Original Article

Mass fluctuations suggest different functions of bimodal foraging trips in a central-place forager

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The function of a foraging trip (self-feeding or provisioning) and the spatial distribution of food resources play an essential role in foraging decisions of central-place foragers. Theory predicts that if foraging patches optimal for self-feeding and provisioning are spatially separated, a bimodal foraging strategy should often be favored. A bimodal foraging strategy involves the alternation of short feeding trips (ST) to collect food for offspring with long trips (LT) for self-feeding, as previously described in some procellariiform seabirds. Using an automated passage recording and weighing system, we tested whether the bimodal trip pattern observed in little auks (*Alle alle*), a small Arctic alcid, reflects a corresponding functional difference of bimodal foraging trips. We found that the body mass trajectory of little auks was closely related to their bimodal trip pattern. Little auks weighed significantly more returning from a LT and lost an equivalent amount of mass during subsequent ST. The decision to start a LT was not directly related to body mass but seemed to depend on the individual strategy of a bird. During LT, birds likely utilized distant foraging areas suitable for self-feeding while relying on near-shore areas during ST. These results support predictions of recent foraging models and indicate that the function of long and short trips of little auks is similar to procellariiforms independent of large differences in the temporal and spatial scale of feeding trips among these taxa. We suggest that bimodal foraging might be more widespread among central-place foragers than previously thought. *Key words: Alle alle*, bimodal foraging, body mass, foraging success, foraging trip duration, resource geometry. *[Behav Ecol]*

INTRODUCTION

Foraging decisions of central-place foragers are constrained by their need to regularly return to a central place, usually their breeding site (e.g., Orians and Pearson 1979). Time and energy costs of commuting between foraging and breeding sites are believed to have a strong impact on foraging efficiency and provisioning rates in these animals (Kacelnik et al. 1986; Ricklefs 1990; Ichii et al. 2007). As foraging currencies to be maximized may differ for whether animals self-feed or provision offspring, foraging decisions are likely to depend on the function of a feeding trip (e.g., Orians and Pearson 1979; Ydenberg et al. 1994; Ydenberg and Hurd 1998). Furthermore, the state of the animal (Lorentsen 1996; Varpe et al. 2004; Ballard et al. 2010) and the spatial distribution of the food resources (Catard et al. 2000; Ydenberg and Davies 2010) may have important consequences for the foraging behavior of central-place foragers.

Recently, Ydenberg and Davis (2010) suggested that resource geometry is especially important for foraging decisions of central-place foragers if foraging patches for self-feeding and offspring provisioning are spatially separated. The location of feeding areas for self-feeding and provisioning may vary because the characteristics of optimal food for offspring and parents may differ. Although food sources that maximize foraging efficiency are in theory optimal for self-feeding, characteristics that maximize energy flow to the offspring or enhance their development are important for

provisioning (Orians and Pearson 1979; Golet et al. 2000; Markman et al. 2004). Even in the absence of differences in prey type, the utilization of different foraging areas may be beneficial with respect to chick feeding rates. It may help provisioners to maximize delivery rate while satisfying their own energy needs if, for example, increased efficiency of self-feeding due to differences in prey density at distant foraging patches outweighs additional travel and time costs (c.f. Ydenberg and Davies 2010).

Ydenberg and Davies (2010) model predicts that if foraging patches optimal for provisioning are less distant from the delivery point than patches optimal for self-feeding, an alternating or bimodal foraging strategy should often be favored. They argue that under these conditions provisioners should conduct as many trips to the provisioning patch as possible before embarking on a self-feeding trip (Ydenberg and Davies 2010). However, such a foraging strategy depends on the ability of a species to accept a negative energy balance during provisioning trips and to delay re-fuelling, that is, to tolerate short-term fluctuations of body reserves. Even though the work of Ydenberg and Davies (2010) suggests that a bimodal foraging strategy should be fairly widespread among central-place foragers, it has to our knowledge so far only been documented for pelagic seabirds.

The bimodal foraging strategy of a number of procellariiform seabird species (Chaurand and Weimerskirch 1994; Weimerskirch et al. 1994) is characterized by the regular alternation of foraging trips of short (ST) and long duration (LT) (e.g., Weimerskirch 1998; Congdon et al. 2005). There is good evidence that during LT, these species access distant foraging areas that are highly productive providing birds with a suitable food resource for self-feeding and thus enabling them to maximize foraging efficiency despite high travel costs (Weimerskirch 1998; Weimerskirch et al. 2003). In contrast,

during ST birds forage in areas that are located near shore to primarily collect food for their chicks. During ST, foraging effort is high (i.e., energy expenditure, Weimerskirch et al. 2003) and birds are in a negative energy balance. Although a chick meal is also provided at the end of a LT, dual foragers use these trips mainly to replenish body reserves at the cost of reduced energy flow to the offspring (Chaurand and Weimerskirch 1994; Weimerskirch 1998). Hence, short-term body mass fluctuations of bimodal foragers likely facilitate the maximization of chick provisioning and simultaneously allow birds to remain in energy balance.

The recently described alternation of a single long with several (usually 3–4) short feeding trips of little auks resembles the bimodal foraging strategy of procellariiform seabirds despite large differences in both spatial and temporal extent of trips between the taxa (Steen et al. 2007; Welcker et al. 2009a, 2009c). We tested whether the bimodal foraging trip pattern in little auks reflects a functional difference as predicted by Ydenberg and Davies (2010). We expected that if little auks utilized foraging areas optimal for self-feeding during LT but foraging patches best for delivery during ST (i) parent birds would return heavier after a LT than after ST, (ii) body mass would decrease during consecutive STs, and (iii) reaching low body mass would prompt birds to conduct a LT. To test these predictions, we recorded trip durations and body mass fluctuations in chick rearing little auks over multiple days using an automatic passage and weight recording system.

MATERIALS AND METHODS

Study area and species

Data for this study were collected during the chick-rearing period of little auks in a colony at Isfjorden (Bjørndalen, 78°13'N, 15°20'E) on the west coast of Spitsbergen, Norway from July to August 2008. The little auk (*Alle alle*) is a small (body mass c. 160 g), planktivorous seabird with a breeding distribution confined to high Arctic latitudes (Stempniewicz 2001). With an estimated population size of about 20 million breeding pairs, it is among the most abundant seabirds of the world (Stempniewicz 2001). Little auks breed in large colonies in talus slopes where they lay a single egg in small rock crevices. Both parents provision the chick, carrying food back to the colony in an expandable gular pouch. Throughout the chick-rearing period, little auks adopt a bimodal foraging pattern alternating several ST (c. 2 h duration) with single LT (usually lasting >10 h; Welcker et al. 2009a, 2009c). After chicks fledge at 25–28 days of age, the period of bi-parental care at the colony is followed by a period of male-only care at sea (Stempniewicz 2001; Harding et al. 2004).

Field work

We used a tube-shaped automatic passage and weight recording system based on passive integrated transponder (PIT) tags and an electronic balance (referred to as "bird tube" hereafter) to determine foraging trip durations and body mass changes of little auks arriving and departing from their nests. To avoid disturbance of little auks during their most sensitive part of the breeding cycle (early incubation; Harding et al. 2009), parent birds were caught during late incubation and the early chick-rearing period using mist nets and noose carpets. Captured birds were immediately removed from the trapping devices and marked with an individual color ring combination for visual identification. In addition, an 11×2 mm ID 100 A PIT tag (EID Aalten BV, Aalten, the Netherlands) was subcutaneously injected at the dorsal side of the bird's neck. Handling procedures did not last longer

than 10 min. Recaptures of birds treated similarly in previous years confirmed that PIT tags remained stationary at the area where injected.

A bird tube was placed at the entrance of nests of which at least 1 parent bird was equipped with a PIT tag. If necessary, nest entrances were slightly modified so as to secure that birds had to pass through the system to enter or leave the nest. Every 3–5 days (with time intervals being shorter during the hatching period), we identified the content (egg/chick) of all experimental nests using light scopes (Moritex Europe Ltd., Cambridge, UK) in order to determine hatching dates and to confirm the presence of a live chick throughout data collection.

Bird tubes were c. 30 cm in length and c. 10 cm in diameter and consisted of a PIT tag antenna and a photoelectric switch at the front and rear end of the tube, respectively, and an electronic weighing cell its mid-section. The system was connected to a TROVAN LID 665 OEM PIT tag recorder that, each time a PIT-tagged bird passed through the instrument, recorded the individual identification number, as well as date and time, the bird triggered antenna and photoelectric switch (Steen et al. 2007). The logging of body mass measurements by the electronic balance commenced as soon as the bird stepped on the weighing cell. The device recorded 50 weighings within 2 s after the bird triggered the balance.

The instruments were maintained every 2–3 days and data were downloaded to a computer. The electronic balances in all bird tubes were calibrated before placement and were re-calibrated on a weekly basis throughout the field season. Despite high maintenance effort, system failures occurred occasionally. Out of 9 bird tubes installed, 6 delivered continuous readings of 8 individual birds (including both partners of 2 pairs) for time periods between 3 and 17 days. This corresponds to 1702.5 h of continuous data. Data recording started after chicks had obtained homeothermy (chick age, 4 days).

To our knowledge, the deployment of the bird tubes had no effect on foraging behavior and chick provisioning of the birds. Observations confirmed that parent birds continued to feed their chick normally after the installation of the devices and all studied individuals succeeded in rearing their single chick. We are therefore confident that the data collected in this study reflect natural behavior of little auks.

Data analysis

We determined whether a bird was moving in or out of the nest by the chronological order of the 3 different readings (PIT-tag antenna, electronic balance, and photoelectric switch) recorded by the bird tubes. The duration of a foraging trip was defined as the time period between departure and subsequent re-entry of the nest. Consequently, this comprised the time birds spent at the colony outside the nest (Steen et al. 2007). Extensive direct observations of chick provisioning showed 30 min to be the minimum duration of foraging trips at the study colony (Steen H, unpublished data). All absences from the nest longer than 30 min were therefore regarded to be foraging trips.

Due to technical reasons, 2 bird tubes recorded only ingoing movements. For these data, trip duration was calculated from 2 consecutive ingoing movements. Therefore, trip duration in these cases included also the time birds spent in the nest. The time spent in the nest is relatively short compared with the duration of the feeding trip, especially after parents stop brooding the chick (the median time spent in the nest between foraging trips was only 0.1 h in this study; see also Welcker et al. 2009c). As data recorded by the 2 malfunctioning tubes started at chick age 7 and 16 days, respectively,

derived trip times are unlikely to be confounded by brooding activity by parent birds.

Foraging trip durations were bimodally distributed with only few trips of intermediate length. To avoid a subjective separation of long (LT) and short (ST) trips based solely on visual inspection of frequency distributions, we calculated the cut-off value between ST and LT based on the minimization of the sum of variances (given their log-normal distribution) as detailed in Welcker et al. (2009a). Calculations were done separately for the 2 individuals for which only in-movements were recorded as estimated trip durations were derived differently (see above). The derived cut-off values were 5.4 h and 6.1 h, respectively.

Body mass analysis

Data recorded by the weighing cell (in mA) was transformed to body mass (g) based on the regular calibrations. As calibrations varied slightly among instruments, this was done separately for each bird tube. The fact that most birds were moving during a weighing cycle led to substantial variation across the 50 recordings made at each weighing (Figure 1). Depending on the degree and speed of movement of the bird during a weighing, the sequence of 50 measurements displayed a relatively stable "plateau" in the mid section of the cycle and highly erratic data at the beginning and, often, also at the end of the weighing. By visualizing the data of each weighing cycle, we manually selected the sequence of the weighing that represented the plateau and removed all other data. However, the length of the plateau and the degree to which weightings of the plateau phase fluctuated varied substantially (Figure 1). In some cases, no distinct plateau could be defined and in these cases all 50 data points were kept. As simply taking the mean for the plateau would not take into account the large differences in variance among weightings, we included all single measurements of a weighing cycle in our models (see below).

Statistical analysis

First, we determined differences in body mass between a bird entering the nest and its subsequent departure as an approximation of the food load delivered to the chick using a linear mixed effects model. To test for differences in food load with trip duration, trip type (LT versus ST) was included as a fixed factor in the model; chick age was additionally included to control for changes across the chick-rearing period. To account for nonindependence of partners within a pair and the fact that our data consisted of repeated measurements from individual birds and within each weighing cycle, models contained "weighing ID" within "bird ID" within "nest ID" as a nested random term. The 2 individuals for which only in-movements were recorded were excluded from this analysis.

We fitted a similar mixed effects model to evaluate relative changes in body mass over a bimodal foraging trip cycle. To this end, we calculated the deviation (%) of each body mass measurement from the overall mean of each individual. ST were categorized according to their position in the trip cycle (ST1, ST2, …). As only few individuals conducted 6 or more ST in between LT, these trips were combined into 1 category (ST6+, see Figure 2). In a second step, we included only the first and last ST of a trip cycle to evaluate mass loss during a series of ST. These models contained movement (in versus out) and chick age as a fixed factor and covariate, respectively, and the same random term as the model described above.

To assess which factors drive the decision of the birds to initiate a LT, we ran a generalized linear mixed model (GLMM) with a logit link function and a binomial error structure. Factors evaluated were current body mass, body mass after the preceding LT, duration of the preceding LT and ST, and the number of preceding ST. Bird identity within nest identity was included as a random term. Similarly, a GLMM with Poisson error structure was used to test whether the duration of and/or the body mass after the preceding LT affected the number of ST birds conducted within a foraging trip cycle.

We started by fitting maximum models; model simplification was done by likelihood ratio tests (LRT) starting with the highest interaction terms. Interactions and factors were eliminated from the model if their removal did not significantly increase deviance.

To determine whether there were consistent differences in foraging decisions between individuals, specifically in the number of ST individual birds conducted before embarking on a LT, we estimated their within-individual repeatability. To this end, we estimated GLMM-based repeatabilities ($R \pm$ credibility intervals) fitted by Markov Chain Monte Carlo sampling using the rptR package in R (Nakagawa and Schielzeth 2010).

Trip durations were log-transformed before the analyses. All statistical tests were performed in R 2.12 (R Development Core Team 2011). Mean values are given ±1 SE unless stated otherwise.

RESULTS

Overall, we recorded 372 foraging trips, 292 (78.5%) ST, and 80 (21.5%) LT. The average duration of feeding trips was 2.17 ± 0.08 h (ST) and 12.26 ± 0.56 h (LT). All individuals adopted a bimodal foraging strategy alternating a single LT with a series of approximately 4 (median: 4, range 0–11) ST; none of the examined birds went on only ST or LT. Occasionally, however, a parent bird conducted 2 consecutive LT (5 out of 75 occasions).

Body mass of birds returning to their nest was significantly lower after a ST compared with a LT ($\beta = -5.30 \pm 0.89$ g, $t_{278} = -5.94$, $P < 0.001$; Figure 2). Mean food load (body mass difference between an ingoing and outgoing movement) was estimated to be 2.89 ± 0.74 g ($t_{278} = -3.92$, $P = 0.001$; Figure 1). There was no indication that food load varied between birds returning from a ST versus LT (LRT, $\chi^2_1 = 0.39$, $P = 0.53$). We found a slight but significant increase in body mass with chick age ($\beta = 0.27 \pm 0.11$, $t_{267} = 2.45$, $P = 0.015$), but no evidence that food load co-varied with chick age (i.e., interaction chick age × movement (in/out); LRT, $\chi^2_1 = 0.04$, $P = 0.83$).

Body mass varied significantly in the course of a bimodal foraging trip cycle ($F_{7,386} = 4.64$, $P < 0.001$). After a LT, little auks weighed approximately 3% more than on average ($\beta = 2.70 \pm 0.50\%$, $t_{381} = 5.37$, $P < 0.001$). Compared with their body mass after LT, birds lost $1.90 \pm 0.71\%$ body mass after the first ST ($t_{381} = -2.67$, $P = 0.008$; Figure 3). Birds lost $2.88 \pm 0.73\%$ mass by the second ST ($t_{381} = -3.96$, $P < 0.001$) but maintained relatively stable body mass during ST 4 and 5 (Figure 3). Mass loss compared with LT was highest after ST 5 ($\beta = -3.94 \pm 0.94\%$, $t_{381} = -4.21$, $P < 0.001$; Figure 3). There was no indication that body mass loss varied with chick age (LRT, $\chi^2_1 = 0.11$, $P = 0.74$).

Analysis of body mass change including only the first and the last ST of a foraging trip cycle showed that birds lost on average $1.69 \pm 0.70\%$ body mass after the first ST ($t_{205} = -2.42$, $P = 0.017$). Birds lost another $1.56 \pm 0.76\%$ during the remaining ST of a ST cycle ($t_{205} = -2.03$, $P = 0.043$) but gained on average $3.24 \pm 0.72\%$ mass during a LT ($t_{205} = 4.49$, $P < 0.001$; Figure 4).

The decision to embark on a LT was mainly driven by the number of ST conducted prior to the LT (LRT, $\chi^2_1 = 7.13$,
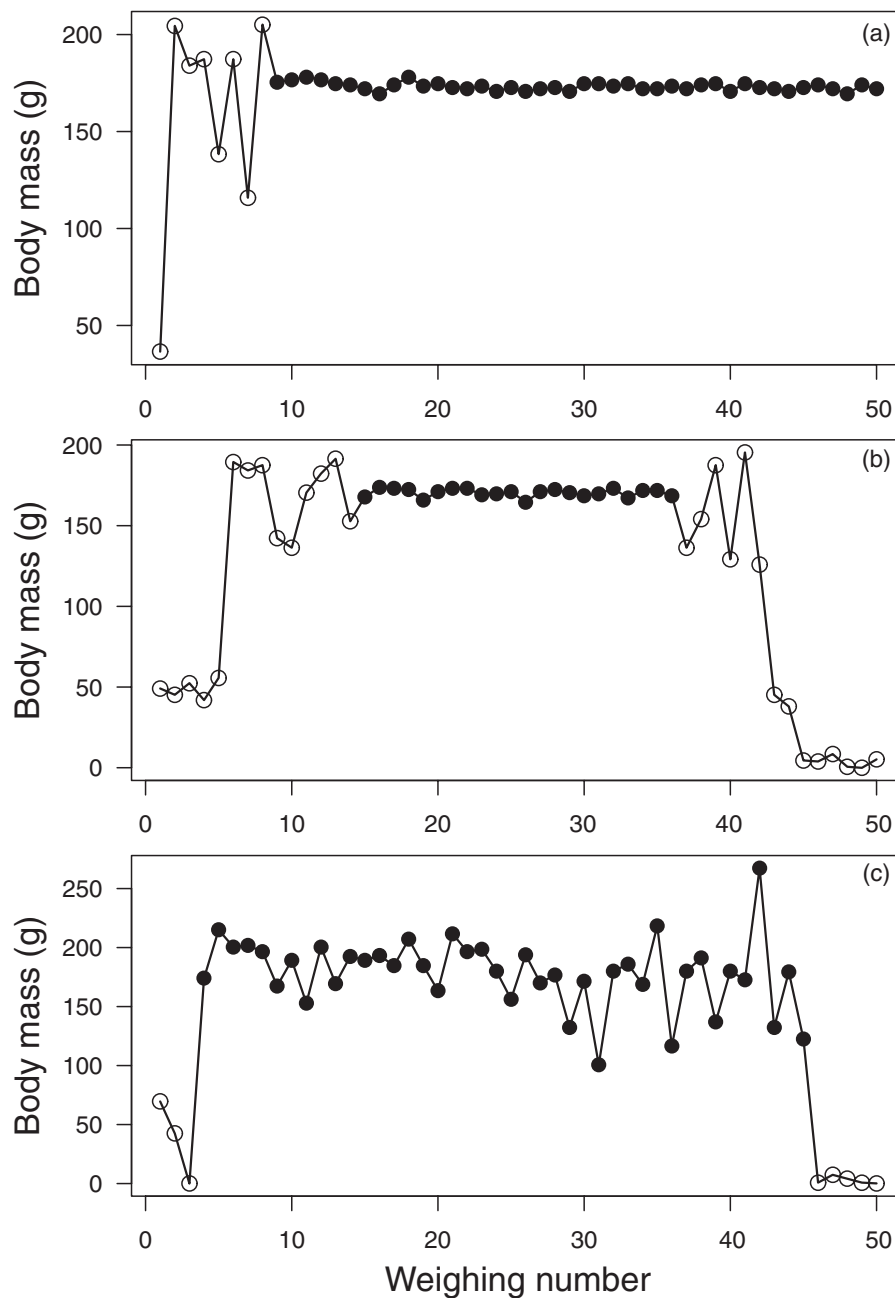
Figure 1
Three examples of automatic weightings of little auks recorded by the electronic weighing system. 50 body mass measurements were recorded within 2 s after the birds stepped on the weighing cell. (a) Example of weight recordings of a bird presumably sitting on the weighing cell resulting in stable weight recordings except during initial movement. (b) Weight recordings of a bird presumably slowly moving over the weighing cell resulting in high variability at the beginning and end of the weight recording cycle. (c) Weight recordings of a bird presumably quickly moving over the weighing cell resulting in high variability throughout the weighing cycle. Filled symbols indicate data used for the analysis; open symbols show data removed.

$P = 0.008$). Neither current body mass (LRT, $\chi^2_1 = 0.37$, $P = 0.54$) nor body mass after the preceding LT ($\chi^2_1 = 2.17$, $P = 0.14$), the duration of the preceding LT ($\chi^2_1 = 2.39$, $P = 0.12$) or the preceding ST ($\chi^2_1 = 2.60$, $P = 0.11$) seemed to play a role in triggering a LT. Similarly, the number of ST within a foraging trip cycle was independent of body mass after the preceding LT ($\chi^2_1 = 3.15$, $P = 0.08$) and the duration of the preceding LT ($\chi^2_1 = 0.41$, $P = 0.52$).

We found that foraging decisions differed consistently between individuals. The number of ST within a foraging cycle was highly repeatable within individuals ($R = 0.564$ [0.258, 0.905]), indicating that individuals had a strong tendency to conduct a consistent number of ST between LT.

DISCUSSION

Our study suggests that the bimodal foraging strategy of little auks (Steen et al. 2007; Welcker et al. 2009a, 2009c) is functionally equivalent to that of pelagic seabirds (e.g., Chaurand
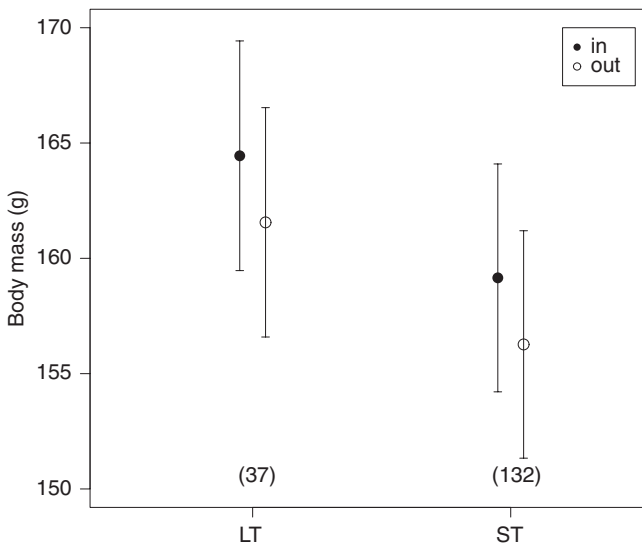
Figure 2
Body mass (parameter estimates $\beta \pm$ SE) of little auks entering and leaving the nest after a long and short foraging trip as predicted by a linear mixed effects model (see text for details). Sample sizes (number of foraging trips) are given in parentheses.

Figure 3
Body mass fluctuations (deviation from mean body mass (%)) of little auks during a bimodal foraging trip cycle as predicted by a linear mixed effects model (parameter estimates $\beta \pm$ SE; see text for details). Sample sizes (number of foraging trips) are given in parentheses.

and Weimerskirch 1994; Weimerskirch et al. 1994; Congdon et al. 2005), namely that LTs are devoted to self-feeding and to store body reserves that are subsequently depleted during ST in order to maximize chick-feeding rates. Our results are also consistent with recent theoretical considerations that dual foraging is the response of central-place foragers to certain resource geometries under the condition that energy balance can be delayed (Ydenberg and Davies 2010).

Our data show that the body mass of little auks fluctuates systematically over the course of a bimodal foraging trip cycle. Body mass of birds was significantly higher returning from a LT compared with ST; individuals gained more than 3% body mass during a LT at the end of a series of ST. A corresponding mass loss was observed during the ST cycle. This strongly suggests 2 different functions of foraging trips; ST mainly serve to collect food for the offspring while during LT birds replenished body reserves depleted during ST. Birds did not balance their energy budget on every trip but accepted to be in negative energy balance during ST, a pivotal precondition for bimodal foraging (Ydenberg and Davies 2010). This strategy allowed birds to optimize foraging decisions over longer time periods, that is, the course of a whole bimodal trip cycle.

It has been estimated that adult little auks need to consume approximately 131g fresh zooplankton each day to fuel their high metabolic rate (Gabrielsen et al. 1991). Our results show that during ST (mean duration ~2h; see also Welcker et al. 2009a), little auks are able to capture about 3g of food (assuming negligible self-feeding; see, e.g., Weimerskirch et al. 2003). Assuming a total travel time of approximately 1h during ST (as reported for a nearby colony; Welcker et al. 2009a) and about 50% of the remaining time used for prey search, resting etc., we can, conservatively estimated, expect birds to be able to capture 3g zooplankton within 0.5h during ST. This implies that little auks would need more than 21.6h if they were to meet their own daily energy requirements at ST foraging areas. In comparison, as birds usually conduct only 1 LT (~12.3h) per day, little auks were presumably capable of satisfying their needs in only about 57% of that time during LT including travel time. Recent studies have shown that during LT little auks
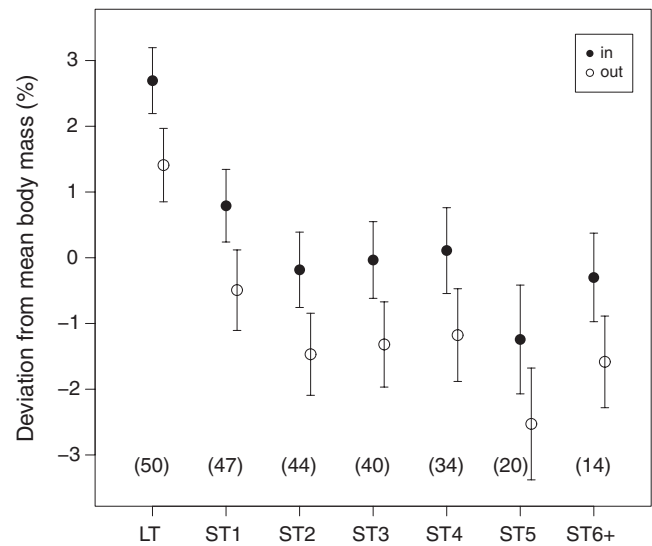
specifically access distant foraging areas that are characterized by high abundance of relatively large, lipid-rich zooplankton, their preferred prey (Jakubas et al. 2012; Brown et al. 2012). In contrast, smaller, less energy-rich prey species are prevalent in near-shore areas where little auks collect food for their offspring (Steen et al. 2007; Welcker et al. 2009a; Kwasniewski et al. 2010). This may explain why little auks can maximize self-feeding efficiency during LT despite relatively long travel distances (presumably up to 200 km one way; (Welcker et al. 2009a; Brown et al. 2012) and their high energetic costs of flight (Gabrielsen et al. 1991; Welcker et al. 2009b). These observations are also in line with predictions made by Ydenberg and Davies (2010), specifically that bimodal foraging should be favored when the distance between the foraging patches for self-feeding and provisioning is large and when the travel distance to the self-feeding patch exceeds that of the provisioning patch.

Body mass fluctuations of little auks were comparatively moderate. In several other bimodal foragers, body mass changes between LT and ST amount to 7–10% (e.g., Weimerskirch et al. 1999; Duriez et al. 2000; Congdon et al. 2005, but see Weimerskirch et al. 1997). In comparison, little auks gained much less weight during LT (~3%). However, the moderate mass changes in little auks may be ecologically relevant as it has previously been shown that mass loss of about 5% substantially reduced local survival in this species (Welcker et al. 2009b). This suggests that mass fluctuations of little auks during the bimodal foraging cycle stays above the margin below which survival costs might be incurred.

Little auks did not lose mass continuously throughout the course of a ST cycle. Roughly half of the mass loss was incurred after the first ST alone, indicating that birds were able to stabilize body mass to some extent during the remaining foraging trips of a ST cycle. This suggests that little auks engage at least in some self-feeding during ST, enabling them to attenuate mass loss and thus extend their series of ST.

In line with this, but contrary to earlier findings (Weimerskirch 1998; Duriez et al. 2000), the decision to initiate a LT seemed not to be directly related to body mass in little auks. The probability of embarking on a LT increased
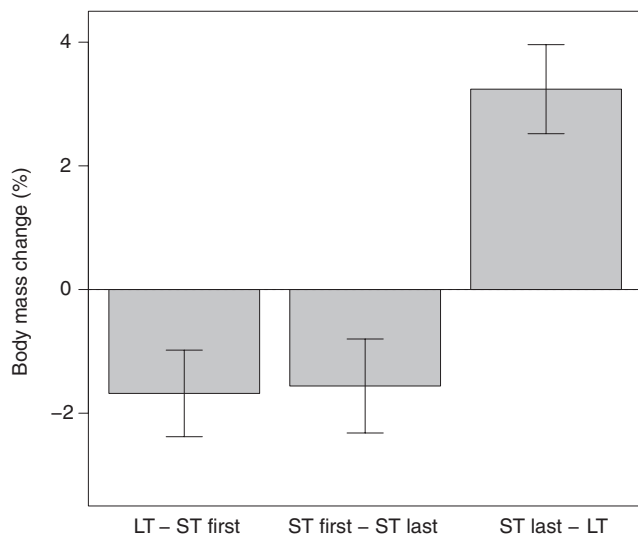
Figure 4
Body mass changes (%) of little auks during the long (LT) and the first and last short (ST) foraging trip of a bimodal foraging trip cycle based on a linear mixed effects model (see text for details).

with increasing numbers of ST but did not depend on either current body mass or body mass after the preceding LT. Ydenberg and Davies (2010) predict that if bimodal foraging is favored, provisioners should make as many ST to collect food for the offspring as possible. However, their model does not take into account the fact that bimodal foragers need to carry the body reserves required to fuel those foraging trips without self-feeding. Our study has shown that little auks avoid body mass losses that would decrease their probability of survival. Nonetheless, they seem to increase the number of ST by engaging to some degree in self-feeding during those trips, thereby maximizing energy flow to their offspring.

We found that the number of ST within a ST cycle was highly repeatable within individuals. This suggests that individuals may differ in their ability to retain body mass during ST and therefore the number of ST may reflect individual quality in terms of foraging efficiency. Individuals with high foraging efficiency may be able to conduct more ST before they have to replenish body reserves during a LT. On the other hand, individuals may consistently differ in their foraging strategy, that is, they may pursuit either a high or a low ST strategy that is only secondarily related to body mass. For example, apparent individual strategies may arise due to differences between the sexes (e.g., Welcker et al. 2009c) or as the result of differences in personality, age, or experience (e.g., Bell et al. 2009; Lecomte et al. 2010).

A food load of about 3 g as estimated in this study using an automated weighing system corresponds well with previous estimates (e.g., 2.68 g; Pedersen and Falk 2001). However, we did not find a difference between LT and ST in the amount of food birds brought back to the colony. This contrasts with studies in other bimodal foragers, which unanimously report higher mass and energy content of chick meals brought back after LT (e.g., Chaurand and Weimerskirch 1994; Granadeiro et al. 1998; Catard et al. 2000). Larger meals after LT mitigate to some extent the detrimental effect of the longer duration of LT to the energy flow to offspring, thereby decreasing the threshold above which a bimodal foraging strategy becomes profitable (sensu Ydenberg and Davies 2010).

Two explanations may account for the lack of difference in food load between trip types in little auks. First, the amount of food little auks are capable to transport may be strongly limited

by the size of the extensible gular pouch and it may be most profitable for birds to fill up the pouch completely before returning to the colony irrespective of trip type. Second, during LT little auks may not collect food for the chick at the foraging area used for self-feeding but rather stop on their way back to the colony to collect the chick meal, thus avoiding high energetic costs of transport (Welcker et al. 2009a; Brown et al. 2012). Hence, little auk chicks are unlikely to benefit from LT through either higher quality food and/or larger meal size. Therefore, the contribution of LT to delivery rate is restricted to their frequency of occurrence (about 20% of all foraging trips while they accounted for more than 58% of the time birds spent foraging), increasing the threshold above which bimodal foraging should be adopted by this species.

Taken together, our results suggest that bimodal foraging in little auks is functionally equivalent to that of tube-nosed seabirds for which the dual strategy has been widely described (e.g., Weimerskirch et al. 1994; Baduini and Hyrenbach 2003). This functional similarity occurs independent of large differences in the temporal and spatial scale of their foraging trips and despite considerable differences in their foraging ecology. Recently, Ydenberg and Davis (2010) have demonstrated in simple models that resource geometry alone, namely the divergent location of foraging patches to self-feed and to collect food for delivery, may under certain conditions promote bimodal foraging in central-place foragers. We have shown that the bimodal foraging strategy of little auks is consistent with their predictions and suggest that bimodal foraging might be more widespread among central-place foragers than currently known.

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