

Sex-specific parental care by incubating Little Auks (*Alle alle*)

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The evolution of sex-specific reproductive behavior among species with biparental care promotes sexual conflict over care. Such conflict may be less intense in species with long-term pair bonds. We examined sex-specific patterns of care during the incubation period in a monogamous, colonially breeding seabird of the high Arctic region, the Little Auk (*Alle alle*). We recorded time spent by birds of known sex in- and outside the nest, and the frequency of particular activities (aggressive interactions and collection of nest material), during four continuous 24-h watches. Males and females shared the incubation duty equally. Both sexes participated in the off-incubation duty behavior with similar frequency. However, males attended nest-site territories more than females and were thus more often involved in aggressive interactions and nest-material collection. These results suggest that there were sex-specific patterns of engagement in different forms of parental care during the incubation period.



1. Introduction

For many bird species, biparental care is crucial for successful breeding (Lack 1968, Gowaty 1996, Sydeman *et al.* 1996). The participation of both partners in brood care allows each of them to save energy, thereby enabling them to increase their own fitness. Particularly, in species with long-term monogamy, such as many seabirds (e.g., del Hoyo *et al.* 1996, Gaston & Jones 1998), individuals are less likely to exploit their partners because maintaining the condition of their partner enhances the fitness of both members of the pair and

favors their future breeding success (Mock & Fuijoka 1990, Flower 1995).

Although both parents have to cooperate during reproduction, sex-specific patterns of parental care are commonly found. Such sex-specific patterns of parental care reflect a variety of male and female constraints imposed by physiological, behavioral and environmental factors, with members of each sex aiming to maximize their own lifetime reproductive success (Trivers 1972). Consequently, understanding sex-specific patterns of parental care is important to comprehend the evolution of parental strategies.

Most studies dealing with sex differences in parental care have been focused on the chick-rearing period. While that period has traditionally been regarded as the most demanding period of avian reproduction (e.g., Drent & Daan 1980), incubation has been evidenced to be an important component of the reproductive cost, and birds expend a considerable amount of energy both during egg incubation in the nest and also during doing parental duties outside the nest, including nest-site defense and maintenance (e.g., Monaghan & Nager 1997, Thomson *et al.* 1998, Reid *et al.* 2002, Tinbergen & Williams 2002). The behavior of parents during incubation may reflect their earlier investments and affect their behavior in later stages of the breeding cycle, and also their future reproduction (e.g., Minguez 1998, Reid *et al.* 2002, Hanssen *et al.* 2005, Heij *et al.* 2006). Therefore, knowledge on behavioral complexity during the incubation period appears crucial for estimating parental investment of males and females both at that time and also during the whole reproductive season.

Here, we investigated sex-specific patterns of parental care during the incubation period in the Little Auk (*Alle alle*), a small, planktivorous seabird that breeds in rock crevices at coastal Atlantic areas of the High Arctic region (Stempniewicz 2001). Like many other seabirds, Little Auks are socially monogamous with negligible sexual dimorphism (Jakubas & Wojczulanis 2007). Both partners incubate the single egg and feed the chick, although females tend to cease chick feeding towards the end of chick rearing, and males exclusively take care of the young (Stempniewicz 2001, Harding *et al.* 2004). Three studies have examined sex differences in parental duties during the chick-rearing period (Harding *et al.* 2004, Wojczulanis *et al.* 2006, Welcker *et al.* 2009), but relatively little is known about the parental activities of each sex throughout the breeding season. To our knowledge, the only study focusing on Little Auk incubation behavior found that both partners contributed to incubation, but the sex of the studied birds was unknown (Stempniewicz & Jezierski 1987). Jakubas *et al.* (2008) demonstrated a different pattern of stress level, as expressed by heterophil/leucocyte (H/L) ratio changes, in Little Auk males and females during the incubation period. The stress level in females decreased (higher H/L ratio) with the progress of the incubation peri-

od, whereas it increased (lower H/L ratio) in males. This difference may indicate sex-specific differences in parental behavior during incubation.

To compare sex-specific parental care of incubating Little Auks we considered not only the incubation duties but also time spent and behavior performed during the birds' attendance in their territory, but outside the nest chamber. Seven types of behavior, performed by birds during territory attendance, were as follows: laying down/sitting, walking, preening, sleeping, head-wagging (head movements from side to side, performed in pairs, with unknown behavioral meaning; Evans 1981), aggressive interactions and collection of nest material. We paid special attention to the latter two as these entail potentially the most stressful and/or costly behaviors and are directly related to parental care (guarding, and improving conditions at the nest site). Assuming an equal contribution of the parents in incubation duty (Stempniewicz & Jezierski 1987), we hypothesized that males, with an increased stress level during incubation (Jakubas *et al.* 2008), would spend more time and/or participate in more aggressive interactions and collecting of nest material than females, whose stress level decreased during incubation.

2. Material and methods

2.1. Study area, field and laboratory work

The study was conducted at a breeding colony of Little Auks at Ariekammen slopes (77°00' N, 15°33' E) in Hornsund, South Spitsbergen in 2006. For detailed monitoring of the time spent in and outside the nest and behavior performed outside the nest during the incubation period, birds were caught using mist nets or noose carpets (pieces of thick net with tiny monofilament loops tied in "nooses" to capture the birds' legs; Williams *et al.* 2000), spread over the colony surface in a restricted sampling patch (hereafter the monitored colony patch).

The monitored colony patch was situated in the central part of a colony, and the number of birds present on that patch was comparable with the neighboring areas. Before egg-laying, 55 individuals were caught and marked individually (distinct

color marks, dyed on breast feathers, and a combination of color rings). A small drop of blood from the brachial vein of caught individuals was taken and stored in 1 ml of 96% ethanol for later DNA-based sex identification. All birds caught were adults (i.e., two years old or older; distinguished from subadults based on the appearance of flight feathers and upper-wing coverts; Stempniewicz 2001).

The breeding status, partner and location of the nest entrances of the caught birds were defined during 22 continuous watches (1–12 h) carried out during the pre-laying and early incubation periods, and during four 24-h continuous watches during the incubation period. Social pairs could be easily recognized as pair mates. They continuously stay close together and copulate frequently with each other during the pre-laying period, and later on in the season use a shared nest. Extra-pair copulations are easily distinguished from within-pair ones, as females do not usually accept extra-pair contacts and perform rejection behavior (Wojczulanis-Jakubas *et al.* 2009). In total, we observed behavior of 21 pairs with both partners marked, and 13 additional individuals (7 males and 6 females) paired with unmarked partners. Nest sites of all observed birds were situated in close proximity, allowing two observers to reliably watch the whole colony that encompassed all the studied birds.

Access to many nests was limited due to the Little Auk nesting in rock crevices. To establish the timing of breeding for birds from the whole monitored colony area, day-to-day examination of a group of 67 nests was performed during the pre-laying period (4–15 June). The monitored nests were situated in the part of the colony where marked birds were observed and the surveys of unmarked birds were conducted. Seven of these 67 nests were those of marked birds. The egg laying was highly synchronous in the colony, 96% of eggs being laid during four days (10–13 June), and was completed in six days. Therefore, median date of the egg-laying (12 June) was considered as the first day of incubation for all marked and unmarked birds from the studied colony. Location of the inspected nests was known from the previous seasons.

Four continuous 24-h watches were performed across the incubation period. The watches were

conducted on the 9th, 15th, 19th, and 27th day after laying. Time spent inside the nest cavity and in the vicinity of the nest (expressed further as territory attendance) was calculated based on the presence/absence of marked individuals on the surface of the monitored colony patch watched continuously and noted at least every 10 minutes. The exact time of birds entering and exiting nests and/or departures from and arrivals to the monitored colony patch were recorded. All occurrences of aggressive interactions and collecting nest material were recorded and described in detail. Threatening, attacking and defending, expressed by characteristic postures (upright position, tense body, bristled head's feathers) and/or mutual physical contact, against other individuals were considered aggressive interactions. The initiator and the receiver of each aggressive interaction were recorded. For occasions of nest material collecting, the type of item (pebbles, lichen and moss pieces, etc.) and the success rate of its delivery to the nest were also recorded. The material was considered successfully delivered if a bird with item entered the nest cavity.

To evaluate the importance of the incubation period for the occurrence of the selected behavioral patterns, surveys of aggressive interactions and nest material collection by unmarked individuals were performed. These surveys were conducted during the three weeks preceding the egg laying, the whole of the incubation period, and for the first nine days of the chick-rearing period (according to median data of egg laying in the inspected nests, established backwards for pre-laying period).

All occurrences of aggressive encounters and birds carrying nest material in the bill were noted during 5-min continuous scanning of the area of 900 m² with nests of ca. 300 pairs and with ca. 200–300 birds observed during each survey. The monitored colony patch, with the marked birds, was within the scanned area. Surveys were performed up to five times per day at different hours to account for the potential influence of time of day on bird activity. In total, 133 surveys (68, 52, 13 during the pre-laying, incubation and chick rearing period, respectively) were performed.

The DNA for sexing was extracted from coagulated pieces of blood (after the ethanol evaporation) using the Blood Mini kit (A&A Biotechnol-

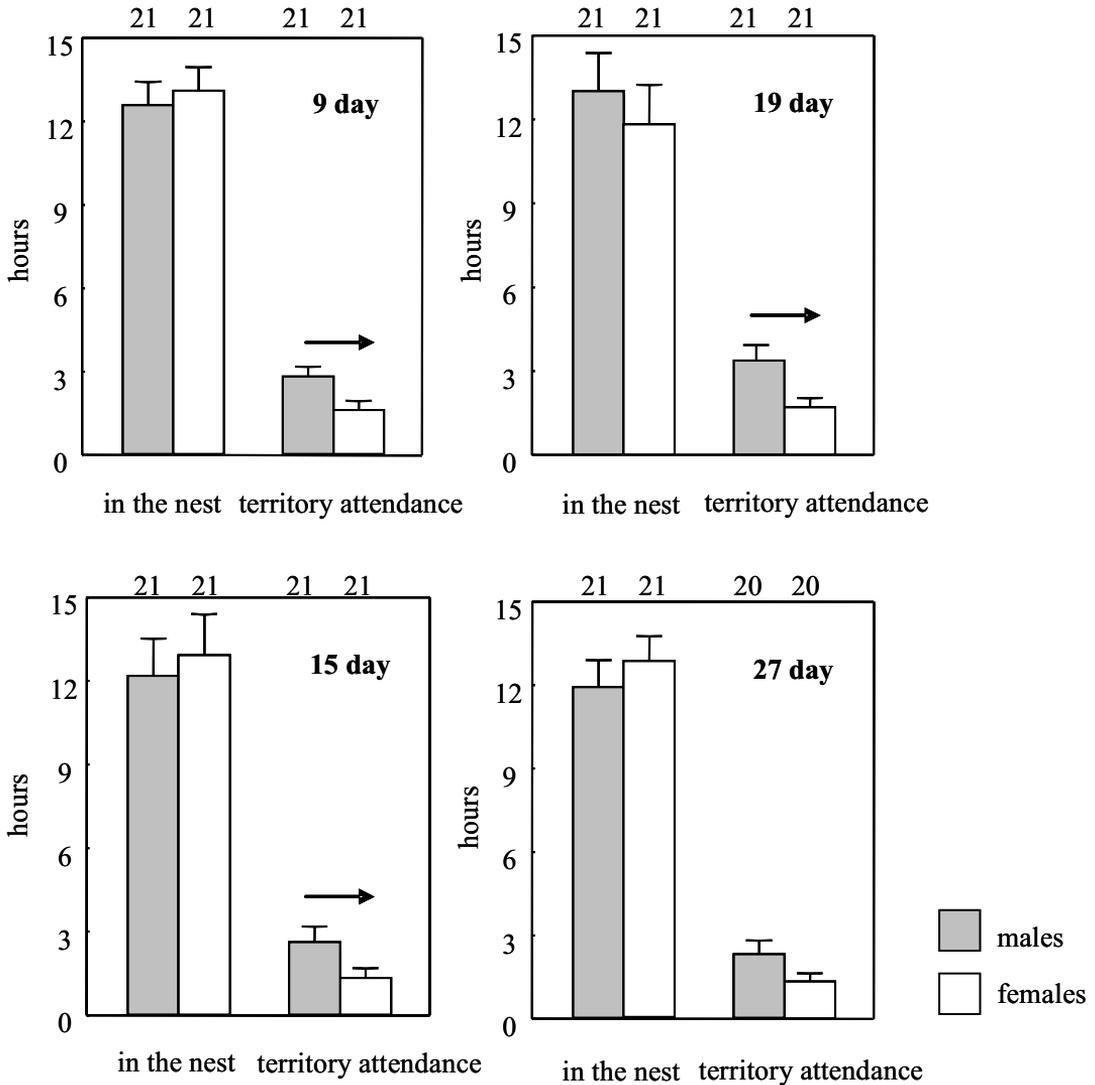


Fig. 1. Time spent by Little Auk males and females (mean and SE) in the colony: in- and outside the nest and in the vicinity of the nest (territory attendance) during the incubation period in Hornsund in 2006. Numbers above the diagrams indicate the number of observed birds. The arrows indicate significant sex differences (paired t test).

ogy, Gdynia, Poland). Subsequent molecular analyses were performed with the primer pair F2550 and R2718, according to Griffith *et al.* (1998), using 50° annealing temperature for the PCR reaction. These primers amplify a 430 bp fragment on the W chromosome for females only, and a 600 bp fragment on the Z chromosome for both sexes (Fridolfsoon & Ellegren 1999). This size difference was clearly visible when separating the fragments on a 2% agarose gel.

2.2. Statistical analyses

Intersexual comparisons of the time spent in- and outside the nest were made only for pairs with both partners marked using paired t -tests [$N = 21$ for the first three watches and $N = 20$ for the last watch; one nest was predated by the Arctic Fox (*Alopex lagopus*)]. The data on time spent outside the nest were logarithmically transformed before the analysis due to the slight divergence from the normal

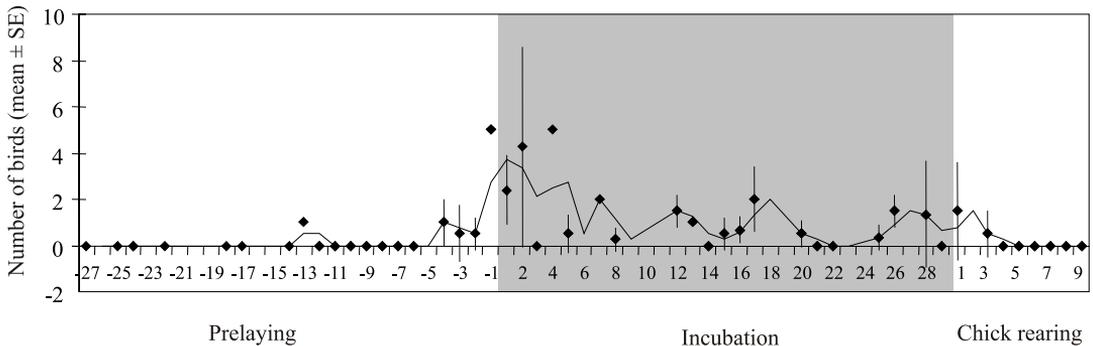


Fig. 2. Number of Little Auks in the monitored colony patch observed with nest material in bill during prelaying, incubation and early chick-rearing periods in Hornsund in 2006.

distribution. To compare the diurnal rhythm of incubation of both sexes, the identity of a bird incubating during the observation period (only for pairs with both partners marked) was established every two hours during the four watches. The frequency of male and female presence at the nest during the 12 checks was compared using Chi-square test for the four watches combined. The frequency of aggressive behavior and occurrences of nest-material collecting were calculated for all marked individuals and compared between sexes using *t*-test for independent variables. To compare the frequency of aggressive encounters and occasions of nest-material collecting noted during surveys of unmarked birds between breeding stages, Mann-Whitney and Kruskal-Wallis tests were used due to the heterogeneous variance of data. Descriptive statistics are expressed in the text as mean and standard error. The critical alpha level was 0.05. The statistical analyses were performed using STATISTICA 8.0.

3. Results

Marked males and females spent similar amounts of time in the nest cavity during the 24-h watches (first watch: $t_{20} = 0.33$, $P = 0.75$; second: $t_{20} = 0.27$, $P = 0.79$; third: $t_{20} = 0.43$, $P = 0.67$; fourth: $t_{19} = 0.51$, $P = 0.62$) (Fig. 1). The frequency of male and female presence at the nest cavity was similar during the 12 checks, performed every two hours during each of the four 24-h watches (χ^2 test, $\chi^2_{11} = 3.92$, $P = 0.97$). Males attended the nest territory more than females during the first three watches,

and the difference was marginally significant also for the fourth watch (first watch: $t_{20} = -3.60$, $P = 0.002$; second: $t_{20} = -2.20$, $P = 0.04$; third: $t_{20} = -2.59$, $P = 0.02$; fourth: $t_{19} = -1.85$, $P = 0.08$) (Fig. 1).

Aggressive encounters noted during the surveys of unmarked birds were observed relatively rarely during the incubation period (0.73 ± 0.09 SE encounters per survey; $N = 68$) compared with the prelaying period (1.74 ± 0.05 SE, $N = 52$; Mann-Whitney $Z = 2.57$, $P = 0.01$). During the incubation period, marked males and females participated in aggressive interactions both as initiators and receivers. Males initialized such interactions more frequently than females (7.89 ± 1.13 SE and 2.60 ± 0.73 SE, respectively; $t_{53} = -3.85$, $P = 0.0003$). However, considering the number of initialized aggressive interactions per time spent at the territory, sexes behaved in a similar way (males: 0.32 ± 0.04 SE and females: 0.24 ± 0.06 SE events per bird per hour; $t_{53} = -0.98$, $P = 0.33$).

Nest material collection during the survey, expressed as the number of unmarked birds carrying nest material, was more frequent during the incubation period compared with pre-laying and chick rearing periods (Kruskal-Wallis $H_2 = 28.70$, $N = 133$, $P < 0.001$; Fig. 2). Both marked males and females participated in collecting nest material, but males were observed more often with nest material in the bill (78% of the total of 427 observations; $\chi^2_1 = 89.11$, $P < 0.001$). However, most marked birds (all the males and 89% of the females; Fisher's exact test, $P = 0.85$) were observed collecting nest material. On average for these birds, the behavior occurred 17 ± 0.9 SE times (range 2–139). Sexes

were similar in terms of the frequency of nest material collection attempts per time spent on the surface of the monitored colony patch (males: 0.2 ± 0.06 SE observations of an individual with item per hour, females: 0.3 ± 0.12 ; $t_{53} = -0.54$, $P = 0.59$).

The most often observed nest material items carried by marked birds were pebbles (males 62% of the collected items, $N = 333$; females 52%, $N = 94$) followed by dry pieces of mosses and lichens (males 37%; females 47%). The rest consisted of bird sternum, dry goose faeces and grass blades. Both sexes collected particular types of nest material with similar frequency (pebbles: $\chi^2_1 = 0.53$, $P = 0.47$; and mosses and lichens: $\chi^2_1 = 0.88$, $P = 0.35$). The majority of the observations of nest material collection led to a successful delivery to the nest, with similar success rates for males and females (76% and 75%, respectively; $\chi^2_1 = 0.01$, $P = 0.94$).

4. Discussion

Both sexes incubated for about 12 hours per day, a result similar to that observed earlier for the Little Auk and other auks (Stempniewicz & Jezierski 1987, Gaston & Jones 1998). Incubation bouts lasting about twelve hours in the Little Auk are presumably long enough to allow the off-duty parent to replenish its body reserves. Foraging flights of Little Auks, performed to collect food for chicks, may sometimes last only ca. 30 min but are usually 3–5 h (Harding *et al.* 2004, Steen *et al.* 2007, Wojczulanis-Jakubas 2007). Thus, it seems plausible that adults are able to feed themselves during the few hours of their off-duty time during the incubation period. Indeed, the body mass of males and females increased in the course of incubation (Taylor 1994, Jakubas *et al.* 2008).

The daily rhythm of incubation of Little Auks were similar for males and females in the present study, although other studies have reported differences in staying frequencies for some auk species breeding in lower latitudes (e.g., Gaston & Jones 1998, Paredes *et al.* 2006). Little Auks, however, breed in the High Arctic region, with the summer months having 24-hour sunlight, little diurnal variation in the availability of zooplankton resources (Błachowiak-Samołyk *et al.* 2006) and relatively low variation in daily air temperature

(IGF, PAS unpublished data). These relatively constant environmental conditions may explain the lack of diurnal pattern in changes of the incubating partners.

In seabirds, costs of physical activity while attending the territory are relatively higher than incubation costs (Thomson *et al.* 1998, Tinbergen & Williams 2002). Little Auk individuals that were not on incubation duty actively participated in aggressive interactions and collected nest material, thereby also devoting their foraging time on parental care behaviors. Both sexes performed these behaviours, yet males attended the territory more than females. Consequently, the contribution of males to duties was greater, which presumably is reflected in the increase of stress level of males during incubation (Jakubas *et al.* 2008). The apparent unequal division of labor between sexes might be a consequence of the large female investment during egg formation. There are no data on the costs of egg production in Little Auks, but a high energy expenditure could be assumed for auks. For example, egg formation in guillemots costs 85% of female basic metabolism rate (references in Nettleship & Birkhead 1985). After the costly egg formation females might be unable to participate in the off-duty activities. Instead, they may have to spend more time foraging to physically recover. The longer staying of males in the colony during the incubation has also been observed in other species of auks: for example, Brünnich Guillemot (*Uria lomvia*), Razorbill (*Alca torda*) (Paredes *et al.* 2006) and Atlantic Puffin (*Fractecula arctica*) (Creelman & Storey 1991). This difference may result from males guarding nests against disturbance from breeding and non-breeding neighbors. Physiological determinants such as higher levels of testosterone (e.g., Ball & Balthazar 2004, Błaszczyk *et al.* 2006), may make males better prepared and thereby become more efficient than females in nest defending. Hence, it would be beneficial for both partners if the male spent more time and effort defending the nest. An alternative explanation for the higher territory attendance of males might be that males had more time than females for staying in the colony. Foraging flights performed by males during the chick-rearing period may be shorter than those done by females (Welcker *et al.* 2009). The causes of that difference are unknown, but foraging areas or for-

aging efficiency may be different between males and females. Another possibility is that, during the incubation period, males might forage closer to the colony or more effectively than females and therefore might stay longer periods in the colony.

Although the aggressive behaviour of Little Auks was most pronounced during the pre-laying period, it was still noticeable during the incubation period and might play an important role in manifestation of the site possession by the nest holder. High nest-site fidelity and long-term pair bonds (authors' unpubl. data) may promote nest-site guarding for possible future seasons. Moreover, nest-site guarding by off-duty partners may allow the incubating bird to remain undisturbed (Birkhead 1978, 1985).

Collection of pebbles and other nest material by Little Auks was almost exclusively performed during the incubation period. This is probably related with the fact that the species do not build a true nest and only gathers items in the nest cavity to improve conditions inside for the breeding season. Pebbles may prevent the egg from rolling and crushing against the hard rock walls of the nest chamber (Ferdinand 1969, Stempniewicz 1981). Soft items, such as pieces of dry mosses and lichens, might insulate the egg by limiting its contact with bare nest floor, as suggested for Chinstrap Penguins (*Pygoscelis antarctica*; Moreno *et al.* 1995). The present results showed that collection of nest material was common and seems to be intentional – the majority of items were successfully delivered to the nest. In contrast, in Razorbills and Common Guillemots (*Uria aalge*), nest-material collecting appears to be more ritualized, as the birds usually drop the pebbles on the ground outside the nest (Bedard 1969, Birkhead 1976, Lloyd 1976, cited after Cramp 1998). It is difficult to estimate the costs of nest material collecting by Little Auks. Pebbles found in the inspected nests weighed on average 3.9 ± 0.48 SE g ($N = 165$; the equivalent to 2.3% average body mass of males and 2.4% of females during the incubation; Wojczulanis-Jakubas 2007). Thus, the mass of a single pebble appears negligible. On the other hand, pebbles were transported in the bill, which is beyond the central point of the body, sometimes for large distances, i.e., a few dozen meters. In Chinstrap Penguins, intensive pebble collecting decreased the body condition of individuals and as

such might be regarded as an important part of parental care (Fargallo *et al.* 2001).

Subtle sex differences in parental care seem to be the rule for seabirds, and the Little Auk is not an exception. Our results suggest that parental care during the incubation period is slightly biased towards greater male participation. Higher stress level of males in that period (Jakubas *et al.* 2008) suggests allocation of resources from the immune function to parental care. Both male and female are likely to benefit from adopting sex-specific parental roles during incubation. Various parental strategies of resource allocation in both sexes during the incubation might be related to their specific parental roles and efforts, both at pre-laying and subsequent stages of the breeding season. However, to understand the causality of the labor division between the sexes in Little Auk, further observational and experimental studies of the energy expenditure of both sexes at the particular stages of reproductive cycle are needed.

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Sukupuoliriippuvainen investointi vanhemmuuteen pikkuruokilla

Sukupuolisidonnainen käyttäytyminen lajeilla, joilla molemmat puolisot osallistuvat poikasten hoitoon, johtaa evolutiivisesti ristiriitaan sukupuolten välisen työnjaon ja huolenpidon välillä. Tämä ristiriita saattaa olla vähäisempää lajeilla, joilla on pitkäaikaiset parisuhteet. Tutkimme tätä kysymystä haudonta-aikana yksiavioisella, yhdyskunnissa pesivällä, arktisen alueen merilinnulla, pikkuruokilla (*Alle alle*). Selvitimme sukupuoleltaan tunnistamattomien yksilöiden pesässä ja sen ulkopuolella viettämää aikaa sekä ajankäyttöä tiettyihin tarkoituksiin (aggressiiviset kohtaamiset ja pesämateriaalin keruu) neljän 24 tuntia kestä-

neen tarkkailujakson aikana. Koiraat ja naaraat ja-koivat haudontavastuun ja sen ulkopuolisen ajan tasaisesti. Koiraat kuitenkin oleskelivät naaraita enemmän reviirillä ja sitä kautta osallistuivat useammin aggressiivisiin yksilöiden välisiin kohtaamisiin ja pesämateriaalin keräämiseen. Tulokset viittaavat siihen, että sukupuolet käyttävät tiettyihin pesintään liittyviin toimiin aikaansa eri tavoin.

References

- Ball, G.F. & Balthazar, J. 2004: Hormonal regulation of brain circuits mediating male sexual behavior in birds. — *Physiology & Behavior* 83: 329–346.
- Birkhead, T.R. 1978: Behavioural adaptations to high density nesting in the common guillemot, *Uria aalge*. — *Animal Behaviour* 26: 321–331.
- Birkhead, T.R. 1985: Coloniality and social behaviour in the Atlantic Alcidae. — In *The Atlantic Alcidae* (eds. Nettleship, D.N. & Birkhead, T.R.): 355–383. Academic Press, London.
- Błachowiak-Samołyk, K., Kwaśniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Petersen, S. & Mouritsen, L.T. 2006: Arctic zooplankton do not perform daily vertical migration (DVM) during periods of midnight sun. — *Marine Ecology Progress Series* 308: 101–116.
- Błaszczuk, B., Tarasewicz, Z., Udała, J., Gączarzewicz, D., Stankiewicz, T., Szczerbińska, D., Romaniszyn, K. & Jasieniecka, J. 2006: Changes in the blood plasma testosterone and cholesterol concentrations during sexual maturation of Pharaoh quails. — *Animal Science Papers and Reports* 24: 259–266.
- Cramp, S. 1998: *The Complete Birds of the Western Palearctic on CD-ROM*. Oxford University Press, Optimedia.
- Creelman, E. & Storey, A.E. 1991: Sex differences in reproductive behavior of Atlantic Puffins. — *Condor* 93: 390–398.
- Drent, R.H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. — *Ardea* 68: 225–252.
- Evans, P.G.H. 1981. Ecology and behaviour of the Little Auk *Alle alle* in west Greenland. — *Ibis* 123: 1–18.
- Fargallo, J.A., De Leon, A. & Potti, J. 2001: Nest-maintenance effort and health status in chinstrap penguins, *Pygoscelis antarctica*: the functional significance of stone-provisioning behaviour. — *Behavioural Ecology and Sociobiology* 50: 141–150.
- Ferdinand, L. 1969: Some observations on the behaviour of the Little Auk (*Plautus alle*) on the breeding ground, with special reference to voice production. — *Dansk Ornitologisk Forenings Tidsskrift* 63: 19–45.
- Flower, G.S. 1995: Stages of age-related reproductive success in birds: Simultaneous effects of age, pair-bond duration and reproductive experience. — *American Zoology* 35: 318–328.
- Fridolfsoon, A. K. & Ellegren, H. 1999: A simple and universal method for molecular sexing of non-ratite birds. — *Journal of Avian Biology* 30: 116–121.
- Gaston, A.J. & Jones, I.A. 1998: *Bird Families of the World. The Auks Alcidae*. — Oxford University Press, Oxford.
- Gowaty, P. 1996: Field studies of parental care in birds: new data focus on question on variation among females. — *Advances in the Study of Behavior* 25: 477–531.
- Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998: A DNA test to sex most birds. — *Molecular Ecology* 7: 1071–1075.
- Hanssen, S.A., Hasselquist, D., Folstad, I. & Erikstad, K.E. 2005: Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. — *Proceedings of the Royal Society Ser. B* 272: 1039–1046.
- Harding, A.M.A., Pelt, T.I.V., Lifjeld, J.T. & Mehlum, F. 2004: Sex differences in Little Auk *Alle alle* parental care: transition from biparental to parental-only care. — *Ibis* 146: 642–651.
- de Heij, M.E, van den Hout, P.J. & Tinbergen, J.M. 2006: Fitness cost of incubation in great tits (*Parus major*) is related to clutch size. *Proceedings of Royal Society Ser. B* 273: 2353–2361.
- del Hoyo, J., Elliot, A. & Sargatal, J. (eds.) 1996: *Handbook of the Birds of the World. Vol. 3. Hoatzin to Auks*. — Lynx Edicions, Barcelona.
- Jakubas, D. & Wojczulanis K. 2007: Predicting the sex of dovekeys by discriminant analysis. — *Waterbirds* 30: 92–96.
- Jakubas, D., Wojczulanis-Jakubas, K. & Kreft, R. 2008: Sex differences in body condition and hematological parameters in Little Auk *Alle alle* during the incubation period. — *Ornis Fennica* 85: 90–97.
- Lack, D. 1968: *Ecological adaptations for breeding in birds*. — Methuen, London.
- Minguez, E. 1998: The cost of incubation in the British Storm Petrel: an experimental study in a single-egg layer. — *Journal of Avian Biology* 29: 183–189.
- Mock, D.W. & Fuijoka, M. 1990: Monogamy and long-term pair bonding in vertebrates. — *Trends in Ecology and Evolution* 5: 39–43.
- Monaghan, P. & Nager R.G. 1997: Why don't birds lay more eggs? — *Trends in Ecology & Evolution* 12: 270–274.
- Moreno, J., Bustamente, J. & Viñuela, J. 1995: Nest maintenance and stone theft in the chinstrap penguin (*Pygoscelis antarctica*). I. Sex roles and effects on fitness. — *Polar Biology* 15: 533–540.
- Nettleship, D. N. & Birkhead, T. R. (eds.) 1985: *The Atlantic Alcidae. The evolution, distribution and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas*. — Academic Press, New York.

- Paredes, R., Jones, I.L. & Boness, D.J. 2006: Parental roles of male and female thick-billed murres and razorbills at the Gannet Islands, Labrador. — *Behaviour* 143: 451–481.
- Reid, J.M., Monaghan, P. & Ruxton G.D. 2002: The consequences of clutch size for incubation conditions and hatching success in starlings. — *Functional Ecology* 14: 560–565.
- Steen, H., Vogedes, D., Broms, F., Falk-Petersen, S. & Berge, J. 2007: Little auks (*Alle alle*) breeding in a High Arctic fjord system: bimodal strategies as a response to poor food quality? — *Polar Research* 26: 118–125.
- Stempniewicz, L. 1981: Breeding biology of the Little Auk *Plautus alle* in the Hornsund region, Spitsbergen. — *Acta Ornithologica* 18: 1–26.
- Stempniewicz, L. 2001: Little Auk *Alle alle*. BWP Update. — *Journal of Birds of the Western Palearctic* 3: 45–201.
- Stempniewicz, L. & Jezierski, J. 1987: Incubation shifts and chick feeding rate in the Little Auk *Alle alle* in Svalbard. — *Ornis Scandinavica* 18: 152–155.
- Sydeman, W.J., Pyle, P., Emslie, S.D. & McLaren, E.B. 1996: Causes and consequences of long-term partnerships in Cassin's Auklets. — In *Partnerships in birds* (ed. Black, J.M.): 211–222. Oxford University Press, Oxford.
- Taylor, J.R.E. 1994: Changes in body mass and body reserves of breeding Little Auks (*Alle alle* L.). — *Polish Polar Research* 123: 149–168.
- Thomson, D.I., Furness, R.W. & Monaghan, P. 1998: Field metabolic rates of Kittiwakes *Rissa tridactyla* during incubation and chick rearing. — *Ardea* 86: 169–175.
- Tinbergen, J.M. & Williams, J.B. 2002: Energetics of incubation. — In *Avian incubation: behaviour, environment and evolution* (ed. Deeming, D.C.): 299–313. Oxford University Press, New York.
- Trivers, R.L. 1972: Parental investment and sexual selection. — In *Sexual selection and the descent of man* (ed. Campbell, B.): 139–179. Aldine Publication Corporation, Chicago.
- Welcker, J., Steen, H., Harding, A.M.A. & Gabrielsen, G.W. 2009. Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. — *Ibis* 151: 502–513.
- Williams, J.C., Scharf, L., & Byrd, G.V. 2000: Ecological monitoring methods of the Aleutian Islands Unit, Alaska Maritime National Wildlife Refuge. — U.S. Fish and Wildlife Service Technical Report AMNWR 00/01.
- Wojczulanis, K., Jakubas, D., Walkusz, W. & Wennerberg, L. 2006: Differences in food delivered to chicks by males and females of little auks (*Alle alle*) on South Spitsbergen. — *Journal of Ornithology* 147: 543–548.
- Wojczulanis-Jakubas, K. 2007: Inwestycje rodzicielskie samca i samicy u monogamicznego gatunku ptaka morskiego (alczyk *Alle alle*) w warunkach dnia polarnego. [Male and female parental investments in the monogamous seabird (little auk *Alle alle*) in the conditions of the midnight sun]. — PhD thesis, University of Gdańsk. (In Polish)
- Wojczulanis-Jakubas, K., Jakubas, D., Øigarden, T. & Lifjeld, J.T. 2009: Extrapair copulations are frequent but unsuccessful in a highly colonial seabird, the little auk, *Alle alle*. — *Animal Behaviour* 77: 433–438.