



Comparison of optimal foraging versus life-history decisions during nestling care in Lincoln's Sparrows *Melospiza lincolnii* through stable isotope analysis

MICHAEL BEAULIEU^{1*} & KEITH W. SOCKMAN^{1,2*}

¹Department of Biology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA

²Curriculum in Neurobiology, University of North Carolina at Chapel Hill, Chapel Hill, NC, USA

In short-lived species, parents are expected to favour their offspring and may therefore have to sacrifice the best part of their diet to feed their young ('conflict hypothesis'). In addition, they need to maximize energy delivered per unit of time to the young ('delivery hypothesis'). We examined the influence of these two factors on food allocation in Lincoln's Sparrows *Melospiza lincolnii* by measuring plasma $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in both parents and offspring. Adults' isotopic values were unchanged when feeding chicks, but their $\delta^{15}\text{N}$ values were higher than those of their chicks. Using the isotopic signature of Lincoln's Sparrows and that of prey available in their habitat, we reconstructed the diet of parents and chicks using mixing models for stable isotope analyses. The main difference between the diet of chicks and that of adults was that the proportion of spiders was lower in chicks than in adults, while the proportion of grasshoppers was higher. Spiders appear more valuable than grasshoppers, as they are more easily digested and richer in lipids, proteins and essential amino acids. However, grasshoppers are larger than spiders and are therefore likely to be better suited to maximize energy delivery to chicks. As parents keep their diet constant when breeding and as the contribution of large prey is higher in the diet of chicks than in that of their parents, our results suggest that the influence of optimal foraging strategy is predominant over the influence of parent–offspring conflict on food allocation in Lincoln's Sparrows, thereby supporting our delivery hypothesis. However, this relative influence may differ when resource availability constraining parent–offspring conflict varies.

Keywords: food provisioning, parental care, resource allocation, SIAR.

Two theories have been proposed to explain how parents allocate food resources between themselves and their offspring. On the one hand, central place foragers such as parents provisioning their chicks are expected to select prey to feed their offspring to maximize energy delivery per unit of time. In that case, they may have to select large prey to feed their young and use small prey for self-feeding (Orians & Pearson 1979). This is likely to be crucial when parents need long periods of time to find food for their offspring because of long travelling distances or prolonged search effort (Kaspari 1991, Grieco 2002), or when commuting

between breeding and foraging areas exposes parents or young to high predation risk (Skutch 1949). In the latter case, feeding young with large prey would allow parents to decrease provisioning rate and hence reduce predation risk without compromising energy delivery rate. On the other hand, because food resources are finite, a conflict of interest may arise between adults and their offspring, both generations being expected to take advantage of resources at the expense of the other (Trivers 1974). The decision to favour one component at the expense of the other depends on life-history characteristics (Stearns 1989); in long-lived species, allocating too many resources to current reproduction may reduce survival and therefore lifetime reproductive success more than in short-lived species. Thus, in parent–offspring conflict,

*Corresponding author.

Email: miklvet@hotmail.fr (Michael Beaulieu); kws@unc.edu (Keith W. Sockman)

long-lived parents may be expected to retain the most beneficial prey for themselves, while the opposite is expected in short-lived species. Even though these two theories on resource allocation between parents and offspring have been formulated separately, they are likely to act together on parental feeding decisions. Yet, the importance of one relative to the other has not been examined.

Food allocation between parents and young has mostly been examined through visual observations of the solicitation behaviour of the young and the associated feeding behaviour of their parents (e.g. Cameron-Macmillan *et al.* 2007, Beaulieu *et al.* 2009a). Even though this approach has led to a better understanding of food allocation, it has drawbacks: behaviour is difficult to observe in furtive species, human presence is stressful and can modify parental foraging and allocation decisions (McDonald *et al.* 2007), and individual behavioural observations give only a snapshot of how parents allocate food to their offspring and do not necessarily reflect the whole young-rearing period. In this context, the use of stable isotope analyses can be useful. Indeed, as the incorporation rate of isotopes depends on the turnover rate in tissues, the isotopic signature of a tissue with turnover rate corresponding to the young-rearing period integrates all of the parental feeding decisions over the same period of time. The comparison of the isotopic signature of parents to that of their offspring can therefore provide a more complete picture of food allocation between parents and young than individual behavioural observations.

Despite the advantages of stable isotope analysis to study food allocation between parents and their offspring, investigators have so far only simultaneously measured the isotopic signature of adults and young to look for general intraspecific patterns. Two-thirds of studies conducted in birds (mostly in seabirds) report that adults and juveniles show different (either lower or higher) $\delta^{15}\text{N}$ values and/or $\delta^{13}\text{C}$ values (see Supporting Information Table S1 for a list of these studies and a brief description of their results). This suggests that the division of food resources by parents between their own feeding and the provisioning of their young is common in bird species. Although some of these studies measured stable isotope ratios from both chicks and their parents, only two explicitly examined how the isotopic signature of the young was related to the isotopic signature of their parents (Nisbet *et al.* 2002, Koenig *et al.*

2008). In Common Terns *Sterna hirundo*, parents and their offspring exhibit similar isotopic signatures, suggesting that parents feed their chicks as they feed themselves (Nisbet *et al.* 2002). This may be explained by the fact that (1) Common Terns feed on very few prey species (Granadeiro *et al.* 2002), which limits the possibility for parents to select a given prey type for chick provisioning or self-feeding, and (2) they are long-lived (maximum life expectancy: 33 years; The Animal Ageing & Longevity Database 2013) and are therefore expected to sacrifice relatively less of their diet and self-maintenance to feed their chicks (Stearns 1992).

Terrestrial birds, which tend to have shorter life expectancy than most seabirds, may be more likely to sacrifice the most profitable part of their diet to feed their young. Moreover, they often feed on a wider range of prey from different trophic levels, from plant material to arthropods, which exhibit distinct $\delta^{15}\text{N}$ signatures (Girard *et al.* 2011, Beaulieu & Sockman 2012) and therefore provide the possibility to discriminate food for chick provisioning and self-feeding. In agreement with this hypothesis, Acorn Woodpeckers *Melanerpes formicivorus* (maximum life expectancy: 17 years; The Animal Ageing & Longevity Database 2013) appear more flexible than Common Terns in terms of feeding their chicks. In this species, even though the diet of chicks depends heavily on the diet of their parents, adults feed their offspring proportionally more arthropods than they feed themselves, which is reflected by different isotopic values between adults and chicks (Koenig *et al.* 2008). As arthropods are rich in proteins, one explanation for this high proportion of arthropods in the diet of chicks is that parents regulate the diet of chicks as a function of their demand for proteins. However, the composition of arthropods is not constant and some species may be more advantageous than others for adults and for chicks. For instance, spiders represent a highly valuable prey both for adults and developing young, as they have a high content of lipids, proteins and essential amino-acids, a low content of indigestible chitin, and can be easily handled relative to most other arthropod prey (Bañbura *et al.* 1999, Brodmann & Reyer 1999, Ramsay & Houston 2003, Magrath *et al.* 2004). Considering that short-lived parents are expected to favour their current reproduction at the expense of their own maintenance, short-lived terrestrial birds may withhold this highly

profitable prey from their own diet in order to feed their young (what we call the 'conflict hypothesis'). As spiders are at the top of the arthropod trophic chain, they have the highest $\delta^{15}\text{N}$ values among arthropods (Beaulieu & Sockman 2012, Wimp *et al.* 2013). Consequently, if parents withhold spiders from their diet to feed their chicks, this should be reflected (1) by lower $\delta^{15}\text{N}$ values in adults during the chick-rearing period than before, and (2) by lower $\delta^{15}\text{N}$ values in parents than in their young. Alternatively, because spiders are generally smaller than other arthropod prey, feeding chicks with this prey may not maximize the amount of energy delivered to the young per unit of time as much as feeding them with larger arthropods, such as grasshoppers. Consequently, spiders may not be best suited for chick feeding but rather for parents' self-feeding. In that case, parents may not have to withhold spiders from their own diet to feed their young but should feed chicks with larger prey species from lower trophic levels, such as grasshoppers (what we call the 'delivery hypothesis'). This should be reflected (1) by constant $\delta^{15}\text{N}$ values in adults before and during the chick-rearing period, and (2) by lower $\delta^{15}\text{N}$ values in young than in their parents.

To examine these two hypotheses, we considered here two key aspects in the short-lived Lincoln's Sparrow *Melospiza lincolnii* (maximum life expectancy: 7.6 years; The Animal Ageing & Longevity Database 2013). First, we assessed how feeding offspring impacts adults' diet. Secondly, we examined within Lincoln's Sparrow families how parents allocate food resources to their chicks. We used stable isotope analyses to examine (1) the isotopic signature of adults before and when feeding chicks, (2) the isotopic signature of parents and that of their chicks, and (3) the composition of the diet of parents and chicks.

METHODS

Fieldwork

We conducted fieldwork from late May to late July 2010 in a sub-alpine meadow located in the Rocky Mountains close to Molas Pass (37.74°N, 107.69°W), Colorado, USA (see Sockman 2008, 2009 for details of the study system). Each day during the field season, five people searched for Sparrow nests in the grass under bushes for 3 or 4 h each. Nests were found at four different

stages: before and during egg-laying, during incubation and after hatching. We checked nests daily (except during the first 7 days of incubation to limit disturbance) and noted each breeding event (egg-laying, clutch completion, hatching) until chicks were 8 days old (i.e. just before they fledged). Over the season we found 76 Lincoln's Sparrow nests in which birds initiated clutches from early June to early July (mean \pm se: 20 June \pm 0.88 days; Beaulieu & Sockman 2012). Because of nest desertion and predation, one nest produced no eggs, 22 nests with eggs produced no hatchlings, 24 nests with chicks were depredated and nine nests lost at least one chick during the first 8 days of the chick-rearing period. Among the 20 remaining nests, 8 days after hatching, one nest had one chick, five had two chicks, six had three chicks and eight had four chicks. To limit the potential effect of brood size on parental feeding decisions, we focused on nests with a constant number of chicks from hatching to fledging and composed of three or four chicks. We used mist-nets to capture both parents from 10 of these 14 nests (from 29 June to 23 July) while they were provisioning their chicks (seven nests with four chicks and three nests with three chicks, i.e. 20 adults and 37 chicks). We collected blood (50–100 μL) for isotopic measurement from the wing vein with a heparinized capillary tube (Natelson blood collecting tubes, Fisherbrand[®]; Fisher Scientific, Pittsburgh, PA, USA). As with the adults, we collected blood (50 μL) from the chicks when they were 8 days old (i.e. before fledging).

We also captured adults with 50 seed-baited trapping stations placed throughout the meadow before capturing birds provisioning their chicks. These birds were bled and identified with a US Geological Service identification ring and a unique combination of coloured leg rings. In the second half of June (17 June–1 July), we captured 14 individuals, which we later knew did not have chicks at the time they were captured (i.e. their nest was found later with chicks, and on our field site Lincoln's Sparrows typically breed only once over one breeding season: we observed only once a bird breeding twice over one breeding season in 8 years of fieldwork). These 14 birds were not the same as those feeding chicks described above. Most of these 14 birds visited seed-baited traps several times over the season. Importantly, we did not find any relationship between their isotopic values (see below) and the frequency with which

they visited seed-baited traps before we took blood for isotopic measurements (between 0 and 10 times) (Pearson correlations: $r = -0.276$, $P = 0.340$ for $\delta^{13}\text{C}$ values, and $r = -0.442$, $P = 0.114$ for $\delta^{15}\text{N}$ values), suggesting that the consumption of seeds from baited-traps did not interfere with isotopic measurements. This may be because we used very few seeds to bait birds in traps and because birds spent a short period of time (between a few minutes and an hour) in the traps for each capture.

Once collected, blood was transferred into Eppendorf tubes, held on ice for a few hours and centrifuged (4600 g, 9 min). Plasma was then separated from red blood cells and both were frozen until analysis.

Bird sexing

As Lincoln's Sparrows are slightly sexually dimorphic (males being 2–10% heavier than females; Ammon 1995), feeding allocation can be affected by the sex of the parents and the sex of the chicks (Quillfeldt *et al.* 2004, Beaulieu *et al.* 2009b). We therefore took the sex of birds into consideration in our analyses. We sexed adults using cloacal inspection and, because the young are sexually monomorphic, we sent chick red blood cells to Zoogen Incorporated (Davis, CA, USA) for molecular sexing. We also sent to Zoogen the red blood cells from three known males and three known females (sexed as adults by cloacal inspection), which enabled us to confirm that the molecular technique was accurate (each of these six was identified as the correct sex).

Isotopic analyses

To reflect the 8 days of the chick-rearing period, we chose to measure isotopic ratios in plasma, as opposed to red blood cells. In White-spectacled Bulbuls *Pycnonotus xanthopygos*, plasma ^{15}N retention time (i.e. the amount of time isotopes spend in plasma) ranges from 5 to 8 days (i.e. the age of Lincoln's Sparrow chicks when they were bled), whereas in red blood cells, it ranges from 22 to 32 days (Tsahar *et al.* 2008). Moreover, in Myrtle Warblers *Setophaga coronata*, the plasma half-life of C lasts 24 h vs. 11 days in red blood cells, and 8 days after a switch from C4 to C3 diet, birds' plasma isotopic values are stable and reflect their C3 diet (Podlesak *et al.* 2005). These durations are presumably even shorter in growing individuals

like chicks (Fry & Arnold 1982, MacAvoy *et al.* 2005). Finally, in altricial birds, the yolk sac, which constitutes only 5–10% of the total body mass of hatchlings (Schmidt *et al.* 1985), is quickly resorbed after hatching (Tully *et al.* 2000). Therefore, we can be confident that plasma isotopic measurements of 8-day-old Sparrow chicks reflect entirely or almost entirely the isotopic signature of the diet provided by parental feeding rather than the isotopic signature of the yolk.

After the field season, we freeze-dried plasma samples from adults and chicks overnight, homogenized them and loaded them in tin cups for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analyses. Isotopic assays were carried out at the Duke Environmental Stable Isotope Laboratory (Duke University, NC, USA). Results are expressed as the standard δ notation (‰) relative to Pee Dee belemnite for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$. The mean difference between two standards of acetanilide within the same assay was $0.24 \pm 0.06\text{‰}$ for $\delta^{15}\text{N}$ and $0.12 \pm 0.06\text{‰}$ for $\delta^{13}\text{C}$ (mean \pm se, $n = 4$ assays). The mean difference between two measurements of standard acetanilide in different assays was $0.07 \pm 0.02\text{‰}$ for $\delta^{15}\text{N}$ and $0.09 \pm 0.02\text{‰}$ for $\delta^{13}\text{C}$ (mean \pm se, $n = 4$ assays).

Data analyses

When possible, lipids should be removed from plasma samples before measuring isotopic ratios because lipids are depleted in ^{13}C (Post *et al.* 2007). In our study, because of the small size of Lincoln's Sparrows, we only collected a small amount of plasma, which did not allow us to remove lipids chemically from our samples. Therefore, to each of the statistical models with $\delta^{13}\text{C}$ as a response, we added the C : N ratio as a covariate, as it strongly predicts lipid content in animal samples (Post *et al.* 2007). Additionally, we previously discovered that the isotopic signature of Lincoln's Sparrows could change with time (between spring and summer; Beaulieu & Sockman 2012). We thus first checked the effects of date on the isotopic signature of the birds considered in the present study; we did not find any effect, presumably because the time scale in the present study is much shorter than in our previous study.

For statistical analyses, we used mixed effects linear regressions, which become general linear models in the absence of a nested random effect. These models use Z-tests, which assume a standard

normal sampling distribution under the null hypothesis that a coefficient equals zero. To compare the isotopic signatures of adults with and without chicks, we used sex, breeding status (absence or presence of chicks) and their interaction as fixed factors in each of two general linear models, one with $\delta^{13}\text{C}$ and one with $\delta^{15}\text{N}$ as the response.

To compare isotopic ratios between chicks and adults, we used age category (adult or chick), sex and their interaction as fixed factors, and nested individual within family as a random intercept and random coefficient for age and sex (covariance structure: unstructured) in each of two mixed effects linear regressions, one with $\delta^{13}\text{C}$ (in which the C : N ratio was included as a covariate, see above) and one with $\delta^{15}\text{N}$ as the response.

Finally, we estimated the proportion of each prey in the diet of adult Lincoln's Sparrows (without and with chicks) and in the diet of chicks by using mixing models for stable isotope analyses in R (SIAR v4). SIAR offers the possibility through a Bayesian approach to investigate complex dietary systems by considering uncertainties related to consumers, multiple food resources and diet-tissue isotopic fractionation (Parnell *et al.* 2010). As such, SIAR models incorporate the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ means and standard deviations of consumers and of food resources, as well as trophic enrichment factors for ^{13}C and ^{15}N , and generate probability distributions for food resources in the diet of consumers. Based on three studies comparing plasma and diet isotopic values in passerine birds (Hobson & Clark 1993, Evans-Ogden *et al.* 2004, Tsahar *et al.* 2008), we used for these analyses the following trophic enrichment factors (mean \pm sd): $0.5 \pm 0.3\text{‰}$ for $\delta^{13}\text{C}$ and $3.3 \pm 0.5\text{‰}$ for $\delta^{15}\text{N}$. However, these trophic enrichment factors can be impacted by growth in chicks. For instance, by feeding growing chicks and adults of Rhinoceros Auklets *Cerorhinca monocerata* with the same diet in captivity, Sears *et al.* (2009) found lower $\delta^{15}\text{N}$ values in chicks than in adults. This difference is likely to be due to a difference in ^{15}N fractionation between growing chicks and adults, growth being related to a better nitrogen-use efficiency responsible for ^{15}N depletion. Indeed, at fledging (i.e. after most growth had occurred), these differences of trophic enrichment factors between adults and chicks disappear (Sears *et al.* 2009).

We did not have direct information about isotopic fractionation in 8-day-old Lincoln's Sparrows

(i.e. at fledging). Thus, we conducted SIAR analyses first by using the same trophic enrichment factor in chicks and in adults, and secondly after correcting them in chicks because of the potential ^{15}N depletion in growing chicks. We applied correction factors only in SIAR models and not directly in our analyses of isotopic values because correction factors are likely to vary between individual chicks. Because SIAR models do not use individual values but the mean of isotopic values for a group of individuals (chicks), we were able to use the mean correction factor for ^{13}C and ^{15}N values given by Sears *et al.* (2009) in these analyses. For this correction, we subtracted 0.2‰ from the ^{15}N trophic enrichment factor of adults and 0.3‰ from the ^{13}C trophic enrichment factor of adults (Sears *et al.* 2009). The 95% range of the high-density regions of residual variance for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from SIAR models with and without correction of trophic enrichment factors was similar (Table 1), indicating similar fit of both models. Moreover, both models recovered prey proportions in the diet of chicks that were very close. For these reasons, we present below only the results of the model including corrected trophic enrichment factors in chicks.

For SIAR models, we used the isotopic values of six groups of potential food types: dandelion (*Taraxacum*) seeds, willow (*Salix*) seeds, grasshoppers (Orthoptera), insect 1, insect 2 and spiders (Araneae). These were collected over the field season in 2010 at our field site that we measured in another study (Beaulieu & Sockman 2012). Because of isotopic similarity, 'insect 1' comprised crane flies (Tipulidae), ants (Formicidae) and caterpillars, and 'insect 2' comprised ladybirds

Table 1. The 95% high-density region values for residual variance (standard deviation (sd)) from SIAR models for adult Lincoln's Sparrows (without and with chicks) and for chicks. For chicks, calculations were carried out with and without correction of the trophic enrichment factor due to the potential effects of growth on isotopic enrichment (see Methods). Lower residual variance values reflect better fit for the models.

	sd $\delta^{15}\text{N}$		sd $\delta^{13}\text{C}$	
	Low 95%	High 95%	Low 95%	High 95%
Adults with no chicks	0.00	1.00	0.51	1.71
Adults with chicks	0.00	0.66	0.55	1.33
Chicks	0.00	0.54	0.78	1.36
Chicks (corrected)	0.00	0.51	0.79	1.37

Table 2. Mean isotopic values and standard deviations of each prey type used in SIAR models. Values are expressed as the standard δ notation (‰) relative to atmospheric N_2 for $\delta^{15}N$ and Pee Dee belemnite for $\delta^{13}C$. Crane flies, ants and caterpillars were combined into 'Insect 1', and ladybirds, damselflies and flies into 'Insect 2' due to isotopic similarities. For more details, see Beaulieu and Sockman (2012).

	$\delta^{15}N$		$\delta^{13}C$	
	Mean	sd	Mean	sd
Dandelion seeds	0.57	0.28	-28.61	0.21
Willow seeds	1.32	0.25	-23.49	0.04
Grasshoppers	1.10	0.17	-26.20	0.24
Insect 1	3.62	1.76	-25.83	1.80
Insect 2	5.55	1.47	-24.68	0.74
Spiders	7.83	0.58	-24.49	0.28

(Coccinellidae), damselflies (Odonata) and non-tipulid flies (Diptera). Among these prey items, spiders had the highest $\delta^{15}N$ and $\delta^{13}C$ values, whereas dandelion seeds, willow seeds and grasshoppers had the lowest $\delta^{15}N$ values. The mean isotopic values of each prey type used in our SIAR models as well as their respective standard deviations are presented in Table 2. Statistical analyses were conducted in STATA IC 10.1 for Macintosh (Stata Corporation, College Station, TX, USA). Results are expressed as means \pm 1 se.

RESULTS

We found no difference in the isotopic signatures of adults feeding nestlings and those not raising young (breeding-status-effect on $\delta^{15}N$: $z = -0.35$, $P = 0.729$; $\delta^{13}C$: $z = -1.40$, $P = 0.161$; Fig. 1), and the effect of the breeding status did not vary by sex of the adult (sex-by-breeding status interaction effect on $\delta^{15}N$: $z = 1.09$, $P = 0.275$; $\delta^{13}C$: $z = 1.26$, $P = 0.208$). Males and females had similar isotopic signatures (sex effect on $\delta^{15}N$: $z = -0.66$, $P = 0.512$; $\delta^{13}C$: $z = -1.08$, $P = 0.282$).

Similarly, we found no differences in isotopic signature between males and females in our tests comparing the isotopic values of parents to those of their offspring (sex effect on $\delta^{15}N$: $z = -0.31$, $P = 0.754$; $\delta^{13}C$: $z = -0.59$, $P = 0.557$). However, although chicks had similar $\delta^{13}C$ values to adults (age effect on $\delta^{13}C$: $z = 0.74$, $P = 0.459$; Fig. 1), they exhibited significantly lower $\delta^{15}N$ values (age effect on $\delta^{15}N$: $z = 3.05$, $P = 0.002$; Fig. 1). We found no evidence of a reliable sex-by-age

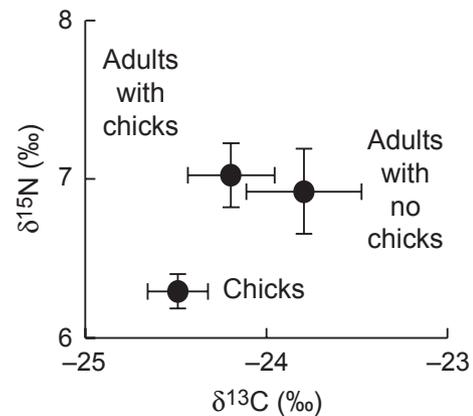


Figure 1. Isotopic signatures (mean \pm se) of adult Lincoln's Sparrows with and without chicks, and of 8-day-old chicks (at fledging). Raw values (i.e. uncorrected because of potential different isotopic fractionations in adults and chicks) are represented.

interaction ($\delta^{15}N$: $z = 1.87$, $P = 0.062$; $\delta^{13}C$: $z = 1.61$, $P = 0.108$).

Having established using frequentist statistics that plasma $\delta^{15}N$ values were lower in chicks than in adults, we took a Bayesian approach using SIAR mixing models to determine the likely cause of that difference. SIAR mixing models suggested that willow seeds and 'Insects 2' (ladybirds, damselflies and flies) were the main food sources both for adults and for chicks, as they represented together half of their diet (Fig. 2). The proportion of willow seeds was higher in adults with no chicks than in adults provisioning chicks (modal values: 35 and 26%, respectively). In contrast, the proportion of grasshoppers was higher in adults provisioning chicks than in adults with no chicks (modal values: 12 and 2%, respectively), suggesting that provisioning adults partially abandoned willow seeds as a feeding resource in favour of grasshoppers (although these apparent diet differences were not reflected by significantly different isotopic values between adults without and with chicks; Fig. 1). The proportion of spiders was high in adults both with and without chicks (modal values: 24 and 22%, respectively). Interestingly, spiders contributed less to the diet of chicks (modal value: 14%) than to the diet of adults (Fig. 2). Instead, the proportion of grasshoppers was higher in the diet of chicks than in the diet of their parents (modal values: 18 and 12%, respectively). Finally, and to a lesser extent, differences in the contribution of plant material in the diets of chicks and their

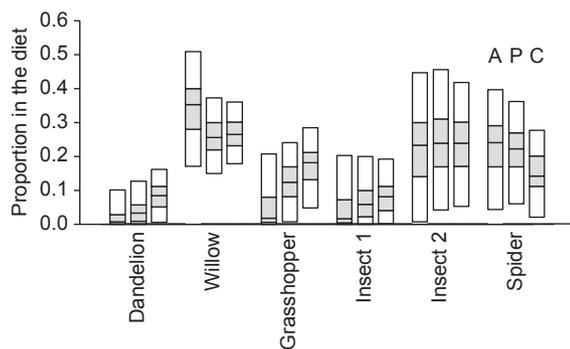


Figure 2. Proportion of prey in the diet of adult Lincoln's Sparrows without chicks (A), of adults provisioning chicks (P) and of the chicks (C). The bars show the credibility intervals at 50% (grey) and 95% (white), as well as the modal values given by SIAR for each food resource. For chicks, calculations were carried out with correction of the trophic enrichment factor due to the potential effects of growth on isotopic enrichment (see Methods). Some insect sources were combined into two categories (Insect 1: crane flies, ants, caterpillars, and Insect 2: ladybirds, damselflies, flies) because of isotopic similarities.

parents were also observed, with higher proportions in the diet of chicks than in the diet of their parents (modal values for dandelion seeds: 8 and 3%, respectively; Fig. 2). No obvious difference was apparent between the respective diet of adults and chicks for the other prey categories (Fig. 2).

DISCUSSION

We found in Lincoln's Sparrows that feeding chicks did not appreciably alter the isotopic signature of adults, and that chicks had lower $\delta^{15}\text{N}$ values than their parents. This difference in $\delta^{15}\text{N}$ values between parents and young appears to be the result of a lower relative contribution of prey from high trophic levels (spiders) and a higher relative consumption of prey from lower trophic levels (grasshoppers and plant material) in the diet of chicks than in the diet of their parents. Altogether, these results support our 'delivery hypothesis' about food allocation between parents and young in Lincoln's Sparrows. These results also illustrate the use of stable isotope analysis in determining the general outcome of food allocation decisions between parents and young.

Considering that spiders represent the most profitable part of the diet of Lincoln's Sparrows and that Lincoln's Sparrows are relatively short-lived, our 'conflict hypothesis' predicts that parent Lincoln's Sparrows should withhold this prey from

their own diet and that the contribution of spiders should be more important in the diet of chicks than in the diet of their parents. In contrast, we found that the proportion of spiders was similar in the diet of adults with no chicks and in the diet of adults provisioning chicks, and that the diet of chicks was characterized by lower proportions of spiders than was the diet of adults, thereby discrediting our 'conflict hypothesis'.

To explain this discrepancy, it is possible that Lincoln's Sparrow chicks have to be fed spiders at a low and fixed level (with a proportion of about 14%). Indeed, other studies conducted in passerine birds (and using techniques other than stable isotope analysis) show proportions of spiders in the diet of their chicks very close to the proportions observed in our study: 9% in Water Pipits *Anthus spinoletta* (Brodmann & Reyer 1999), 12% in Brown Songlarks *Megalurus cruralis* (Magrath *et al.* 2004), 9% in Great Tits *Parus major* (Wilkin *et al.* 2009) and 6–14% in Eurasian Blue Tits *Cyanistes caeruleus* (Grieco 2002). Moreover, even experimentally supplementing parents with extra food does not affect this proportion in Eurasian Blue Tits (Grieco 2002), suggesting that this proportion is fixed in the diet of passerine chicks.

It is interesting to note that the main difference in food contribution between the diet of chicks and that of adults was observed for spiders, the prey that was expected to be the most profitable for adults and chicks. It is therefore also possible that, contrary to our 'conflict hypothesis' in a short-lived species, Lincoln's Sparrow parents invest more in their own diet than in the diet of their young, as they consume more spiders than their chicks. This hypothesis is reinforced by the fact that they feed their chicks slightly more plant material (which has been associated with higher chick mortality rate in House Sparrows *Passer domesticus*; Peach *et al.* 2008). However, consistent with our 'delivery hypothesis' predicting that larger prey species maximize energy delivery to young, spiders smaller than grasshoppers may be better suited for adults' self-feeding than for chick provisioning. Because of the absence of delivery constraint on self-feeding, parents may be able to include a higher proportion of spiders in their diet than in the diet of their offspring, and may thus optimize their energy intake with small and energetic prey. This may be especially true when parents forage far away from their nest or for a long period of time. Indeed, studies conducted in passerine birds have shown that parents are more likely to bring

larger prey to their chicks when foraging for a long time and in distant foraging patches (Kaspari 1991, Grieco 2002). In this case, parents may consume smaller prey such as spiders to satisfy their own energy requirements, while provisioning their young with larger prey, such as grasshoppers, as we observed in the present study. As Lincoln's Sparrows forage relatively close to their nest (on average < 60 m, Beaulieu & Sockman 2012), this suggests that allocation decisions by adults may not be due to foraging distances but to searching time. Moreover, provisioning chicks with large prey may be a way for parents to limit nest detection by predators by reducing provisioning rate to the nest without compromising energy delivery rate to the chicks (as suggested by the high number of depredated nests; predation risk was high in our field site). Therefore, optimal foraging theory appears more likely to explain the differences in the diet of Lincoln's Sparrow parents and chicks that we observed in our study than does parent-offspring conflict. However, this does not mean that life-history traits do not have any influence on food allocation decisions made by Lincoln's Sparrow parents (as mentioned in the Introduction, both parent-offspring conflict and optimal foraging strategies are expected to act together on parental feeding decisions). It is likely that the influence of life-history traits is minor relative to (and therefore overwhelmed by) the influence of optimal foraging strategy. Therefore studies examining the influence of these two factors under variable environmental conditions would be of great interest. Indeed, the influence of life-history traits may become important only when the availability of prey devoted to provisioning chicks or self-feeding is limited in the environment, and the parent-offspring conflict becomes more critical.

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REFERENCES

- Ammon, E.M. 1995. Lincoln's Sparrow (*Melospiza lincolni*). In Poole, A. (ed.) *The Birds of North America Online*. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/191>
- Bañbura, J., Lambrechts, M.M., Blondel, J., Perret, P. & Cartan-Son, M. 1999. Food handling-time of Blue Tit chicks: constraints and adaptation to different prey types. *J. Avian Biol.* **30**: 263–270.
- Beaulieu, M. & Sockman, K.W. 2012. One meadow for two sparrows: resource partitioning in a high elevation habitat. *Oecologia* **170**: 529–540.
- Beaulieu, M., Raclot, T., Le Maho, Y., Ropert-Coudert, Y. & Ancel, A. 2009a. Can a handicapped parent rely on its partner? An experimental study within Adélie Penguin pairs. *Anim. Behav.* **78**: 313–320.
- Beaulieu, M., Thierry, A.M., Raclot, T., Le Maho, Y., Ropert-Coudert, Y., Gachot-Neveu, H. & Ancel, A. 2009b. Sex-specific parental strategies according to the sex of offspring in the Adélie Penguin. *Behav. Ecol.* **20**: 878–883.
- Brodmann, P.A. & Reyer, H.U. 1999. Nestling provisioning in Water Pipits (*Anthus spinoletta*): do parents go for specific nutrients or profitable prey? *Oecologia* **120**: 506–514.
- Cameron-Macmillan, M.L., Walsh, C.J., Wilhelm, S.I. & Storey, A.E. 2007. Male chicks are more costly to rear than females in a monogamous seabird, the Common Murre. *Behav. Ecol.* **18**: 81–85.
- Evans-Ogden, L.J., Hobson, K.A. & Lank, D.B. 2004. Blood isotopic ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) turnover and diet-tissue fractionation factors in captive Dunlin (*Calidris alpina pacifica*). *Auk* **121**: 170–177.
- Fry, B. & Arnold, C. 1982. Rapid $^{13}\text{C}/^{12}\text{C}$ turnover during growth of Brown Shrimp (*Penaeus aztecus*). *Oecologia* **54**: 200–204.
- Girard, J., Baril, A., Mineau, P. & Fahrig, L. 2011. Carbon and nitrogen stable isotope ratios differ among invertebrates from field crops, forage crops, and non-cropped land uses. *Ecoscience* **18**: 98–109.
- Granadeiro, J.P., Monteiro, L.R., Silva, M.C. & Furness, W. 2002. Diet of Common Terns in the Azores, Northeast Atlantic. *Waterbirds* **25**: 149–155.
- Grieco, F. 2002. Time constraint on food choice in provisioning Blue Tits, *Parus caeruleus*: the relationship between feeding rate and prey size. *Anim. Behav.* **64**: 517–526.
- Hobson, K.A. & Clark, R.G. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *Auk* **110**: 638–641.
- Kaspari, M. 1991. Central place foraging in Grasshopper Sparrows: opportunism or optimal foraging in a variable environment? *Oikos* **60**: 3017–3312.
- Koenig, W.D., Schaefer, D.J., Mambelli, S. & Dawson, T.E. 2008. Acorns, insects, and the diet of adults versus nestling Acorn Woodpeckers. *J. Field Ornithol.* **79**: 280–285.
- MacAvoy, S.E., Macko, S.A. & Arneson, L.S. 2005. Growth versus metabolic tissue replacement in mouse tissues determined by stable carbon and nitrogen isotope analysis. *Can. J. Zool.* **83**: 631–641.

- Magrath, M.J.L., Van Lieshout, E., Visser, G.H. & Komdeur, J. 2004. Nutritional bias as a new mode of adjusting sex allocation. *Biol. Lett.* **271**: 347–349.
- McDonald, P.G., Kazem, A.J.N. & Wright, J. 2007. A critical analysis of 'false-feeding' behavior in a cooperatively breeding bird: disturbance effects, satiated nestlings or deception? *Behav. Ecol. Sociobiol.* **61**: 1623–1635.
- Nisbet, I.C.T., Montoya, J.P., Burger, J. & Hatch, J.J. 2002. Use of stable isotopes to investigate individual differences in diets and mercury exposures among Common Terns *Sterna hirundo* in breeding and wintering grounds. *Mar. Ecol. Prog. Ser.* **242**: 267–274.
- Orians, G.H. & Pearson, N.E. 1979. On the theory of central place foraging. In: Horn, D.J., Mitchell, R.D. & Stairs, G.R. (eds) *Analysis of Ecological Systems*: 154–177, Columbus, OH: Ohio State University Press.
- Parnell, A., Inger, R., Bearhop, S. & Jackson, A.L. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* **5**: e9672.
- Peach, W.J., Vincent, K.E., Fowler, J.A. & Grice, P.V. 2008. Reproductive success of House Sparrows along an urban gradient. *Anim. Conserv.* **11**: 493–503.
- Podlesak, D.W., McWilliams, S.R. & Hatch, K.A. 2005. Stable isotopes in breath, blood, faeces and feathers can indicate intra-individual changes in the diet of migratory songbirds. *Oecologia* **142**: 501–510.
- Post, D.M., Layman, C.A., Albrecht Arrington, D., Takimoto, G., Quattochi, J. & Montana, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**: 179–189.
- Quillfeldt, P., Masello, J.F. & Hamer, K.C. 2004. Sex differences in provisioning rules and honest signalling of need in Manx Shearwaters, *Puffinus puffinus*. *Anim. Behav.* **68**: 613–620.
- Ramsay, S.L. & Houston, D.C. 2003. Amino acid composition of some woodland arthropods and its implications for breeding tits and other passerines. *Ibis* **145**: 227–237.
- Schmidt, G.P., Domermuth, G.H. & Potter, L.M. 1985. Dietary protein and yolk sac inoculation with *Escherichia coli* in young turkeys. *Poultry Sci.* **64**: 1343–1349.
- Sears, J., Hatch, S.A. & O'Brien, D.M. 2009. Disentangling effects of growth and nutritional status on seabird stable isotope ratios. *Oecologia* **159**: 41–48.
- Skutch, A.F. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* **91**: 430–455.
- Sockman, K.W. 2008. Ovulation order mediates a trade-off between pre-hatching and post-hatching viability in an altricial bird. *PLoS ONE* **3**: e1785.
- Sockman, K.W. 2009. Annual variation in vocal performance and its relationship with bill morphology in Lincoln's Sparrows, *Melospiza lincolnii*. *Anim. Behav.* **77**: 663–671.
- Stearns, S.C. 1989. Trade-offs in life-history evolution. *Funct. Ecol.* **3**: 259–268.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. New York: Oxford University Press.
- The Animal Ageing & Longevity Database. 2013. Available at <http://genomics.senescence.info/species/> (accessed 11 July 2013).
- Trivers, R. 1974. Parent-offspring conflict. *Am. Zool.* **14**: 249–264.
- Tsahar, E., Wolf, N., Izhaki, I., Arad, Z. & Martinez del Rio, C. 2008. Dietary protein influences the rate of ¹⁵N incorporation in blood cells and plasma of Yellow-Vented Bulbuls (*Pycnonotus xanthopygus*). *J. Exp. Biol.* **211**: 459–465.
- Tully, T.N., Lawton, M.P.C. & Dorrestein, G.M. 2000. *Avian Medicine*. Edinburgh: Elsevier Science Limited & Butterworth-Heinemann.
- Wilkin, T.A., King, L.E. & Sheldon, B.C. 2009. Habitat quality, nestling diet, and provisioning behavior in Great Tits *Parus major*. *J. Avian Biol.* **40**: 135–145.
- Wimp, G.M., Murphy, S.M., Lewis, D., Douglas, M.R., Ambikapathi, R., Van-Tull, L.A., Gratton, C. & Denno, R.F. 2013. Predator hunting mode influences patterns of prey use from grazing and epigeic food webs. *Oecologia* **171**: 505–515.

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SUPPORTING INFORMATION

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

Table S1. Summary of previous studies examining $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values both in adults and in chicks.

Table S1. Summary of previous studies examining $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values both in adults (A) and chicks (C) (without taking into account possible differential affects of fractionation in adults and chicks). Kinship refers to the parental relationship between adults and chicks: ‘yes’ indicates that adults were the biological parents of the chicks, ‘no’ indicates that adults were not related to the chicks, and ‘?’ indicates that the study does not provide details about kinship. The difference (or the absence of difference) between the isotopic signature of adults and chicks is given in parentheses (= identical, > higher, < smaller, M: males, F: females). Sears *et al.* (2009) refers to the field experiment of this study, and not to the captive experiment where food was controlled.

Species	Kinship	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	Tissue	Reference
<i>Melanerpes formicivorus</i>	Yes	C < A (1.1 ‰)	C > A (0.6 ‰)	Blood	Koenig <i>et al.</i> 2008
<i>Sula sula</i>	?	C = A	C > A (1.5 ‰)	Feather (C) / Blood (A)	Young <i>et al.</i> 2010
<i>Fregata minor</i>	Yes	C = A	C = A	Blood	Cherel <i>et al.</i> 2008
<i>Onychoprion fuscatus</i>	Yes	C > A (1.0 ‰)	C < A (0.5 ‰)	Blood	Cherel <i>et al.</i> 2008
<i>Sterna hirundo</i>	Yes	C = A	C = A	Feather	Nisbet <i>et al.</i> 2002
<i>Alle alle</i>	Yes/No	C < A (0.3-1.0 ‰)	C > A (0.3-1.7 ‰)	Blood	Harding <i>et al.</i> 2008
	No	C = A	C = A	Blood	Fort <i>et al.</i> 2010
<i>Uria aalge</i>	Yes	C < A (1.0 ‰)	C < A (0.7 ‰)	Blood	Davies <i>et al.</i> 2009
<i>Ptychoramphus alentius</i>	Yes	C > A (0.5 ‰)	C = A	Blood	Davies <i>et al.</i> 2009
<i>Fratercula cirrhata</i>	Yes	C = A	C = A	Blood	Davies <i>et al.</i> 2009
	Yes	C < A (0.1 ‰)	C < A (0.3 ‰)	Blood	Davies <i>et al.</i> 2009
<i>Cerorhinca monocerata</i>	?	C < A (0.2 ‰)	C < A (0.3 ‰)	Red blood cells	Sears <i>et al.</i> 2009
	Yes	C < A (0.1 ‰)	C < A (0.1 ‰)	Blood	Hipfner <i>et al.</i> 2013
<i>Rissa tridactyla</i>	Yes	C > A (0.4 ‰)	?	Muscle	Hobson 1993
<i>Uria lomvia</i>	No	C > A (0.5 ‰)	?	Muscle	Hobson 1993
<i>Larus hyperboreus</i>	No	C = A	?	Muscle	Hobson 1993
<i>Fulmarus glacialis</i>	No	C = A	?	Muscle	Hobson 1993
	Yes	C > A (F) (1.0 ‰) C = A (M)	C > A (F) (0.5 ‰) C = A (M)	Blood	Forero <i>et al.</i> 2005
<i>Macronectes giganteus</i>	Yes	C < A (F) (2.6 ‰) C < A (M) (1.8 ‰)	C < A (F) (1.4 ‰) C < A (M) (1.0 ‰)	Blood	Raya Rey <i>et al.</i> 2012
	No	C > A (0.4 ‰) C = A	C < A (0.5-1.3 ‰)	Feather	Hedd <i>et al.</i> 2006
<i>Puffinus tenuirostris</i>	Yes	C > A (2.0 ‰)	C > A (0.6 ‰)	Plasma	Cherel <i>et al.</i> 2005
<i>Bulweria bulwerii</i>	?	C < A (2.0 ‰)	C > A (1.0 ‰)	Blood	Bond <i>et al.</i> 2010
<i>Oceanodroma tristrami</i>	?	C < A (2.0 ‰)	C < A (2.0 ‰)	Blood	Bond <i>et al.</i> 2010
<i>Puffinus pacificus</i>	?	C > A (9.0 ‰)	C = A	Blood	Bond <i>et al.</i> 2010
<i>Puffinus nativitatis</i>	?	C = A	C = A	Blood	Bond <i>et al.</i> 2010
<i>Fulmarus glacialisoides</i>	?	C > A (1.0 ‰)	C < A (0.5 ‰)	Red blood cells	Hodum & Hobson 2000
<i>Thalassoica antarctica</i>	?	C > A (1.0 ‰)	C < A (0.5 ‰)	Red blood cells	Hodum & Hobson 2000

<i>Daption capense</i>	?	C > A (1.0 ‰)	C < A (0.5 ‰)	Red blood cells	Hodum & Hobson 2000
<i>Pagodroma nivea</i>	?	C > A (2.0 ‰)	C < A (0.2 ‰)	Red blood cells	Hodum & Hobson 2000
<i>Pachyptila belcheri</i>	Yes	C = A	C = A	Red blood cells	Quillfeldt <i>et al.</i> 2008
	No	C > A (3.8 ‰)	C > A (5.5 ‰)	Down (C) / Feather (A)	Weiss <i>et al.</i> 2009
<i>Thalassarche melanophris</i>	No	C = A	C = A	Down (C) / Feather (A)	Weiss <i>et al.</i> 2009
<i>Procellaria aequinoctialis</i>	No	C = A	C = A	Down (C) / Feather (A)	Weiss <i>et al.</i> 2009
<i>Pygoscelis papua</i>	No	C = A	C < A (1.0 ‰)	Down (C) / Feather (A)	Weiss <i>et al.</i> 2009
<i>Endyptes chrysocome</i>	No	C = A	C = A	Down (C) / Feather (A)	Weiss <i>et al.</i> 2009
	No	C = A	C = A	Blood	Cherel <i>et al.</i> 2007
<i>Aptenodytes patagonicus</i>	No	C = A	C = A	Blood	Cherel <i>et al.</i> 2007
<i>Endyptes chrysolophus</i>	No	C > A (0.5 ‰)	C = A	Blood	Cherel <i>et al.</i> 2007
<i>Endyptes moseleyi</i>	Yes/No	C < A (F) (1.0-1.9 ‰)	C < A (F) (0.7 ‰)	Blood	Booth & McQuaid 2013
	No	C = A	C > A (0.5 ‰)	Blood	Tierney <i>et al.</i> 2008
<i>Pygoscelis adeliae</i>	Yes	C = A (M)	C < A (M) (0.7 ‰)	Blood	Thierry <i>et al.</i> 2013
	No	C > A (1.0 ‰)	C = A	Blood	Cherel 2008
<i>Aptenodytes forsteri</i>	No	C = A	C = A	Blood	Cherel 2008
<i>Spheniscus magellanicus</i>	Yes	C > A (0.2 ‰)	C < A (0.3 ‰)	Blood	Forero <i>et al.</i> 2002
<i>Megadyptes antipodes</i>	No	C > A (1.0 ‰)	C > A (0.7 ‰)	Feather (C) / Blood (A)	Browne <i>et al.</i> 2011
<i>Endyptula minor</i>	Yes/No	C < A (0.2-1.0 ‰)	C < A (0.3-0.6 ‰)	Blood	Chiaradia <i>et al.</i> 2010

REFERENCES

- Bond, A.L., McClelland, G.T.W., Jones, I.L., Lavers, J.L. & Kyser, T.K.** 2010. Stable isotopes confirm community patterns in foraging among Hawaiian Procelariiformes. *Waterbirds* **33**: 50-58.
- Booth, J.M. & McQuaid, C.D** 2013. Northern rockhopper penguins prioritise future reproduction over chick provisioning. *Mar. Ecol. Prog. Ser.* **486**: 289-304.
- Browne, T., Lalas, C., Mattern, T. & Van Heezik, Y.** 2011 Chick starvation in Yellow-Eyed Penguins: evidence for poor diet quality and selective provisioning of chicks from conventional diet analysis and stable isotopes. *Austral Ecol.* **36**: 99-108.
- Cherel, Y., Hobson, K.A. & Weimerskirch, H.** 2005. Using stable isotopes to study resource acquisition and allocation in procelariiform seabirds. *Oecologia* **145**: 533-540.
- Cherel, Y., Hobson, K.A., Guinet, C. & Vanpe, C.** 2007. Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. *J. Anim. Ecol.* **76**: 826-836.
- Cherel, Y.** 2008. Isotopic niches of emperor and Adélie Penguins in Adélie Land, Antarctica. *Mar. Biol.* **154**: 813-821.
- Cherel, Y., Le Corre, M., Jaquemet, S., Ménard, F., Richard, P. & Weimerskirch, H.** 2008. Resource partitioning within a tropical seabird community: new information from stable isotopes. *Mar. Ecol. Prog. Ser.* **366**: 281-291.
- Chiaradia, A., Forero, M.G., Hobson, K.A. & Cullen, J.M.** 2010. Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey. *ICES J. Mar. Sci.* **67**: 1710-1720.

- Davies, W.E., Hipfner, J.M., Hobson, K.A. & Ydenberg, R.C.** 2009. Seabird seasonal trophodynamics: isotopic patterns in a community of Pacific alcids. *Mar. Ecol. Prog. Ser.* **382**: 211-219.
- Forero, M.G., Hobson, K.A., Bortolotti, G.R., Doñazar, J.A., Bertellotti, M. & Blanco, G.** 2002. Food resource utilization by the Magellanic Penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on offspring quality. *Mar. Ecol. Prog. Ser.* **234**: 289-299.
- Forero, M.G., González-Solís, J., Hobson, K.A., Doñazar, J.A., Bertellotti, M., Blanco, G. & Bortolotti, G.R.** 2005. Stable isotopes reveal trophic segregation by sex and age in the Southern Giant Petrel in two different food webs. *Mar. Ecol. Prog. Ser.* **296**: 107-113.
- Fort, J., Cherel, Y., Harding, A.M.A., Welcker, J., Jakubas, D., Steen, H., Karnovsky, N.J. & Grémillet, D.** 2010. Geographic and seasonal variability in the isotopic niche of Little Auks. *Mar. Ecol. Prog. Ser.* **414**: 293-302.
- Harding, A.M.A., Hobson, K.A., Walkusz, W., Dmoch, K., Karnovsky, N.J., Van Pelt, T.I. & Lifjeld, J.T.** 2010. Can stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) measurements of Little Auk (*Alle alle*) adults and chicks be used to track changes in high-Arctic marine foodwebs? *Polar Biol.* **31**: 725-733.
- Hedd, A. & Montevecchi, W.A.** 2006. Diet and trophic position of Leach's Storm-Petrel *Oceanodroma leucorhoa* during breeding and moult, inferred from stable isotope analysis of feathers. *Mar. Ecol. Prog. Ser.* **322**: 291-301.

- Hipfner, J.M., McFarlane-Tranquilla, L., Addison, B., & Hobson, F.A.** 2013. Trophic responses to the hatching of offspring in a central-place foraging seabird. *J. Ornithol.* **154**: 965-970.
- Hobson, K.A.** 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent stable-isotope models. *Mar. Ecol. Prog. Ser.* **95**: 7-18.
- Hodum, P.J. & Hobson, K.A.** 2000. Trophic relationships between Antarctic fulmarine petrel: insights into dietary overlap and chick provisioning strategies inferred from stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses. *Mar. Ecol. Prog. Ser.* **198**: 273-281.
- Koenig, W.D., Schaefer, D.J., Mambelli, S. & Dawson, T.E.** 2008. Acorns, insects, and the diet of adults versus nestling Acorn Woodpeckers. *J. Field Ornithol.* **79**: 280-285.
- Nisbet, I.C.T., Montoya, J.P., Burger, J. & Hatch, J.J.** 2002. Use of stable isotopes to investigate individual differences in diets and mercury exposures among Common Terns *Sterna hirundo* in breeding and wintering grounds. *Mar. Ecol. Prog. Ser.* **242**: 267-274.
- Raya Rey, A., Polito, M., Archuby, D. & Coria, N.** 2012. Stable isotopes identify age- and sex-specific dietary partitioning and foraging habitat segregation in Southern Giant Petrels breeding in Antarctica and Southern Patagonia. *Mar. Biol.* **159**: 1317-1326.
- Sears, J., Hatch, S.A. & O'Brien, D.M.** 2009. Disentangling effects of growth and nutritional status on seabird stable isotope ratios. *Oecologia* **159**: 41-48.
- Thierry, A.M., Ropert-Coudert, Y. & Raclot, T.** 2013. Elevated corticosterone levels decrease reproductive output of chick-rearing Adélie penguins but do not affect chick mass at fledging. *Conserv. Physiol.* **1**: cot007

- Tierney, M., Southwell, C., Emmerson, L.M. & Hindell, M.A.** 2008. Evaluating and using stable-isotope analysis to infer diet composition and foraging ecology of Adélie Penguins *Pygoscelis adeliae*. *Mar. Ecol. Prog. Ser.* **355**: 297-307.
- Weiss, F., Furness, R.W., McGill, R.A.R., Strange, I.J., Masello, J.F. & Quillfeldt, P.** 2009. Trophic segregation of Falkland Islands seabirds: insight from stable isotope analysis. *Polar Biol.* **32**: 1753-1763.
- Young, H.S., Shaffer, S.A., McCauley, D.J., Foley, D.G., Dirzo, R. & Block, B.A.** 2010. Resource partitioning by species but not sex in sympatric boobies in the central Pacific Ocean. *Mar. Ecol. Prog. Ser.* **403**: 291-301.