J Ornithol (2006) 147:543–548
DOI 10.1007/s10336-006-0077-1

ORIGINAL ARTICLE

Differences in food delivered to chicks by males and females of little auks (*Alle alle*) on South Spitsbergen

Katarzyna Wojczulanis · Dariusz Jakubas · Wojciech Walkusz · Liv Wennerberg

Received: 31 October 2005 / Revised: 3 March 2006 / Accepted: 20 March 2006 / Published online: 21 July 2006

Abstract Sex differences in the quality and quantity of food loads brought to little auk (*Alle alle*) chicks were investigated in a large colony in Hornsund (South Spitsbergen). Adults returning to the colony were caught in mist-nets and food loads were taken from their gular pouch. The sex of each bird was determined by means of molecular methods. Females brought significantly more food per single load than males in terms of wet weight (30% more on average), number of prey items (46%) and energy contents (39%). However, there was no difference between the sexes in the size of prey taken. Energy-rich *Calanus glacialis*, originating from cold Arctic waters, was the most frequent prey item and made up the majority of food loads brought by both males and females (75 and 72%, respectively). This indicates that both sexes forage mainly in Arctic waters. However, differences in the proportion of cold water *Calanus* species (*C. glacialis* and *C. hyperboreus*), warm water *Calanus* species (*C. finmarchicus*), as well as other taxa, between males and females may suggest different ways of exploiting the feeding area.

Keywords Chick diet · Feeding ecology · Little auk

Communicated by P.H. Becker

K. Wojczulanis (✉) · D. Jakubas
Department of Vertebrate Ecology and Zoology,
University of Gdańsk, Legionów 9,
80-441 Gdansk, Poland
e-mail: wojczulanis@wp.pl

W. Walkusz
Institute of Oceanology, Polish Academy of Sciences,
Powstanców Warszawy 55, 81-712 Sopot, Poland

L. Wennerberg
Natural History Museum, University of Oslo,
1172, Blindern 0318 Oslo, Norway

Introduction

In severe environmental conditions, in which high-latitude seabirds live, considerable parental investment is required for reproductive success (Ashmole and Ashmole 1967; Lack 1968). Therefore, monogamy, with biparental care, is prevalent among seabirds. Although, in such breeding systems, males and females often divide their parental effort more or less equally, the form of their parental investment may be distributed unevenly over the whole breeding season, and/or they may use different foraging tactics to obtain food for chick provisioning. For example, chicks of thick-billed murres (*Uria lomvia*) are brooded and fed at the colony by both parents for 2–4 weeks, after which they are taken to sea by the males alone and cared for offshore (Gaston and Nettleship 1981; Gaston and Jones 1998). Furthermore, foraging patterns and dive durations differ between males and females during the chick-rearing period (Jones et al. 2002).

Sex differences may be affected by a variety of constraints imposed by anatomical, behavioral and ecological factors, and can result in different strategies of males and females in order to maximize fitness (Trivers 1972). Therefore, the cost–benefit functions of parental effort and, hence, the time and energy budgets of the two sexes should be different (Brunton 1988).

Little auks (*Alle alle*) are probably the most numerous colonial seabirds breeding in the high Arctic (Stempniewicz 2001). They are monogamous with very slight sexual dimorphism in size (expressed by slightly longer wing, bill, tarsus and slightly greater body mass among males; Stempniewicz 1981). Both sexes incubate the clutch and feed the young. Towards the end of breeding season, females cease feeding and males exclusively take care of the chicks (Stempniewicz 1995; Harding et al. 2004). There is little known about the investment of each sex in particular breeding activities. The only study is that of Harding et al. (2004) who studied male and female attendance at the colony and found that frequency of feeding trips tended to be higher in males as the breeding season progresses. The purpose of this study was to compare the food delivered to chicks by males and females.

The food of little auk chicks is almost exclusively composed of planktonic crustaceans. There are some regional differences in diet, but chicks are fed mainly copepods (*Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*), supplemented by amphipods (*Themisto* sp., *Apherusa* sp., *Gammarus* sp.) and larval fish (*Boreogadus saida*, *Liparis* sp.) (Stempniewicz 2001). In the Hornsund area of Spitsbergen, little auks feed mainly on copepods, particularly on an energy-rich species (*C. glacialis*) originating from cold Arctic waters (Karnovsky et al. 2003).

The specific objectives of this study were: (1) to compare the wet weight and energetic value of food loads brought by males and females, thus comparing the energy contribution to the chick between parents; (2) to evaluate the proportion of cold- and warm-water species in the food loads in order to identify possible differences in feeding areas of males and females; and (3) to compare the sizes of prey items brought by males and females, to determine if there are differences in food size preference.

Methods

Fieldwork

The fieldwork was conducted in a breeding colony on the Ariekammen slopes (77°00′N, 15°33′E), 1.5 km north of Hornsund fjord, South Spitsbergen. The data were collected during the chick-rearing period (24 July–5 August) in 2003, when chicks were 8–20 days old and both parents were participating in feeding.

Only adult birds (distinguished from subadults based on appearance of flight feathers and upper-wing coverts; Stempniewicz 2001) with filled gular pouches were included in the study. The birds were captured in a mist-net strung perpendicular to the slope with nest crevices. Birds were ringed and the food was gently scooped out from their gular pouch with a small plastic spoon. In total, 56 birds (29 males and 27 females) were captured.

Any food items spilled while releasing the birds from the net were collected on a sheet of plastic spread under the net and were kept with the bird they came from. Each food load was weighed to the nearest 0.1 g, then preserved in 40% alcohol and analyzed later at the Institute of the Oceanology, Polish Academy of Sciences.

A small blood sample (50 μl) was taken from each bird from the brachial vein and stored in 1 ml lysis buffer at 4°C for 2–3 months before laboratory analysis at the Natural History Museum, University of Oslo.

The birds were released unharmed after 5–10 min of handling.

Laboratory analyses

Prior to identification, food samples were rinsed with fresh water. Individuals larger than 1 cm were picked out and identified before the rest of the sample was divided into subsamples by means of micropipette. Organisms were identified to the lowest possible taxonomical level. Copepods were identified to developmental stages on the basis of morphological features (Sars 1903; Brodskii 1967; Mauchline 1998). The identification criteria given by Kwaśniewski et al. (2003) were applied to distinguish the three *Calanus* species. All individuals of each taxa were counted in the subsamples and the number of prey items in the total food load was extrapolated from the subsamples.

DNA was extracted in the laboratory from 100 μl of blood and buffer solution, using the Blood Mini kit (A&A Biotechnology, Gdynia, Poland). Molecular sexing was performed with the primer pair P2 and P8, according to the protocol described by Griffiths et al. (1998), using 50°C annealing temperature for the PCR reaction. These primers amplify a 400-bp fragment on the W chromosome (in females only), and a 430-bp fragment on the Z chromosome (in both sexes) (Griffiths et al. 1998). This size difference is clearly visible when separating the fragments on a 3% agarose gel.

Data analysis

Energetic values of food loads were calculated using dry weights and energy values based on published estimates of the different taxa found in food loads according to the references (Kosobokova 1980; Percy

and Fife 1981; Wołowicz and Szaniawska 1986; Berestovskii et al. 1989; Węsławski and Kwaśniewski 1990; Mumm 1991; Richter 1994; Węsławski et al. 1994, 1999a, b; Hansen 1997; Poltermann 1997; Karnovsky et al. 2003).

Results are presented as mean values and standard deviations (mean±SD). All statistical analyses were computed in STATISTICA 6.0.

Results

Males brought on average less food (wet weight) per load (2.4±1.9 g, range 0.7–5.0, n=29) than females (3.5±1.6 g, range 1.5–6.9 g, n=27; Student's t-test: t_{54}=2.76, $P<0.05$). They also brought fewer prey items per food load (males 990.4±704.2, range 58–2,873, n=29; females 1,853.4±887.4, range 598–3,761, n=27; Student's t-test: t_{54}=–4.22, $P<0.001$). The mean energetic value of food delivered to chicks by males (17.5±9.6 kJ, range 2.7–40.1, n=29) was significantly lower than by females (28.6±12.8 kJ, range 9.9–52.0, n=27; Student's t-test: t_{54}=–3.67, $P<0.05$).

Among the 36 prey categories (taxa and developmental stages), 65% occurred in food loads delivered by both sexes. The remaining prey categories were found exclusively in either males' or females' food loads (22 and 13%, respectively). However, the food diversity, as measured by the Shannon–Wiener index (H') did not differ significantly between sexes (males H'=1.38, females H'=1.42; Hutcheson t-test: t=0.22, n.s.). The most numerous and most frequently occurring taxon in the food loads of both sexes was the copepod species *C. glacialis* [particularly, the fifth copepodite (CV) stage]. The second was *C. finmarchicus* (mainly CV). The rest of the diet consisted mainly of amphipods and decapods (Table 1).

Considering the relative numbers of particular prey categories, males brought more cold water *Calanus* sp. (*C. glacialis* and *C. hyperboreus*), less warm water *C. finmarchicus* and more taxa other than *Calanus* sp. than females (G-test, G_2=842.52, $P<0.05$; Fig. 1).

None of the developmental stages of the most important copepod species exceeded 5 mm in size. Among the other taxa brought by both sexes the most numerous items were up to 5 mm (Fig. 2). There were no differences in the frequency of prey items smaller and larger than 5 mm in food loads brought by males or females (χ^2_1=1.38, n.s.).

Discussion

This study showed that males bring significantly smaller single food loads to chicks by wet weight, number of items and the energy content than females. During the mid-chick-rearing period (when these data were collected) Harding et al. (2004) found a trend towards males delivering food more frequently, and we also found this to be the case (males 2.5±2.1 feedings per

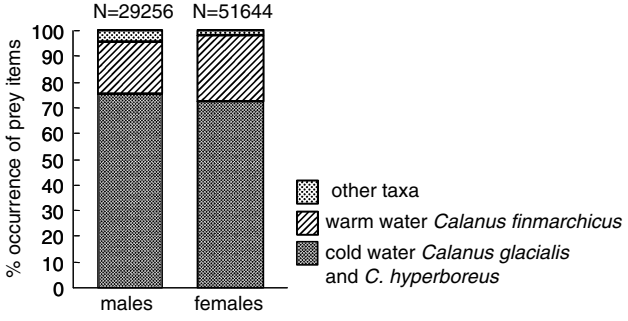

Fig. 1 Occurrence of prey items in food loads delivered to little auk *(Alle alle)* chicks by males and females

Table 1 Mean abundance and occurrence of particular taxa in food loads delivered to little auk *(Alle alle)* chicks by males (n=29) and females (n=27)

Taxon	Females		Males	
	Mean abundance	Occurrence (%)	Mean abundance	Occurrence (%)
Copepoda				
Calanus glacialis CV	1,071.7	97	682.8	94
C. glacialis (other stages)	90.4	100	28.5	94
C. finmarchicus CV	362.6	97	167.8	91
C. finmarchicus (other stages)	59.1	94	20.3	91
Remaining copepods	0.03	16	1.9	22
Decapoda	14.7	97	27.4	97
Euphasiacea	4.9	34	7.4	34
Amphipoda	8.0	56	7.2	56
Gastropoda	0.03	3	0.1	3
Polychaeta	0.0	0	0.1	3

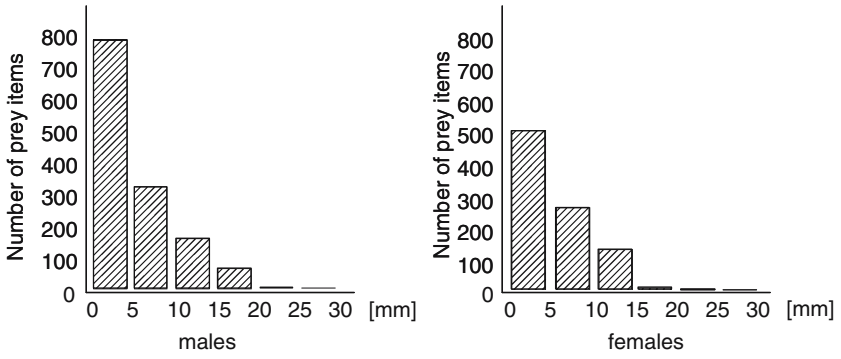

Fig. 2 Number of prey items (other than *Calanus* sp.) in different size classes found in food loads delivered to chicks by males and females

day, females 2.1±1.3; for birds from five nests and for six consecutive days in 2003; own unpublished data). However, the higher feeding rate performed by males does not equalize the energy contribution of the two sexes. Based on the average energy content of each food load and the average number of feedings performed by each sex, males delivered an average of 44 kJ per day and females 60 kJ.

In contrast to our results, Roby et al. (1981) did not find any sex differences in weight of meals delivered to chicks in north-west Greenland. This may be a consequence of the high abundance of food around breeding colonies in Greenland (Nielsen and Hansen 1995; Karnovsky and Hunt 2002). In such circumstances, differences in feeding strategies of males and females may be reduced or disappear. Around Hornsund, where waters tend to be more diversified (cold and warm masses of water co-occur), the zooplankton is more heterogeneous (Węsławski et al. 1988; Koszteyn and Kwaśniewski 1989; Karnovsky et al. 2003).

The most preferred prey item of both males and females was the large and energy-rich *C. glacialis*, which originates from cold Arctic waters. Feeding on this species is far more energetically efficient than feeding on its warm Atlantic water counterpart—*C. finmarchicus* which is much smaller. Indeed, little auks were found in highest numbers feeding in Arctic water (Karnovsky et al. 2003).

The lack of difference between males and females in food trip duration, and the observation that males and females leave and arrive at the colony in mixed-sex groups (Harding et al. 2004), may suggest that males and females forage together in the same feeding areas. However, variation in trip duration was high in that study and we found sex differences in the proportions of cold water *Calanus* sp. (*C. glacialis* and *C. hyperboreus*), warm water *C. finmarchicus* and other prey taxa in food loads. A higher proportion of taxa other than *Calanus* in food delivered by males could indicate they employ a different foraging strategy and utilize shallower water situated closer to the seacoast (where more amphipods and decapods occur). Wagner (1997) reported sexual differences in the composition of prey delivered to razorbill (*Alca torda*) chicks and suggested that it resulted from feeding-niche partitioning.

Little auks select their prey by sight. Prey sizes of 3–6 mm seem to be most profitable (Węsławski et al. 1999a). The present study revealed that both sexes brought mainly prey items up to 5 mm size. Prey items bigger than 5 mm occurred infrequently and with similar frequency in food loads of males and females. This indicates that both sexes have similar size criteria in choosing prey.

The discovery of sex based differences in the foraging behaviour of little auks is important for understanding how the sexes may respond to changes in prey availability due to the variability of oceanographic conditions near their colonies. This study also highlights the importance of examining differences between the sexes in apparently monomorphic species.

Zusammenfassung

Männchen und Weibchen des Krabbentauchers (*Alle alle*) auf Süd-Spitzbergen füttern ihre Jungen mit verschiedener Nahrung

Geschlechtsunterschiede in der Qualität und Quantität der Küken des Krabbentauchers zugetragenen Nahrung wurden in einer großen Kolonie in Hornsund untersucht (Süd-Spitzbergen). Zur Kolonie zurückkehrende Altvögel wurden mit Japannetzen gefangen und die Nahrungsladung aus dem Kehlsack beprobt. Das Geschlecht jedes gefangenen Individuums wurde später mit molekularen Methoden ermittelt. Weibchen brachten signifikant mehr Nahrungstiere pro Ladung als Männchen, bezogen auf Frischgewicht (im Mittel 30% mehr), Anzahl der

Nahrungstiere (46%) und Energiegehalt (39%). Kein Geschlechtsunterschied bestand aber in der Nahrungstiergröße. Energiereiche *Calanus glacialis*, die aus kalten arktischen Gewässern stammen, waren die häufigste Nahrung und machten den größten Anteil an der Ladung bei beiden Geschlechtern aus (75% bei Männchen und 72% bei Weibchen). Das deutet darauf hin, dass beide Geschlechter hauptsächlich in arktischen Gewässern fressen. Unterschiede im Anteil an Kaltwasserarten *Calanus* (besonders an *C. glacialis* und *C. hyperboreus*), Warmwasserarten (*Calanus finmarchicus*) und weiteren Taxa zwischen Männchen und Weibchen aber legen eine geschlechtsabhängige Nutzung von Nahrungsgebieten nahe.

Acknowledgements The authors are very grateful to Katarzyna Dmoch for her help with calculations of caloric values of food samples. We thank Prof. Lech Stempniewicz for critical comments on the first version of the manuscript. Thanks to Nina Karnovsky and two anonymous referees for helpful comments on the earlier version of the paper. This project was supported by grants of the University of Gdańsk (BW 1140-5-0205-4), BioMobil, the Polish State Committee for Scientific Research (2P04F04926) and the National Centre for Biosystematics, Natural History Museum, Oslo University. All birds were handled under the permission of the Norwegian Animal Research Authority and the Governor of Svalbard.

References

Ashmole NP, Ashmole MJ (1967) Comparative feeding ecology of tropical seabirds. Bulletin Peabody Museum of Natural History 24. Yale University Press, New Haven

Berestovskii EG, Anisimova NA, Denisenko CG, Luppova EN, Savinov VM, Timofeev CF (1989) Relationships between size and body mass of some invertebrates and fish of the North-East Atlantic. Academy of Sciences of the USSR, Murman Marine Biological Institute, Apatity

Brodskii KA (1967) Calanoida of the Far Eastern Seas and Polar Basin of the USSR. Keys to the fauna of the USSR No. 35:440 pp. (in Russian)

Brunton DH (1988) Sexual differences in reproductive effort: time-activity budgets of monogamous Killdeer *Charadrius vociferus*. Anim Behav 36:705–717

Gaston AJ, Jones IL (1998) The Auks: Alcidae. Oxford University Press, Oxford

Gaston AJ, Nettleship DN (1981) The thick-billed Murres of Prince Leopold Island. Canadian Wildlife Service Monograph Series, no. 6, Ottawa, Ontario

Griffiths R, Double MC, Orr K, Dawson RJG (1998) A DNA test to sex most birds. Mol Ecol 7:1071–1075

Hansen H (1997) Mesozooplankton of the Laptev Sea and the adjacent eastern Nansen Basin—distribution and community structure in late summer. Rep Polar Res 229:131

Harding AMA, Pelt TIV, Lifjeld JT, Mehlum F (2004) Sex differences in Little Auk *Alle alle* parental care: transition from biparental to parental-only care. Ibis 146:642–651

Jones JL, Rowe S, Carr SM, Fraser G, Taylor P (2002) Different patterns of parental effort during chick-rearing by female and male Thick-billed Murres (*Uria lomvia*) at a low-arctic colony. Auk 119:1061–1074

Karnovsky NJ, Hunt GL Jr (2002) Carbon flux through dovekies (*Alle alle*) in the North Water. J Deep Sea Res II 49:5117–5130

Karnovsky N, Kwaśniewski S, Węsławski JM, Walkusz W, Beszczyńska-Moller A (2003) The foraging behaviour of Little Auks in a heterogenous environment. Mar Ecol Prog Ser 253:289–303

Kosobokova KN (1980) Caloric value of some zooplankton representatives from the Central Arctic Basin and the White Sea. Oceanology 20:84–89

Koszteyn J, Kwaśniewski S (1989) Comparison of fjord and shelf mesozooplankton communities of the southern Spitsbergen region. Rapp P-V Run Cons Int Explor Mer 188:164–169

Kwaśniewski S, Hop H, Falk-Petersen S, Pedersen G (2003) Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. J Plankton Res 25:1–20

Lack D (1968) Ecological adaptations for breeding in Birds. Methuen, London

Mauchline J (1998) The biology of calanoid copepods. Adv Mar Biol 33:1–710

Mumm N (1991) On the summerly distribution of mesozooplankton in the Nansen Basin, Arctic Ocean. Ber Polarforsch 92:1–146

Nielsen TG, Hansen (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. Mar Ecol Prog Ser 125:239–257

Percy JA, Fife FJ (1981) The biochemical composition and energy content of arctic marine macrozooplankton. Arctic 34:307–313

Poltermann M (1997) Biology and ecology of cryopelagic amphipods from Arctic Sea ice. Ber Polarforsch 225:1–170

Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Rep Polar Res 154:1–90

Roby DD, Brink KL, Nettleship DN (1981) Measurements, chick meals and breeding distribution of Dovekies (*Alle alle*) in north-west Greenland. Arctic 34:241–248

Sars GO (1903) An account of the Crustacea of Norway with short descriptions and figures of all the species, vols. I–VII. Bergen Museum, Bergen, Norway

Stempniewicz L (1981) Breeding biology of the Little Auk (*Plautus alle*) in the Hornsund region, SW Spitsbergen. Acta Ornithol 18:141–165

Stempniewicz L (1995) Predator–prey interactions between Glaucous Gull *Larus hyperboreus* and Little Auk *Alle alle* in Spitsbergen. Acta Ornithol 29:155–170

Stempniewicz L (2001) Little Auk *Alle alle*. BWP Update (J Birds West Pal) 3:145–201

Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) Sexual selection and the descent of man 1871–1971. Aldine, Chicago, pp. 136–179

Wagner R (1997) Differences in prey species delivered to nestlings by male and female Razorbills *Alca torda*. Seabird 19:58–59

Węsławski JM, Kwaśniewski S (1990) The consequences of climatic fluctuations for the food web in Svalbard coastal waters. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine environment. Proceedings of the 24th European marine biology symposium. Aberdeen University Press, Aberdeen, pp. 281–295

Węsławski JM, Zajączkowski M, Kwaśniewski S, Jezierski J, Moskal W (1988) Seasonality in an Arctic fjord ecosystem: Hornsund, Spitsbergen. Polar Res 6:185–189

Węsławski JM, Stempniewicz L, Galaktionov KM (1994) The food and feeding of little auk from Franz Josef Land. Polar Res 13:173–181

Węsławski JM, Stempniewicz L, Mehlum F, Kwaśniewski S (1999a) Summer feeding strategy of the little auk (*Alle alle*) from Bjørnoya, Barents Sea. Polar Biol 21:21–134

Węsławski JM, Koszteyn J, Kwaśniewski S, Stempniewicz L, Malinga M (1999b) Summer food resources of the little auk, *Alle alle* (L.) in the European Arctic seas. Pol Polar Res 20:387–403

Wołowicz M, Szaniawska A (1986) Calorific value, lipid content and radioactivity of common species from Hornsund, southwest Spitsbergen. Polar Res 4:79–80