FEEDING STRATEGIES OF THE SHORT-TAILED SHEARWATER VARY BY YEAR AND SEA-SURFACE TEMPERATURE BUT DO NOT AFFECT BREEDING SUCCESS

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Abstract.   To understand how animals cope with environmental variability it is necessary to identify the degree of flexibility in a species' diet and foraging mode and the consequences of this flexibility for reproduction. We examined rates of feeding and energy delivery to chicks by a long-lived pelagic seabird, the Short-tailed Shearwater (*Puffinus tenuirostris*). Individual adults alternated between foraging trips of short and long duration in a dual foraging strategy, but the allocation of time on those trips varied significantly from year to year. In two years when sea-surface temperatures of feeding grounds exploited during short trips were cooler (2005, 2006) adults initially fed their chick more often, then feeding decreased through the chick-rearing period. In the following year of warmer sea-surface temperature (2007), the number of feedings per day was initially low but increased through chick rearing. Despite varied feeding patterns, breeding success was consistently high, yet in 2006 the chicks' poor condition indicates the capacity for buffering chicks from these effects was lower than in other years. The relative contribution of short and long trips to the amount of energy delivered to chicks also varied by year. During local food shortages, shearwaters appeared to deliver more oil from long trips and increased the frequency of short trips. Yet in 2006, low-calorie prey from short trips coincided with low volume of stomach oil from long trips, resulting in chicks' poorer condition. Oil volume and increased short-trip foraging provide potential mechanisms of flexibility enabling adults to buffer prey delivery to chicks during food shortages.

Key words: chick condition, feeding rate, energy flow, flexibility, sea-surface temperature.

Las Estrategias de Alimentación de *Puffinus tenuirostris* Varían según el Año y la Temperatura Superficial del Mar pero no Afectan el Éxito Reproductivo

Resumen.   Para entender como los animales hacen frente a la variabilidad ambiental es necesario identificar el grado de flexibilidad en la dieta de la especie y el modo de forrajeo y sus consecuencias para la reproducción. Examinamos las tasas de alimentación y de entrega de energía a los pichones por parte de una ave pelágica longeva, *Puffinus tenuirostris*. Los individuos adultos combinaron viajes de forrajeo de corta y larga duración en una estrategia dual de forrajeo, pero la asignación de tiempo a estos viajes varió significativamente de año a año. En dos años en los que las temperaturas de la superficie del mar de las áreas de forrajeo utilizadas durante viajes cortos fueron más frías (2005, 2006), los adultos inicialmente alimentaron a sus pichones más frecuentemente y luego la alimentación disminuyó a lo largo del periodo de cría de los pichones. En el año siguiente con una temperatura superficial del más más cálida (2007), el número de alimentaciones por día fue inicialmente bajo pero aumentó a lo largo de la cría de los pichones. A pesar de estos patrones de alimentación variados, el éxito reproductivo fue consistentemente alto, aunque en 2006 la mala condición de los pichones indicó que la capacidad de amortiguar a los pichones de estos efectos fue más baja que en otros años. La contribución relativa de los viajes cortos y largos a la cantidad de energía entregada a los pichones también varió de año en año. Durante los períodos de escasez local de alimentos, los individuos de *P. tenuirostris* parecieron entregar más aceite de los viajes largos e incrementaron la frecuencia de los viajes cortos. Aún en 2006, las presas de bajas calorías de los viajes cortos coincidieron con un bajo volumen de aceite estomacal de los viajes largos, dando como resultado pichones en peores condiciones. El volumen de aceite y el aumento de los viajes cortos de forrajeo brindan los mecanismos potenciales de flexibilidad que permiten que los adultos amortigüen la entrega de presas a los pichones durante los períodos de escasez de alimentos.

INTRODUCTION

Most seabirds are central-place foragers when rearing their chicks because they have to make trips to and from their nest to source food. The balance between food delivery to chicks and self-feeding is influenced primarily by an individual's own needs, the needs of its chick(s), and feeding conditions (Houston 1987, Ydenberg et al. 1992). Coping with varied feeding conditions requires a degree of flexibility in diet, feeding technique, feeding rate, energy-allocation patterns, daily time budgets of adults, or in chick growth (Bednekoff and Houston 1994, Furness 1996). Identifying the extent of flexibility in each of these factors, and the resultant plasticity in feeding, is essential to gauging a species' sensitivity or tolerance to environmental variation and global climate change.

Pelagic seabirds are well suited to coping with fluctuations in their food supply. They share a suite of life-history traits (long life, low fecundity, single egg, slow growth) reducing energy demands at the nest (Baduini and Hyrenbach 2003). Furthermore, the Procellariiformes (shearwaters, petrels, and albatrosses) have additional traits (stomach oil, chick obesity) enabling adults to return to the nest less frequently than most other seabirds such as terns and cormorants (Ricklefs 1990). During chick rearing, adults of some Procellariiformes (Baduini and Hyrenbach 2003), as well as some penguins (Ropert-Coudert et al. 2004) and alcids (Steen et al. 2007, Welcker et al. 2012), alternate foraging trips of short and long duration in a "dual" strategy. After short trips raw prey is delivered to the chick more frequently, and adults maximize energy delivery by fueling most if not all of their needs from stored reserves (Chaurand and Weimerskirch 1994, Tveraa et al. 1998, Weimerskirch 1998). In comparison, on long trips farther from the colony adults restore their depleted reserves (Granadeiro et al. 1998, Weimerskirch and Cherel 1998, Weimerskirch et al. 2003). Flexibility in foraging location means that adults can respond to changes in feeding conditions by using different foraging zones and exploiting different prey (Quillfeldt et al. 2010).

Studies of numerous seabirds that follow a dual strategy have demonstrated colony-wide variation in the extent of short or long trips under varied feeding conditions. Despite a changing food supply, interpreted from variable sea-surface temperatures (SST), adults of some species can maintain the chick's condition (Antarctic Prion, *Pachyptila desolata*, Weimerskirch et al. 1999; Thin-billed Prion, *Pachyptila belcheri*, Quillfeldt et al. 2007, 2010) or breeding success (Cory's Shearwater, *Calonectris diomedea*, Granadeiro et al. 1998; Yellow-nosed Albatross, *Thalassarche chlororhynchos*, Pinaud et al. 2005). This is evidence of the flexibility inherent in a dual strategy, in which adults can buffer the chick from food shortages close to the colony by foraging farther afield (Weimerskirch 2007). Further study combining measures of provisioning with energy allocation is required to identify how and why different feeding strategies are adopted. Such

an approach may reveal the trigger for alternative feeding strategies, how a balance between reproduction and survival is achieved, and the limits of a species' capacity for buffering.

We studied the number of feedings per day and energy flow (joules delivered per second) to chicks of the Short-tailed Shearwater (*Puffinus tenuirostris*) over three consecutive years to identify (1) the extent of variation in averaged feeding strategies and energy delivery; (2) how feeding conditions influenced feeding strategies and energy delivery; and (3) chick condition under varied feeding conditions (i.e., capacity for buffering). We expected that chick condition would be maintained under modest changes in feeding rate but compromised by moderate to large changes. The Short-tailed Shearwater is a wide-ranging seabird whose long trips to feeding grounds 1000–4000 km from its breeding colonies are alternated with short trips of 200 km (Einoder et al. 2011). Long trips of 7–30 days are alternated with multiple short trips of 1–3 days (Weimerskirch and Cherel 1998, Einoder et al. 2011). The colony we studied, on Althorpe Island off South Australia (35° 37′ S, 136° 86′ E), has around 20 000 breeding pairs and is located in a region where productivity available to top predators fluctuates (Ward et al. 2006). Differences in primary productivity are driven by changes in the timing and intensity of winddriven upwelling (Kämpf et al. 2004, Middleton and Bye 2007).

We did not measure prey availability directly but expected that reductions in either local or distant food supply should result in an adjustment in the number or duration of short and long trips. We tested the hypothesis that when the intensity of coastal upwelling increases (cooler SST), adults should increase short-trip foraging to maximize feeding rate. Conversely, when the intensity of coastal upwelling decreases (warmer SST) the number of feedings per day should decrease and the importance of meals returned from long trips should increase. A high level of energy in food delivered from long trips should provide evidence of adults attempting to buffer chicks from locally poor feeding conditions.

MATERIALS AND METHODS

STUDY AREA AND BREEDING CHRONOLOGY

At Althorpe Island, we monitored the rates at which chicks were fed on a daily basis. We classified all data collected during the 90-day chick-rearing period (January–April) into three groups of 30 days to highlight changes within and between years (following Quillfeldt 2001). Laying and hatching within Short-tailed Shearwater colonies is highly synchronous, occurring within a 10-day window (Wooller et al. 1990). We defined early chick rearing as the first 30 days from the first chicks' hatching (average 11 Jan, range 9 Jan 2005, 13 Jan 2006, 12 Jan 2007), including the chick-brooding period and the early growth stage. The middle phase, from 10 Feb to 11 Mar, was the phase of rapid growth and peak mass. Late chick rearing, from 12 Mar to 10 Apr, encompassed

growth of the juvenile plumage and loss of down and the onset of adults' abandonment prior to the chicks' fledging.

MEASURES OF FEEDING

Field technicians monitoring the nest attendance of marked adults in 25 burrows each year recorded feeding rate (number of feedings per day), the duration of short and long trips, and the number of successive short trips an adult made between two long trips. Each member of a breeding pair was captured during incubation and marked with a numbered leg band and a subcutaneous microchip (Aleis, Jandowae, Qld., Australia) for radio identification on the top of the back between the wings. To identify marked adults, we read the microchips with a 2-m wand, precluding the need for recapture. Adults return to the colony only at night, and beyond the brooding period of 2–8 days the chick is left unattended during the daytime while both adults forage. Arrival time at the nest was recorded when an adult knocked down a stick at the burrow entrance, triggering a red light-emitting diode (Baduini 2002). Simultaneous attendance by both adults was identified by retriggering of the reset diode and a positive scan of the partner's microchip, or by double feeding of the chick (feedings over 120 g, determined by weighing chicks after they were fed; Hamer et al. 1997). We calculated the average number of feedings per day for each 30-day stage across all 25 chicks each year. Adults typically departed the colony soon after feeding their chick, so the time elapsed between two arrivals at the nest represented the duration of an individual foraging trip (in days). We classified foraging trips as either short (1 to 3 days) or long (>7 days) because no trips of 4–6 days were recorded (Weimerskirch and Cherel 1998). For all analyses we present standard errors unless otherwise specified.

FEEDING CONDITIONS

We also collected diet samples and assessed their energy density to calculate energy flow from foraging trips, defined as the average quantity of energy delivered to the chick per unit of time in watts (joules delivered per second). Estimates of average energy flow from short and long trips for each chick-rearing stage (early, mid, late) first involved deriving the energy density of meals, the mass of a diet sample multiplied by the calorific value of prey it contained. To calculate energy flow, we divided this energy density by the average duration of short and long trips for each chick-rearing stage (from 25 monitored burrows) and multiplied the result by two (because both parents feed each chick) (Chaurand and Weimerskirch 1994). Diet samples were collected outside the main study area from adults that were not attending chicks in the 25 study burrows. We assumed the composition of prey and mass of stomach contents to represent that delivered to study burrows. We captured adults before they provisioned their chicks and used the water off-loading technique (Wilson 1984) to collect diet samples. The numbers of short-trip samples containing prey items for the early, mid, and late stages were 0, 23, and

26 in 2005, 23, 27, and 18 in 2006, and 38, 12, and 37 in 2007, respectively. The number of long-trip samples containing prey items for the early, mid, and late stages were 0, 3, and 19 in 2005, 14, 18, and 15 in 2006, and 13, 17, and 21 in 2007. We assume that the whole stomach content is fed to the chick and that we collected the entire stomach contents. After diet samples were collected they were frozen at –18 °C in vials for up to 6 months prior to analysis.

Once defrosted, stomach oil from samples was poured into a graduated cylinder for measurement of volume (±1 mL), and mass (±0.001 g). The remaining liquid and solid was separated by gravity over a 0.25-mm sieve, and solids were weighed on an electronic balance (±0.001 g). The mass of stomach oil was added to the wet weight of the solid fraction. Hard and soft parts were sorted and identified under a dissecting microscope. We counted the number of right and left otoliths (fish), upper and lower beaks (squid), or pairs of eyes (crustaceans) of each taxon to estimate the minimum number of individuals (Hull 1999), identifying the prey with reference to collections and Lu and Ickeringill (2002; cephalopods), Ritz et al. (2003; crustaceans), and Williams and McEldowney (1991; bony fishes). Otoliths that could not be identified, or samples containing other hard parts of fish but no otoliths, were recorded as "unidentified fish." To estimate the percentage contribution to total mass we multiplied the percentage of each prey by the total mass of the stomach contents (Duffy and Jackson 1986). We measured the calorific value of the major prey types and stomach oil by blending (whole fish), drying, pulverizing and combusting raw prey in a bomb calorimeter, following Tierney et al. (2002). We estimated the total energy density of each diet sample by multiplying the proportionate wet mass of each prey by the calorific value of that prey type (Chaurand and Weimerskirch 1994).

CHICK CONDITION AND BREEDING SUCCESS

We recorded breeding success (fledged chicks per pair of adults) and body condition of chicks (age 70–80 days) at the same 25 burrows where we monitored feeding by adults. Chicks were weighed at the start of every night at 20:00 with a spring balance (1000 ± 5 g). We regressed the body mass of chicks the night after their last feeding against chick age and derived a body-condition index from the residual of each chick's body mass, expressed as a proportion of predicted body mass from a control group of chicks of the same age (Granadeiro et al. 2000). We monitored a control group of ~100 burrows three times each season to identify eggs (November), newly hatched chicks (January), and the survival and condition of chicks at 70–80 days of age (April). Comparison with the control group was intended to reveal whether there was any effect of this study on the condition of chicks or the breeding success of adults.

SEA-SURFACE TEMPERATURE

A concurrent satellite-tracking study identified the primary foraging area of Short-tailed Shearwaters making short trips from

the study colony (Einoder et al. 2011). All foraging occurred within a 1 square degree (35.4–36.4° S, 135.5–136.5° W) directly southwest of the colony, so we downloaded from IMOS (http://imos.aodn.org.au/webportal/) 8-day averages of SST (ºC) measured by MODIS satellites at a resolution of 4 km. We used 8-day averaged to overcome the lack of data on cloudy days and subsequent issues with SST calculations. We calculated weekly SST anomalies by subtracting the current weekly value from the 15-year (1995–2010) mean for that week.

STATISTICAL ANALYSIS

We compared normally distributed data on feeding rate by year with the unequal-variance t-test (i.e., Welch's t-test), which performs better than both the equal-variance t-test and the Mann–Whitney test (see Ruxton 2006). Intra-annual feeding-rate data, not distributed normally, we examined with Mann–Whitney tests. We compared the frequency of short trips (number of short trips between two long trips) per year by logarithmic transformation of non-normal data, then applying t-tests. Neither trip-duration nor energy-flow data were normally distributed, so we used Mann–Whitney tests for comparisons of inter-annual variation. We compared the oil content of stomach contents from long-trip feedings by year with t-tests or Mann–Whitney tests depending on whether the data were normally distributed. The relationship between oil volume and duration of long trips was assessed with Pearson's correlation coefficients. Relationships between the frequency of short trips and the SST anomaly were assessed with Kendall's tau correlation coefficients. Inter-year comparisons of chick condition involved Kruskal–Wallis χ^2 approximations, while χ^2 tests of breeding-success data were used to test for differences between proportions. For all statistics we used R version 2.13.1. Throughout this paper we report mean values ± 1 SE.

RESULTS

VARIATION IN FEEDING STRATEGIES AND ENERGY DELIVERY

In two successive years the pattern of feeding with chick age varied widely. In 2006 number of feedings per day was highest in early chick rearing (0.49 ± 0.02), decreasing by 51% in late chick rearing (0.25 ± 0.04) (Fig. 1; Welch's t (one-tailed) = 5.0, df = 57, $P < 0.001$). In 2007 the pattern reversed: the rate of food delivery was low initially, then increased 130% by late chick rearing (Fig. 1; Welch's t [one-tailed] = 2.5, df = 37, $P = 0.02$). As a result, in early 2007 chicks were fed at half the rate of 2006 ($U = 689.5$, $P < 0.001$), but by late chick rearing the rate was higher in 2007 than 2006 (Welch's t [one-tailed] = 2.0, df = 49, $P = 0.03$, Fig. 1). In 2005, the number of feedings per day in early chick rearing was not calculated, but the pattern in the remainder of the season followed that of 2006 (Fig. 1).
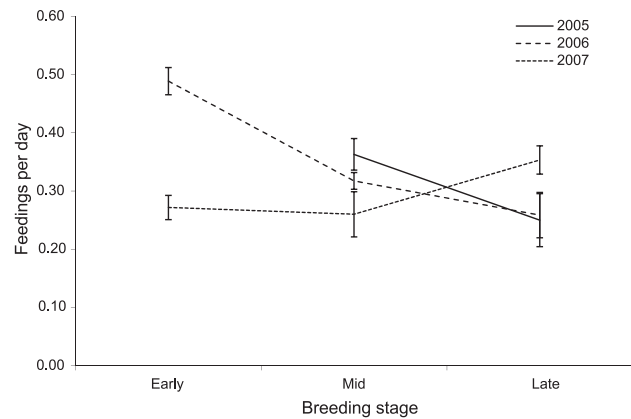

FIGURE 1.   Variation by year in the number of feedings per day by Short-tailed Shearwaters through three stages of chick rearing, 2005–2007.

All individuals alternated between short and long trips, and variation in feeding rates from year to year was attributable to the changes in the number, sequence, and duration of those trips. The low feeding rate in early 2007 was due to lower number of successive short trips performed between two long trips, with one fewer short trip per session than in 2006 (Table 1). Also, in early 2007, short trips were significantly longer than in 2006 (Table 1). The lack of measurements during the early breeding period in 2005 precludes any comparisons. In late chick rearing annual variation in the number of feedings per day was again attributable to the number of short trips, with significantly more short trips performed between two long trips in 2007 than in other years and significantly shorter long trips in 2007 than in 2006 but not 2005 (Table 1).

CHICK CONDITION UNDER VARIED FEEDING CONDITIONS

The feeding pattern of 2005 and 2006—feeding rate decreasing with chick age—occurred when local SST was cooler than average (Fig. 2). Waters were cooler than average through most of chick rearing in 2005 (February–March) and in the first half of chick rearing in 2006 (Fig. 2). In contrast, the alternative feeding pattern of 2007 coincided with SST warmer than average (Fig. 2). The SST anomaly was significantly correlated with the number of successive short trips performed between weeks in 2006, indicating a boost in short trips and subsequent feeding rate when local waters were cooler, a decrease when they were warmer (Fig. 3; $R^2 = -0.74$, $n = 8$, $P = 0.03$). No significant relationships between short-trip foraging and the SST anomaly were detected in other years (2005: $R^2 = -0.25$, $n = 6$, $P = 0.64$, 2007: $R^2 = -0.69$, $n = 6$, $P = 0.13$). Yet in the warm conditions of early 2007 the shearwaters made fewer short trips (Fig. 2, Table 1). Also at this time the short trips were significantly longer (Table 1), contributing to the reduced feeding rate (Fig. 1).

Fish dominated the prey from short trips in 2005, krill dominated in 2006, and 2007 saw a shift from mixed fish/krill/

TABLE 1. Comparison of short and long trips of foraging Short-tailed Shearwaters during early, mid and late stages of chick rearing, by year, showing mean, standard error, and sample size (in parentheses). Short-trip frequency is the number of short trips performed between two long trips. *denotes low sample size of only three diet samples. Values by year compared with Wald's t-test (t), and Mann–Whitney tests (U).

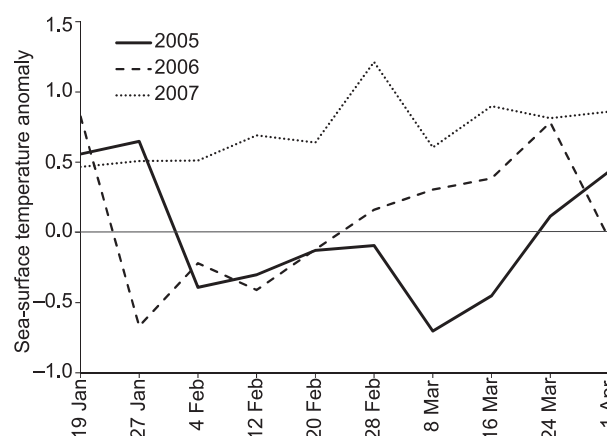| Stage and year	Short trips			Long trips		Test	Short-trip frequency		Short-trip duration		Long-trip duration	
	Frequency	Duration (days)	Mass (g)	Duration (days)	Mass (g)		t	P	U	P	U	P
Early												
2006	3.3 ± 0.2	1.11 ± 0.37 (130)	27.3 ± 5.5	11.3 ± 0.3 (48)	39.8 ± 6.5	2006 vs. 2007	3.69	<0.001	3008	0.004	407.5	0.073
2007	2.0 ± 0.2	1.22 ± 0.03 (180)	41.4 ± 13.6	12.5 ± 0.5 (25)	74.4 ± 24.6							
Mid												
2005	1.4 ± 0.1	1.18 ± 0.04 (111)	44.5 ± 6.2	11.4 ± 0.5 (27)	*55.1 ± 14.1	vs. 2007	3.57	0.001	1169	NS	64	0.036
2006	2.3 ± 2.1	1.07 ± 0.02 (86)	42.2 ± 10.7	13.6 ± 0.3 (82)	63.7 ± 6.5	vs. 2005	6.24	<0.001	16599	0.005	1057	<0.001
2007	2.3 ± 0.2	1.10 ± 0.09 (66)	31.3 ± 5.4	15.1 ± 0.6 (20)	89.9 ± 9.4	vs. 2006	0.51	NS	2612	NS	584	NS
Late												
2005	1.1 ± 0.2	1.09 ± 0.28 (36)	55.1 ± 4.8	13.9 ± 0.7 (56)	65.0 ± 8.3	vs. 2007	2.24	0.031	696	NS	900	NS
2006	1.3 ± 1.0	1.15 ± 0.42 (175)	70.1 ± 14.0	16.8 ± 0.6 (31)	75.4 ± 8.3	vs. 2005	0.47	NS	690	NS	1107	0.033
2007	2.0 ± 0.2	1.26 ± 0.08 (40)	86.0 ± 7.5	13.1 ± 0.7 (11)	89.7 ± 3.7	vs. 2006	2.2	0.035	853	NS	1110	0.013

FIGURE 2. Weekly sea-surface temperature anomaly based on the 15-yr mean (1995–2010) in the zone of ocean where Short-tailed Shearwaters nesting on Althorpe I. made short foraging trips (35.4–36.4° S, 135.5–136.5° W) during chick rearing, 2005–2007.

cephalopod to fish in late chick rearing (Fig. 4). These dietary changes had major implications for energy flow (joules delivered per second), as krill and cephalopod are of lower calorific value than pelagic fish (Table 2). For example, although the masses of short-trip feedings in mid-2005 and 2006 were similar, in 2006 low-calorie krill reduced energy flow from its value in 2005, when the birds returned with higher-calorie fish (Table 1, Fig. 5). Also, despite longer short trips in early 2007, energy flow that year was comparable to that in early 2006, when trips were shorter. Similar energy flow was attributable to the return of larger feedings containing higher-calorie fish in 2007 (Table 1, Fig. 4). High fish content and large feedings also contributed to high energy flow in late 2007 (Table 1, Fig. 4).

Mean energy flow (joules delivered per second) from both parents from short trips ranged between 2.3 and 7.3 W
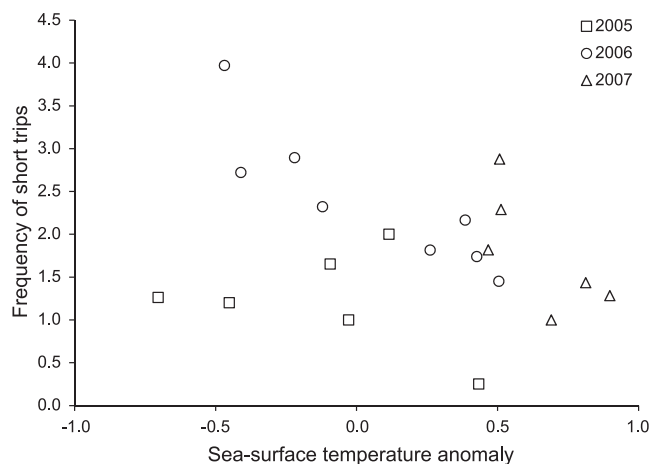

FIGURE 3. Frequency of short trips (number of successive short trips between two long trips) by Short-tailed Shearwaters versus weekly sea-surface temperature anomalies over three breeding seasons. The anomalies were based on values at 35.4–36.4° S, 135.5–136.5° E. A value of zero represents a long trip followed immediately by another long trip.

(mean 4.8 W) and between 1.3 and 3.8 W (mean 2.4 W) from long trips (Fig. 5). Individual variation was extensive, reflected by the wide standard error (Fig. 5). Average energy flow achieved on long trips was commonly 30–60% that of short trips, except in mid-2007 when the value for long trips exceeded that for short trips (Fig. 5). Across years there was no consistent pattern in long-trip energy flow with chick age, as it was stable through 2006, decreased through 2005, and increased significantly through 2007 (Fig. 5). In contrast, short-trip energy flow consistently increased with chick age in all years, significantly so in 2006 and 2007 but not in 2005 (Fig. 5, Table 3).

The pattern of a high initial number of feedings per day decreasing with the chick's age (2005 and 2006) did not present any advantages over the alternative strategy (2007), as breeding success was comparably high in all three years (chicks per breeding pair: 2005 = 0.88; 2006 = 0.80; 2007 = 0.88, Kruskal–Wallis χ^2_{72} = 0.34, df = 2, P = 0.84). Also, breeding success did not significantly differ from that of the control group in any of the three years (chicks per breeding control pair: 2005 = 0.80; 2006 = 0.76; 2007 = 0.82). The alternative strategy of 2007 saw chicks reared to the best condition of any year (mean body-condition index = 0.22 ± 0.06), comparable to the good condition attained in 2005 (mean body-condition index = 0.10 ± 0.03). In contrast, in 2006, a year of more short trips, chicks' condition was poorer (mean body-condition index = –0.17 ± 0.05, Kruskal-Wallis χ^2_{72} = 8.59, df = 2, P = 0.014).
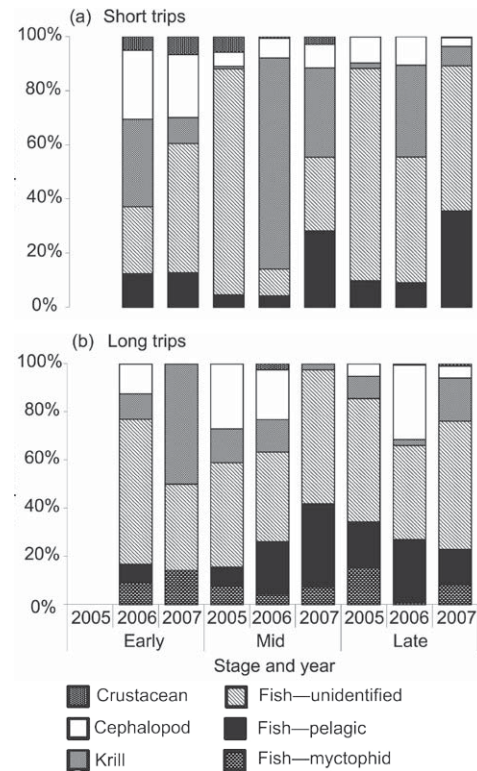

FIGURE 4.   Seasonal and annual variation in prey composition (% biomass) of major prey types in feedings following short and long trips. Asterisk (*) denotes a low sample size of only three diet samples.

TABLE 2.   Mean (± SD) calorific content (kJ g⁻¹ wet weight) of the major prey types and species in the diet of Short-tailed Shearwaters at Althorpe I.

Prey type and species name	Common name	Age	n	Source[a]	Calorific value (kJ g⁻¹)	Mean
Pelagic fish						
Engraulis australis	Anchovy	subadult	7	raw	5.47	4.68 ± 0.73
		juvenile	31	raw	5.12	
Sardinops sagax	Pilchard	subadult	7	raw	4.08	
Trachurus declivis	Jack mackerel	juvenile	4	raw	4.04	
Myctophid fish					8.88[b]	
Cephalopod						
Sepioteuthis australis	Southern calamari	juvenile	3	stomach	2.75[c]	3.20 ± 0.64
Notodarus gouldi	Arrow squid	juvenile	2	stomach	3.65	
Crustacean						
Brachyura sp.	Megalopa	larvae	80	stomach	2.67	3.00 ± 0.47
Nyctiphanes australis	Australian krill	adult	1200	stomach	3.33	
Stomach oil			10[d]	stomach	41.81	41.81 ± 3.44

[a]Raw, caught directly in a net; stomach, retrieved from a fresh (largely undigested) sample from the stomach of an adult returning to the colony.
[b]From Tierney et al. (2002).
[c]From A. Wiebkin (unpubl. data).
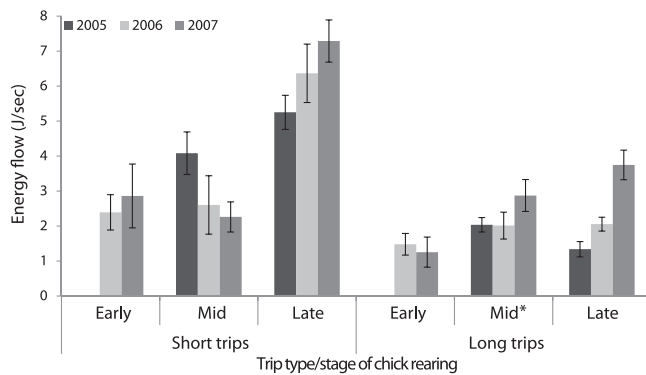[d]Number of samples of collected stomach oil analyzed.

FIGURE 5. Energy flow (watts, joules delivered per second) from short and long trips (oil component included) during rearing of Short-tailed Shearwater chicks over three years at Althorpe I. Asterisk (*) denotes low sample size of only three diet samples.
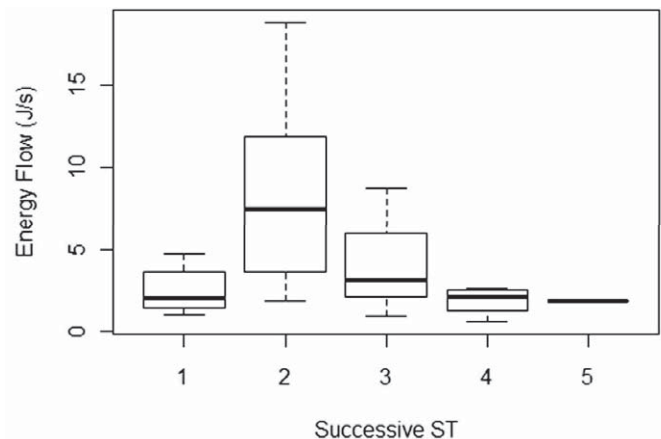
FIGURE 6. Energy flow (watts, joules delivered per second) a Short-tailed Shearwater delivered to its chick after the first to fifth short trips of a succession of short trips between two long trips. Box plot shows the median, 25th and 75th percentiles (edges of box), and entire spread of data (maximum and minimum). Diet samples were not collected from the same individual twice. Numbers of individuals sampled on their first to fifth successive short trips are 8, 11, 5, 4, and 1, respectively.

Where diet samples were collected from successive short trips (up to the 5th in succession) ($n = 30$, pooled years, mid-chick rearing) energy flow was relatively low on the first trip, highest on the second, and low on the third and subsequent trips (Fig. 6).

When adults returned from long trips, their volume of stomach oil was variable (Fig. 7), and this variation strongly influenced the energy density of feedings. At 42 kJ g^{-1} oil has approximately 10 times the calorific value of pelagic fish and 13 times that of krill (Table 2). Oil contributed to energy flow being elevated in late 2007, when its volume was significantly greater than in other years (2005 vs. 2007: $U = 12$, $P < 0.001$; 2006 vs. 2007: $U = 93$, $P < 0.001$, Fig. 7). For a subset of long-trip feedings ($n = 30$, pooled years, mid-chick rearing), time away from the colony was not related to overall energy density ($R^2 = 0.19$, df = 29, $P = 0.35$) or to the volume of oil returned ($R^2 = -0.23$, df = 29, $P = 0.30$). Heavily digested myctophid fish occurred in most long-trip feedings (Fig. 4), and their energy density was higher than that of pelagic prey (Table 2). Pelagic prey constituted the raw component of long-trip feeds, and its composition differed widely from that of short-trip feedings (Fig. 4).

DISCUSSION

We extend previous reports of annual variability in the Short-tailed Shearwater's rate of feeding (Schultz and Klomp 2000) by identifying the elements of the feeding strategy responsible for this variation. The most effective way for the birds to adjust the number of feedings per day was to alter at the number of short trips between two consecutive long trips, as do Cory's Shearwater (Paiva et al. 2010) and the Thin-billed Prion (Duriez et al. 2000). In contrast, a study of the Antarctic Prion (Weimerskirch et al. 1999) and a second study of the Thin-billed Prion (Quillfeldt et al. 2010) found that altering the duration of long trips was the primary means of modifying number of feedings per day. The disparity in energy flow between short and long trips that we observed (4.8 vs. 2.4 W) is similar to previous estimates for the Short-tailed Shearwater
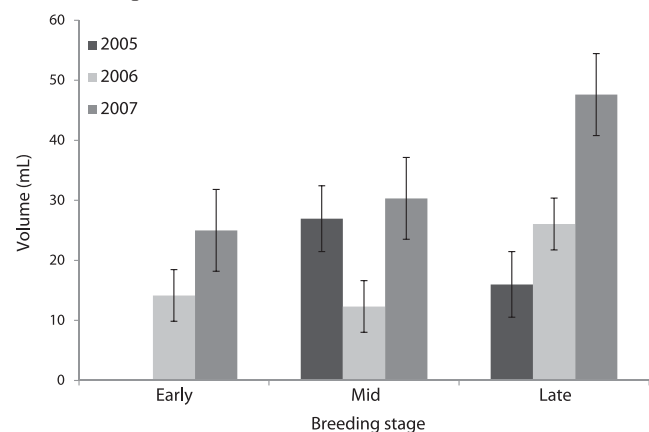
TABLE 3. Results of tests for intra- and inter-year changes in energy flow from short and long trips of Short-tailed Shearwaters at Althorpe I., South Australia. Early = first 30 days of chick rearing, mid = middle 30 days of chick rearing, late = last 30 days of chick rearing.

Effect	Test	Short trips	Long trips
2005 mid vs. late	Mann–Whitney	NS	NS
2006 early vs. mid vs. late	Kruskal–Wallis	$P = 0.008$	NS
2007 early vs. mid vs. late	Kruskal–Wallis	$P < 0.001$	$P = 0.042$
Early 2006 vs. 2007	Mann–Whitney	NS	NS
Mid 2005 vs. 2006 vs. 2007	Kruskal–Wallis	$P = 0.052$	NS
Late 2005 vs. 2006 vs. 2007	Kruskal–Wallis	NS	$P < 0.001$

FIGURE 7. Mean (±1 SE) volume of stomach oil a Short-tailed Shearwater returning from a long trip delivered to its chick at each stage of chick rearing, 2005–2007.

(4.3 vs. 3.1 W, Weimerskirch and Cherel 1998) and for the closely related Sooty Shearwater (*Puffinus puffinus*) (6.4 W vs. 3.3 W, Weimerskirch 1998). Increased energy flow and feeding rate from short trips have a clear benefit to chicks but may incur a long-term disadvantage. For example, we documented reduced energy flow with successive short trips, revealing that prolonged feeding close to the colony has limited benefit to the chick (e.g., 2006). Whether reduced profitability is due to adults feeding themselves (Weimerskirch 1998, but see Chaurand and Weimerskirch 1994, Weimerskirch et al. 2003), or reduced foraging success is unclear. As feeding regimes are largely under the control of the adult's body condition, and short trips bring adults closer to a threshold body mass (Chaurand and Weimerskirch 1994, Tveraa et al. 1998), successive short trips presumably induce longer subsequent long trips as adults restore depleted reserves. Clearly a balance between adults and chicks is required.

Periods of increased oil deliveries (e.g., late 2007) strongly suggest improved feeding conditions in distant waters. However, such interpretations should be made with caution as the primary role of long trips is restoration of the adult's body condition (Chaurand and Weimerskirch 1994), a variable we did not study. Despite the extended duration of long trips the high calorific value of stomach oil (Obst and Nagy 1993) and mesopelagic myctophid fish (Tierney et al. 2002) presents an effective means of boosting energy flow to an average 2.4 W (this study). Neritic species in the fresh component of long-trip feedings (as in Weimerskirch and Cherel 1998) reveal that feeding conditions close to the colony also influence the energy return of long trips. Our expectation of increased energy returns from long trips at times of warmer local SST was poorly supported with no correspondence between these variables from year to year. Instead, long-trip energy flow increased at a time of low short-trip returns (e.g., 2007), and long-trip energy flow decreased when short-trip returns were high (e.g., 2005). The compensatory role of long trips when the yield of short trips was poor warrants a targeted study. Ultimately studying individual variation in energy allocation is a preferred approach as pooling data for estimates of colony-wide variation may mask these patterns. The lack of correlation between oil volume and trip duration reflects the many factors that influence an individual's foraging success and what it subsequently returns from distant feeding areas (Weimerskirch 1998).

Increased short-trip foraging when energy delivery was low (e.g., early 2006) suggests that adults attempt to maintain a suitable rate of energy delivery to chicks (as in Cory's Shearwater; Hamer and Hill 1993). Adjusting provisioning behavior to buffer chicks from food shortages is dependent upon the adult's capacity to balance provisioning with self feeding without jeopardizing its own survival (Erikstad et al. 1998). Under a dramatic deterioration in feeding conditions we expected adults to make fewer short trips, as they have

less scope to modify investment in provisioning. Despite variable conditions the consequences for Short-tailed Shearwater chicks were slight. Our assumption is based on consistent breeding success each year of our study (0.80–0.88), which was at the high end of the range reported for this species (0.17–0.76; Serventy and Curry 1984), and other seabirds following a dual foraging strategy (Granadeiro et al. 1998, Quillfeldt 2001, Pinaud et al. 2005).

We found no consistent relationship between the Short-tailed Shearwater's feeding strategies and SST across three successive years. Despite no record of fluctuations in the intensity of upwelling, our study supports the notion of variable primary productivity (Kämpf et al. 2004, Middleton and Bye 2007), and the variable prey assemblage reflects changed feeding conditions for the shearwater. There are numerous examples of links between indices of coastal upwelling and prey delivered or breeding success of seabirds (Quillfeldt et al. 2007, Thayer and Sydeman 2007). Numerous seabirds with a dual strategy boost short-trip foraging when local waters are more productive (cooler), presumably to capitalize on good feeding conditions and maximize energy delivery to their chick (Thin-billed Prion, Duriez et al. 2000; Yellow-nosed Albatross, Weimerskirch et al. 2001; Cory's Shearwater, Paiva et al. 2010). Our expectation of increased short-trip foraging when SST was cooler was met in one year (2006) but not in another (2005). Also, the assumed link between cooler SST and improved feeding conditions was not consistent from year to year, as energy flow from short trips was low when SST was cooler.

No clear trend across three years suggests either that local feeding conditions don't play a large role in dictating feeding strategies or that SST is a poor reflection of feeding conditions experienced by Short-tailed Shearwaters. In our study area, upwelled water is often sub-surface (Kämpf et al. 2004), and temporal lags associated with productivity through trophic levels to seabird prey (Grémillet et al. 2008) mean that SST may not consistently reflect local productivity.

The prey composition of meals played a large role in Short-tailed Shearwater feeding strategies, however the functional relationship between prey and feeding strategies is unclear. Krill (*Nyctiphanes australis*) has been identified as an important prey for the Short-tailed Shearwater (Montague et al. 1986, Weimerskirch and Cherel 1998), yet its lower energy density may limit its value for provisioning to early chick rearing when chicks' energy demands are low (but see Oka et al. 1987, Oka 2011). The adults made fewer short trips when they exploited higher-calorie fish (2005), more when they exploited low-calorie krill (2006). High-calorie prey and a high rate of energy flow presumably enable adults to meet the energy requirements of chicks more rapidly. This is a benefit to adults, as short trips come at a cost to their body condition (Chaurand and Weimerskirch 1994), and fewer short trips enable adults to depart on a long trip sooner. In comparison, low-calorie prey and

a low rate of energy flow may incur an energy shortage. Increased short-trip foraging when delivering krill could be the adults' response to a change in prey quality to maintain energy delivery to the chick, as in the Common Murre (*Uria aalge*; Wanless et al. 2005). An alternative view is that surface-seizing swarming krill is more cost-effective than pursuit diving for pelagic fish. Hence exploiting krill may elicit an increase in number of feedings per day despite the lower energy density of meals delivered.

We expected that chicks' body condition should be maintained under minor changes in feeding rate but compromised under moderate to large changes (Weimerskirch et al. 1999, Quillfeldt et al. 2010). Yet chicks attained a good condition from alternative feeding patterns. Good condition despite a low number of short-trip feedings in early chick rearing (2007) reveals that the delivery of less raw prey and more oil can meet the chick's requirements. In contrast, chicks' condition was depressed in a year of cooler SST (2006). Consideration of energy flow from both short and long trips revealed a reduction in the middle phase of chick rearing. Fat deposition and mass gain are most rapid then (as they are in antarctic fulmarine petrels, Hodum and Weathers 2003), so shortages in feeding at this stage are likely to be evident at fledging. Chicks of many Procellariiformes are protected from small fluctuations in feeding by adults overfeeding them (Quillfeldt et al. 2007). Among the Procellariiformes, overfeeding is most pronounced in the Short-tailed Shearwater, as chicks accumulate large deposits of fat (up to 50% of body mass; Hamer et al. 1997). So the reduction in chicks' body condition we observed may have had little influence on their post-fledging survival.

The flexible feeding rate, generalist diet, and capability for pursuit diving (up to 70 m; Weimerskirch and Cherel 1998) enable the Short-tailed Shearwater to tolerate considerable changes in its food supply, as can the Japanese Cormorant (*Phalacrocorax filamentosus*; Watanuki et al. 2004) and Common Murre (Burke and Montevecchi 2009). Being able to modify the time spent in close or distant feeding zones is a considerable advantage to seabirds that follow a dual strategy and are faced with variable feeding conditions (Quillfeldt et al. 2007, Welcker et al. 2009, Paiva et al. 2010, but see Smithers et al. 2003). By considering both the short-term and long-term effects of different feeding strategies we have identified that a strategy of fewer short trips of increased energy flow is most beneficial to both adult and chick. However, this strategy may falter when productivity changes dramatically. We recommend our approach of addressing provisioning and diet in combination for future studies of these mechanisms of flexibility in the face of moderate to dramatic changes in feeding conditions and to identify a species' ability to cope with climate change.

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