron Island supplemented chicks (2010 study) (●; dashed regression line) and Lord Howe Island chicks (Peck & Congdon 2005) (○; solid regression line)

In contrast, for Heron Island chicks no significant relationships were observed between rate of tarsal development and treatment type (Wald $\chi^2_{1,157} = 1.379$, $p = 0.240$), meal mass (Wald $\chi^2_{1,157} = 0.087$, $p = 0.768$) and/or individual chicks (nested within supplemented or control categories) (Wald $\chi^2_{1,17} = 18.566$, $p = 0.354$), nor any interactions among these variables (Treatment/Meal mass: Wald $\chi^2_{1,157} = 3.537$, $p = 0.060$) (Chick/Meal mass: Wald $\chi^2_{1,17} = 11.011$, $p = 0.856$) (Fig. 1b). This implies that there was no difference in the relative amount of food Heron Island chicks of either treatment allocated to tarsal growth.

Chick condition

A significant positive relationship was observed between tarsus length and chick mass (Fig. 3, Linear: $F_{1,206} = 560.823$, adj. $r^2 = 0.73$, $p < 0.001$) with the residuals from this analysis providing an index of chick condition. Supplemented chicks were generally heavy (or in relatively good condition) for their size, while control chicks were in general relatively light (or in poor condition). A comparison of means confirmed that on average supplemented chicks were in significantly better condition (mean 0.752 ± 0.122) than controls (mean -0.860 ± 0.152). Regardless of treatment type (supplemented or control) chicks in poorer condition always gained significantly more weight at the next feed than those in better condition (Fig. 4, Wald $\chi^2_{1,17} = 50.129$, adj. $r^2 =$

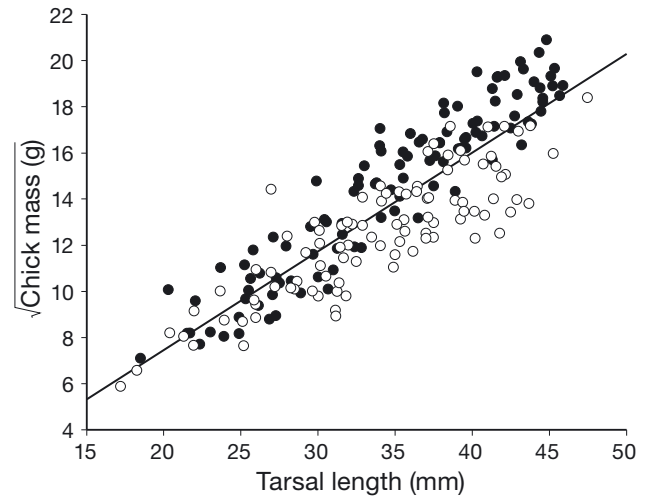


Fig. 3. *Puffinus pacificus*. Chick physical condition: relationship between chick mass and tarsal length, for control chicks (○) and supplemented chicks (●). The generated regression line represents an expectation of weight for size or an index for chick body condition

0.111 , $p < 0.001$). In addition, supplemented chicks ($r^2 = 0.128$) always gained more weight at a given level of condition than did controls ($r^2 = 0.08$) (Wald $\chi^2_{1,17} = 19.483$, $p < 0.001$), with this result likely being a direct consequence of the supplementation. Finally, a significant effect of chicks nested within the control treatment (but not the supplemental treatment) was observed (Fig. 4, Wald $\chi^2_{1,8} = 26.650$, $p < 0.01$; Wald $\chi^2_{1,9} = 14.906$, $p = 0.094$, respectively), indicating that some control chicks were in consistently better condition than others.

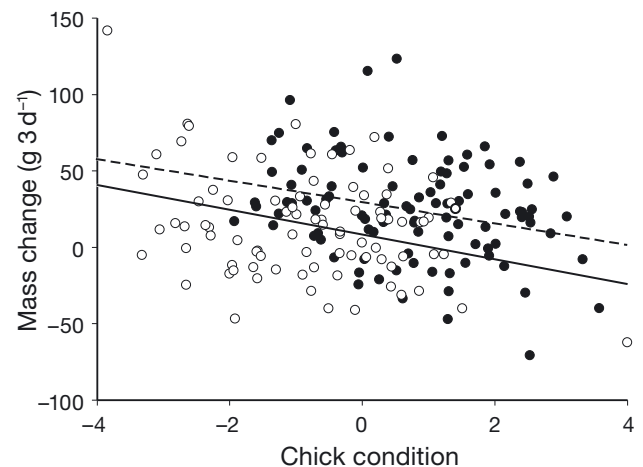


Fig. 4. *Puffinus pacificus*. Relationship between chick body condition and mass change over the 3 d following condition indexing: control chicks (○; solid regression line), supplemented chicks (●; dashed regression line)

ANCOVA comparing tarsus growth in the 3 d following condition indexing showed an effect of treatment (Fig. 5, Wald $\chi^2_{1,17} = 5.108$, adj. $r^2 = 0.194$, $p < 0.05$) and condition (Wald $\chi^2_{1,17} = 16.899$, adj. $r^2 = 0.045$, $p < 0.001$) and an interaction effect between these 2 terms (Wald $\chi^2_{1,17} = 4.899$, $p < 0.05$). The fact that this interaction was significant led to further analyses examining the supplemented and control treatment groups independently. Stepwise multiple regressions demonstrated that when control chicks attained good condition their tarsal growth increased significantly (Fig. 5, $F_{1,86} = 22.492$, adj. $r^2 = 0.198$, $p < 0.001$). In contrast, supplemented chicks did not show any variation in rate of tarsus growth with differences in initial body condition ($F_{1,99} = 2.309$, $r^2 =$

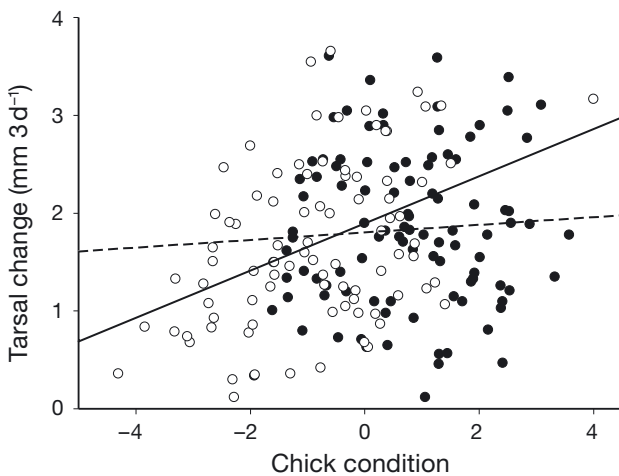


Fig. 5. *Puffinus pacificus*. Relationship between chick body condition and tarsal growth over the 3 d following condition indexing: control chicks (○; solid regression line), supplemented chicks (●; dashed regression line)

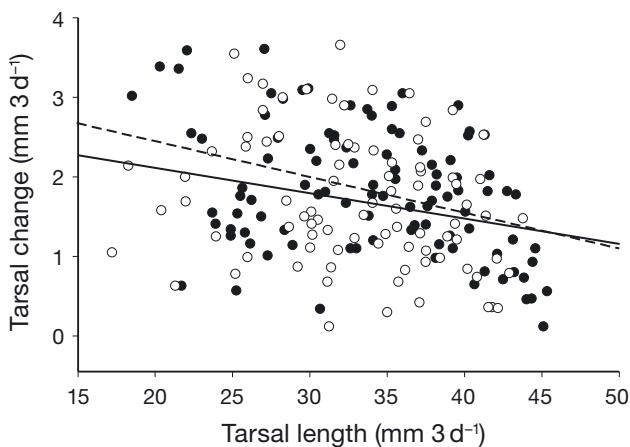


Fig. 6. *Puffinus pacificus*. Change in chick tarsal lengths over the 3 d subsequent to tarsal measurement, relative to initial tarsal length: control chicks (○; solid regression line), supplemented chicks (●; dashed regression line)

0.01, $p = 0.132$). However, it must be noted that supplemented chicks were in consistently good condition. On testing the combined influence of initial tarsus length on tarsal growth over the 3 d following each tarsus/body condition measurement, we found that absolute tarsus length was negatively related to tarsal growth over the subsequent 3 d (Fig. 6, ANCOVA: Wald $\chi^2_{1,189} = 15.882$, $p < 0.001$). There was no difference among treatment groups.

DISCUSSION

Relative mass accumulation and chick condition

Wedge-tailed shearwater chicks at Heron Island significantly reduced the proportion of food allocated to body mass as their body reserves increased. Therefore, changes in the relative amount of food allocated to this component of growth occur as a facultative response to overall body condition. This pattern of allocation suggests that shearwater chicks at Heron Island have a maximum level of body mass accumulation that they can attain at any particular stage of development and that as this level is approached, additional food is either reallocated into unmeasured parameters of growth (i.e. wing/feather development), to additional metabolic costs, or perhaps 'wasted' via defecation. We cannot conclusively identify the fate of additional food, but based on the available literature we believe it most likely that (1) growth is ontogenetically determined, (2) chicks are constrained by some assimilatory capacity (Weimerskirch et al. 2000, Benowitz-Fredericks et al. 2006) and (3) the most likely consequence of this apparent inability to take advantage of food supplementation is increased defecation.

In the previous comparative study by Peck & Congdon (2005), Lord Howe Island chicks that received significantly more food and were in better condition also allocated relatively less to mass storage than did Heron Island chicks. Therefore, our supplementation experiment suggests that the inter-island differences observed in that study likely result from the same facultative ability of chicks to shift allocation in response to their existing level of body reserves and not to a colony-specific difference in the amount of food that is consistently allocated to different components of growth, as was previously suggested (Peck & Congdon 2005).

However, we also found that despite supplemented chicks being in equivalent physical condition (i.e. had similar body reserves for their size) to Lord Howe

Island chicks (Peck & Congdon 2005), their allocation to mass at any particular stage of development was lower than for chicks at Lord Howe Island. This suggests that while chicks at both locations have the ability to change the amount they allocate to body mass in response to current reserves, chicks in each population have a different potential maximum allocation at each stage of development. Unfortunately, this possibility cannot be unequivocally verified without undertaking a similar supplementation experiment at Lord Howe Island.

Relative tarsal growth and chick condition

Based on the model presented by Peck & Congdon (2005), we expected that if the relative allocation of food to one growth parameter (mass) was facultative, then allocations to other growth parameters (i.e. tarsus) would also vary in response to changing body reserves. Specifically, supplementary chicks at Heron Island would show an increase in the amount of food allocated to tarsal growth relative to control chicks. However, regardless of level of food intake, chick condition, or the relative amount of food being allocated to mass, we observed no change in the relative allocation to tarsal growth between supplemented and control chicks. This suggests that the allocation to tarsal growth is a fixed characteristic in this and likely other shearwater populations. Our data also demonstrate that the relative amount of food being allocated to tarsal growth in supplemented chicks on Heron Island differed to that observed on Lord Howe Island (Peck & Congdon 2005). Assuming allocations on Lord Howe Island are also fixed, this suggests that tarsal growth patterns are specific to each colony and divergent between colonies.

Colony-specific divergence in growth

Our findings suggest that the 2 wedge-tailed shearwater colonies examined each have specific patterns of growth and development. Although it remains unclear whether patterns of mass accumulation differ under equivalent levels of provisioning, we have shown that they differ for chicks of equivalent body condition. Our results also confirm that patterns of food allocation to tarsal development are different between colonies and that this growth parameter does not respond to short-term variations in food availability.

So, where do such colony-specific differences originate and how are they maintained? The first possibility is that differences in provisioning rates or food availability between islands/seasons (2004 and 2010) are responsible. However, overall growth rates and body condition of supplemented chicks in the current study matched those previously observed on Lord Howe Island. This implies that supplementation was successful in negating any inter-island differences in development that may have occurred due to differences in total food intake, and implies that differential provisioning or variation in food availability between islands/seasons cannot be responsible.

A second possibility is that the inter-island differences we observed are due to undetected colony-specific maternal effects. Maternal stress and poor maternal condition early in the breeding season are known to translate into negative effects on egg size, which in turn impacts hatching weights, overall chick growth and ultimately fledging success (Galbraith 1988, Wagner & Williams 2007). However, eggs at Heron Island, the colony with slower growing chicks, are consistently larger than those at Lord Howe Island (Peck & Congdon 2005, Peck et al. 2006), a phenomenon that is inconsistent with previously observed maternal effects in other studies. In general, this suggests that facultative changes in female reproductive effort associated with changes in resource availability are unlikely to have caused our observed results.

A third possibility is that differences in diet composition between the 2 locations are responsible for the observed differences in chick growth. If dietary differences drive our results this implies that Heron chicks continue to receive poorer quality meals despite supplementation. We think this possibility unlikely for a number of reasons: (1) overall growth rates in supplemented chicks increased to levels equivalent to those of Lord Howe Island chicks—only relative allocations differed; (2) poor quality diet has previously only been observed to result in either increased mortality (Kitaysky et al. 2006), or reduced growth via decreased body mass or feather development (Romano et al. 2006), not in changes to the relative allocation of nutrients to different components of growth; and (3) our choice of supplementary diet specifically attempted to provide Heron Island chicks with a diet as high in lipid, energy and nutrient content as possible, the main factors considered important in influencing growth (Granadeiro et al. 2000, Benowitz-Fredericks et al. 2006).

We believe that the most likely explanation for the observed inter-island differences in chick growth are

that they are heritable characteristics that result from either genetic drift associated with natal philopatry and a lack of inter-colony movement, or selective adaptation linked to differences in local resource availability. At this time it is not possible to distinguish between these alternatives. However, previous morphological and molecular studies suggest a combination of the two is likely (Peck et al. 2008). Natal philopatry coupled with genetic drift has been invoked as the dominant paradigm driving divergence among seabird populations in a number of studies (e.g. Congdon et al. 2000, Friesen et al. 2007). Similarly, patterns of morphological and molecular variation among wedge-tailed shearwater colonies of the GBR are consistent with divergence due to philopatry and genetic drift alone (Peck et al. 2008).

However, this is not true of divergence among wedge-tailed shearwater colonies in different climatic zones with different levels of natural food availability, such as Heron and Lord Howe Islands (Peck et al. 2008). At these locations, philopatry and genetic drift alone cannot fully explain the patterns of morphological and molecular divergence observed (Peck et al. 2008): natural selection is hypothesized to be partially responsible (Peck et al. 2008). If correct, this suggests that the differences documented in this study are, at least in part, also due to selective divergence driven by long-term patterns of local food availability.

The fact that local resource availability sets an upper limit to colony-specific growth rates in wedge-tailed shearwater chicks is consistent with overall patterns of development in this and other Procellariiform species. Rapid mass accumulation combined with delayed skeletal growth is considered a mechanism that allows food-limited populations to deal with periods of starvation (Lack 1968, Ashmole 1971). As a general rule, as chicks grow larger (skeletal growth) their food requirements increase. If sudden growth surges associated with short-term food increases cause chicks to outgrow future provisioning rates, the risk of starvation is increased (Drent & Daan 1980, Ricklefs 1984, Anderson et al. 1993). This implies that chick growth should be adjusted to levels that can be supported by longer-term expectations of food availability and that developmental constraints are a functional mechanism that could assist chicks to cope with large fluctuations in food availability.

Selection has been invoked as the primary mechanism driving divergence in only one other seabird, the Madeiran storm-petrel *Oceanodroma castro* (Monteiro & Furness 1998). If selection is also a mechanism of seabird population divergence in the

present study, then our findings demonstrate that natural selection, either alone or in combination with other evolutionary processes, is an important driver of seabird diversification.

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