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#### **ORIGINAL ARTICLE**



# Vocal interactions of breeding partners predict duration of incubation bout in an Artic seabird

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#### **Abstract**

In species with biparental care, coordination of parental activities can have important fitness consequences. However, specific behavioral mechanism allowing the coordination of breeding partners remains largely unexplored. Prevalence of biparental care in seabirds makes this group particularly interesting for investigation of behavioral underpinnings of parental coordination. Here, we examined vocal behavior at the nest site of breeding partners and its role in shaping their parental share during incubation in the little auk (*Alle alle*). We evaluated two hypotheses related to the mechanisms involved in parental coordination: (1) behavioral adjustment, where a parent adjusts its effort according to the preceding effort of its partner and (2) vocal negotiation, where effort is adjusted based on information exchanged during the preceding vocal interaction. We found that little auk partners equally share their incubation time, although, duration of nest attendance is highly variable. No immediate reciprocity between partners in the time allocated to parental activity was observed as predicted by behavioral adjustment. However, nest attendance appeared to be related to the vocal interaction between partners during turn-taking. The duration of a given attendance was positively associated to the pair's vocal activity and amount of vocal overlap occurring during turn-taking at the nest. Our results suggest a role of vocalization for coordinating between breeding pairs, providing a potential mechanism for the communication of information enabling this complex interaction.

Keywords Vocalization · Vocal overlap · Parental care · Coordination · Little auk

#### Zusammenfassung

## Vokale Interaktionen zwischen Brutpartnern bestimmen die Dauer der Inkubationsphasen bei einem arktischen Seevogel

Bei Vogelarten mit biparentaler Brutpflege, d. h. gemeinsame Brutpflege durch beide Elternteile, kann die Koordinierung des elterlichen Investments wichtige Auswirkungen auf die Fitness haben. Die spezifischen Verhaltensmechanismen, die die

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Synchronisierung der Brutpartner ermöglichen, sind jedoch noch größtenteils unerforscht. Die Häufigkeit der biparentalen Brutpflege bei Seevögeln macht diese Gruppe besonders interessant für die Untersuchung von Verhaltensweisen, die der Koordination der Elterntiere zugrunde liegen. Wir untersuchten hier das Rufverhalten der Brutpartner am Nest und dessen Rolle bei der Aufteilung der elterlichen Brutpflege während der Brutzeit beim Krabbentaucher (Alle alle). Wir prüften zwei Hypothesen zu den Mechanismen, die an der Koordination zwischen den Elterntieren beteiligt sind: 1) Verhaltensanpassung, d. h. ein Elternteil passt sein Investment Einsatz an den vorangegangenen Einsatz seines Partners an, und 2) Abstimmung über Rufe (engl. "vocal negotiation"), d. h. der Bebrütungseinsatz wird auf Grundlage des Informationsaustausches während der vorangegangenen Rufinteraktion angepasst. Wir fanden heraus, dass Krabbentaucherpartner ihre Brutzeit gleichmäßig untereinander aufteilen, auch wenn die Zeit am Nest stark variiert. Es wurde keine unmittelbare Wechselseitigkeit zwischen den Elternteilen in Bezug auf die Zeit, die für die elterliche Fürsorge aufgewendet wird, beobachtet, wie es die Hypothese der Verhaltensanpassung voraussagt. Die Anwesenheit am Nest schien jedoch mit der vokalen Interaktion der Elterntiere während der Ablösung am Nest verbunden zu sein. Die Dauer der Anwesenheit am Nest stand in einem positiven Zusammenhang mit der Rufaktivität des Paares sowie mit dem Ausmaß an Überschneidungen von Rufen während der Ablösung am Nest. Unsere Ergebnisse lassen vermuten, dass Rufen bei der Koordinierung zwischen den Brutpartnern eine Rolle spielt und einen potenziellen Mechanismus für den Informationsaustausch darstellt, der diese komplexe Interaktion ermöglicht.

#### Introduction

Providing care to the offspring is a widespread behavioral strategy, observed in a large variety of animal taxa (Gonzalez-Voyer and Kolm 2010; Fromhage 2017). The adaptive value of parental care makes the strategy evolutionary stable despite inherent costs (Hamilton 1964). However, when two parents provide care, questions of how and why they should share parental duties arise as each parent may gain shifting the parental burden to its partner (McNamara et al. 2000). A great number of studies has investigated these questions in the context of sexual conflict (Andersson 1994; Balshine et al. 2002), but recently that issue has been considered from a perspective of partners cooperation (as reviewed in Griffith 2019; Wojczulanis-Jakubas 2021). Despite the growing interest in parent cooperation, it remains unclear what are behavioral mechanisms allowing breeding pairs to coordinate their parental care. Several mechanisms have been proposed, among which, vocal communication between partners seems to have a great potential to regulate parents contribution into the care (Hall 1999; Mariette and Griffith 2015; Griffith 2019).

Acoustic signals can carry important information about an individual such as sex (e.g., Kriesell et al. 2018), body size (e.g., Osiecka et al. 2023b), or even current body condition (e.g., Gladbach et al. 2009). It has also been demonstrated that individual's vocalization may reveal some information about behavioral context in which it is produced, as affective states seem to be coded in bioacoustics properties of the emitted sounds (Briefer 2012; Osiecka et al. 2023a). As such, acoustic signals are very much important in social interactions, often being used to defend a territory and/or attract a partner (Andersson 1994). Recent studies clearly demonstrate that vocal interactions are also important for breeding partners to maintain the pair bond (Wickler 2010), and may even shape their parental investment (Wachtmeister

2001; Kavelaars et al. 2019; Mariette 2019; Ferree et al. 2021; Bulla et al. 2022).

Birds provide excellent model systems for investigating dynamics of vocal interaction between breeding partners, and its role in shaping biparental care investment. This is because the majority of species (>80%) exhibit biparental care (Cockburn 2006), so there is a room for parents negotiation, and all the species vocalize to some extent, which creates a channel for partners' communication. Indeed, in some species, a mutual acoustic display of breeding partners has been observed, being associated with partner choice and in this context studied intensively (Andersson 1994). However, in some species, vocal interactions between male and female continue beyond pair formation (Wachtmeister 2001), and this issue has not been studied that extensively (with some notable exceptions of studies on duetting species; Hall 2004, 2009). The role of vocal display in the context of pair communication over the share of parental care has been only recently considered, however, and all so far, studies highlight the fact that vocalization of the breeding partners may be a manifestation of their negotiations over parental care (e.g., Boucaud et al. 2017).

What is a mechanism that shapes male and female contribution into parental care if they both are to share it equally it remains unclear. One of the simplest mechanisms could be a behavioral reciprocity of the partners ("behavioral adjustment hypothesis"), where a parent adjusts its workload to the one performed by its partner just before. For example, duration of an incubation bout of one parent will be adjusted to the duration of the incubation bout being just performed by the partner (Kavelaars et al. 2019). More nuanced mechanism could involve vocal interactions between the partners, where parents adjust their workload accordingly to the information that was vocally transmitted during the partners encounter ("vocal negotiations hypothesis"; Kavelaars et al. 2019; Mariette 2019).



In this study, we considered these two hypotheses: about behavioral adjustment and vocal negotiation, in shaping parental contribution of breeding partners during the incubation period, in a small Arctic seabird, the little auk (also known as dovekie, Alle alle). The species is a vociferous (Evans 1981; Osiecka et al. 2023a), and long-lived monogamous seabird with strong nest and mate fidelity (Stempniewicz 2001). Its breeding biology is well-known, both parents exhibit long and extensive care over a single egg/chick and equally share their parental duty (Wojczulanis-Jakubas et al. 2009; Wojczulanis-Jakubas and Jakubas 2012). It has also been shown that little auk pairs provision their chick in a coordinated manner, alternating with one parent taking care of the egg/chick while the other is foraging for its own maintenance (Wojczulanis-Jakubas et al. 2018). Environmental factors seem to have little influence on coordination, and pair characteristics (such as age, pair bond duration, and assortativity) have been suggested as an alternative source of variability in parental coordination (Grissot et al. 2019). Thus, some sort of communication of the partners over parental care is expected in the species. Vocal interactions of little auk breeding partners are frequently observed during the whole breeding season (Stempniewicz 1980; Evans 1981; Jones et al. 2002), but despite their apparent explanatory potential in partners communication (Mariette 2019), they have never been studied in this context.

To examine behavioral adjustment hypothesis in the little auk for the incubation activity, we explored the link between duration of the nest attendance of one parent and the duration of the following attendance, performed by its partner. We expected this relationship to be positive if behavioral adjustment was the mechanism for parental share, given this simple logic behind: after a long time spent at the colony, an individual may need as much time to forage and restore its body reserves (Dearborn 2001). To investigate the vocal interaction hypothesis for the share of the incubation duty, we explored the link between partners' vocal activity (duration of the vocalization and overlapping vocalization between the partners) during their meeting at the nest (i.e., at the turn-taking, when one parent takes the place of the other on the egg) and the duration of the following incubation bout. We expected vocal activity to be related to the duration of the following nest attendance if the vocal negotiation was involved in parental coordination.

#### Methods

#### **Fieldwork**

Fourteen little auk nests were monitored during the incubation period (mid-June-mid-July) in the breeding season 2020, at their colony in Hornsund (Svalbard, SW

Spitsbergen, 77° 00′ N, 15° 33′ E). Due to travel constraints associated with COVID-19, the fieldwork started when all the eggs were already laid. Thus, the incubation stage was calculated backwards based on the hatching dates and the mean duration of the incubation period as recorded in previous seasons in this colony (29 days; Stempniewicz 2001). Owing to a considerable synchrony of little auk breeding, all the monitored nests were of a similar breeding stage (maximum of seven days difference between the nests in the hatching day). To establish hatching date in the monitored nests, they were checked every day, starting few days before the expected hatching date (established based on multiannual consistency in timing of little auk hatching).

A video recording session of 72 continuous hours was performed for each nest in the middle of the incubation period (8–14 days before hatching). All the nests were recorded on the same days, during relatively stable weather (no strong wind, no precipitation, clouded sky), so a potential effect of meteorological conditions could not affect inter-nests differences in bird activity. We focused on midincubation as at this stage pair bond is expected to be already well-(re)established and both parents are fully engaged in the incubation duty. Importantly, at this stage, partners frequently meet inside their nest, where their vocalization may be reliably separated from their neighbors.

For each nest, a commercial camera (JVC R435REU, Japan) was placed at ca five to seven meters from the entrance, to record the presence and the behavior of focal parents in their nest area (in a radius of three meters from the nest entrance/exit). The recordings were performed with the camera set up in time-lapse mode (one frame per sec). The resolution was sufficient to record all the events of birds' presence/absence in the colony/nest with an accuracy of one second as little auk presence/absence intervals last at least some minutes, and often hours. In parallel to video recording, a miniature microphone (38×14 mm, Olympus ME 51S, OM Digital Solutions GmbH, Hamburg, Germany) was placed inside of each nest (the closest possible to the nest chamber), connected to a digital voice recorder (Olympus LS-3 and LS-P4, OM Digital Solutions GmbH, Hamburg, Germany) via a one-meter long cable, and set up to run for at least 48 h with a sampling rate of 48 kHz and 16-bit resolution (saved in WAV format), fitting the frequency range of little auks (Osiecka et al. 2023a).

To recognize parents in the monitored nests, both were marked with a unique colour-ring combination. The marking was performed in previous season/s, and sex of birds was also already known (molecularly established for the purpose of other studies; e.g., Grissot et al. 2019, with all the methodological details therein).



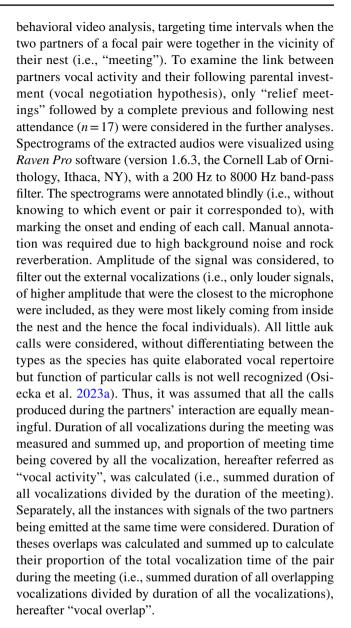
#### **Behavioral analysis**

All the video sessions were trimmed and standardized to last 60 h (from the initial 72 h of recording), starting from 1:00 pm. This is because the starting point for different nests differed a bit in time of the day and little auks tend to exhibit some daily patterns of activity, being more present at the colony during "night" hours (Wojczulanis-Jakubas et al. 2020). Trimming videos allowed us to keep a similar time window for all the pairs, equally represented over the time of the day (i.e., with similar amounts of "day" and "night" hours, considering the polar day). The time window of 60 h allowed us to register for each focal parent at least one complete incubation bout with partners exchange on the nest in between, and the longest nest attendance recorded for an individual in this colony during mid-incubation period lasted 30 h (this study).

Video analysis was performed using VLC software (VideoLAN, France) or QuickTime player (Apple Inc. USA) by manually annotating each appearance and disappearance of a focal bird from its nest area, as well as the time it entered and exited the nest. Two activity categories were defined for each nest based on the annotation for the two partners: "nest attendance", when only one of the parents stays at the colony on duty of parental care (e.g., incubating, nest guarding) while the other is foraging, and "meeting", when both parents are at the nest site. When at the colony, little auks usually stay in an area close to their nest (personal observations). However, the range of this area may vary from one nest to the other and thus not always be entirely covered by our camera view. Nevertheless, birds disappearing and reappearing within one hour were considered present in the colony. Beyond one hour, they were considered foraging. We established this threshold of one hour based on direct observations of presence/absence in the colony of colourmarked and/or GPS-deployed individuals in the colony (unpublished; Grissot et al. 2019). Duration (per 60 h) of all the "meeting events" was calculated, as well as duration of associated previous and following nest attendances (i.e., respectively the time elapsed since the last "meeting", and until the next one). Based on the identity of the bird who stayed at the nest before and after a given meeting, the meetings were classified into two categories: "relief" (i.e., with a change of the parent staying at the nest) or "visit" (i.e., with the same parent remaining at the nest before and after the meeting). For each pair, the proportion of male and female nest attendance was calculated during the 60-h time window.

#### **Acoustical analysis**

Audio recordings were extracted using the package *warbleR* (Araya-Salas and Smith-Vidaurre 2017) in the R environment (version 4.1.2; R Core Team 2021), and based on the



#### Statistical analyses

All statistical analyses were performed in R (version 4.1.2, R Core Team 2021). Assumptions of homoscedasticity and normal distribution of residuals were verified in all the models by visual inspection of models' plots. Statistical significance was considered at alpha level of < 0.05. Significance of explanatory variables was tested with *anova* function from the package *Rstats*.

#### Parental duty share

Durations of the incubation bouts were compared between the sexes using Student's *t* test. Additionally, to examine sex difference in the proportion of the nest attendance, binomial generalized linear mixed-effect model was fitted. The model



was carried out with the *lme4* package (Bates et al. 2015) with proportion of incubation time as response variables, sex being a fixed factor, and nest identity as a random effect to account for pseudo-replication associated with the fact that one pair is represented by two individuals.

#### Behavioral adjustment

To investigate the behavioral adjustment hypothesis, a generalized linear mixed-effects model was fitted with the duration of an incubation bout as response variable, the duration of the previous incubation bout (of the partner), and the duration of the relief meeting as fixed factors. To account for pseudo-replication associated with multiple representation of the same individuals and pairs, the sex of the nest-attending bird and the nest identity were included in the model as random effects. The sex was nested into the identity of the nest as a breeding pair always consists of male and female, and behavior of an individual could be affected by the behavior of its partner.

#### **Vocal negotiation**

To investigate the vocal negotiations hypothesis, a generalized mixed model was fitted with the duration of incubation bout as a response variable being explained by duration of the preceding relief meeting, and "vocal activity" and "vocal overlap" during this meeting. Since each pair may have its own specificity, pair identity was included in the model as a random effect (the effect of the pair was significant when comparing model with and without it, anova, X = 5.587, p = 0.018). The non-multicollinearity of the factors was checked by calculating the variance inflation factors (duration of the relief meeting: 1.30, "vocal activity": 1.79, and "vocal overlap": 1.44) using the vif function from car package (Fox and Weisberg 2018).

#### Results

#### Parental duty share

Females and males nest attendance lasted on average 8.8 h ( $\pm$ 0.97), and 9.7 h ( $\pm$ 1.05) respectively, and the sex difference was not significant (t=-0.65, p=0.51). Also, when considering the proportion of time spent attending the nest, female and male did not differ considerably (GLMM, p=0.451), and most of the pairs showed an equal contribution of each individual (Fig. 1).

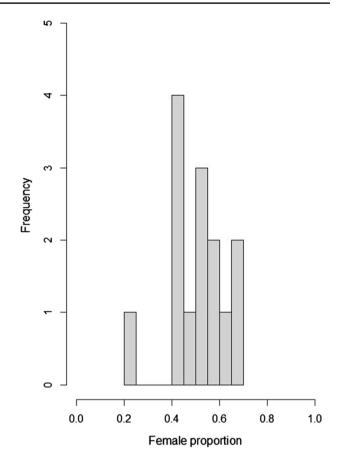


Fig. 1 Distribution of the proportion of nest attendance performed by females during the 60-h continuous video recording (n = 14 pairs)

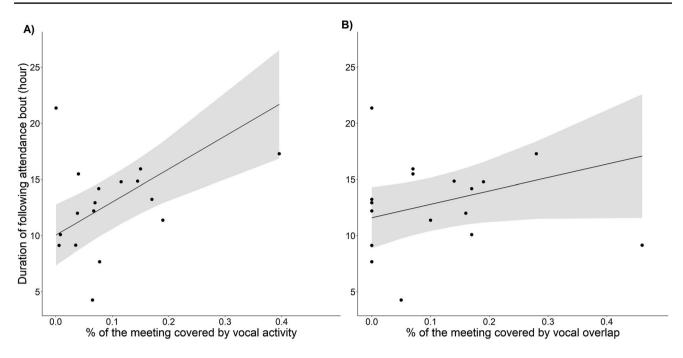
#### **Behavioral adjustment**

The nest attendance ended by a meeting of the two partners at the colony. There was no significant relationship between the duration of nest attendance and the one performed just before, by the partner (GLMM, t=0.829, p=0.407, n=30) nor between the duration of nest attendance and duration of the preceding meeting (GLMM, t=1.300, p=0.193, n=30).

#### **Vocal negotiation**

The duration of a given nest attendance after a relief meeting was not related to the duration of this meeting (GLMM, t=-1.831, p=0.067), but it was significantly and positively related to both to the "vocal activity" (GLMM, t=-4.369, p<0.001, Fig. 2a) and "vocal overlap" (GLMM, t=-2.591, p=0.009, Fig. 2b).





**Fig. 2** A duration of a nest attendance in relation to the vocal activity during the previous meeting (% of the meeting covered by vocalization of both partners) and **B** duration of a nest attendance in relation

to the vocal overlap during the previous meeting (% of overlapping vocalization of the partners in the total vocalization time), n=17 meetings of 14 pairs)

#### **Discussion**

This study was the first attempt to examine partners' behavioral and vocal interactions in the context of mechanisms for sharing parental care in the little auk. Our results support previous findings of equal sharing over parental care between breeding partners during the incubation (Stempniewicz 1980, 2001; Wojczulanis-Jakubas et al. 2009). However, we did not find similarity in duration of consecutive incubation bouts of the two partners, which could manifest a behavioral reciprocity, being support of behavioral adjustment hypothesis. Nevertheless, we did find that vocal activity during the nest-relief meetings was the best predictor of duration of the following incubation bout, this way providing some evidence in support of vocal negotiation over parental share.

The lack of support for the behavioral adjustment hypothesis in our study system is puzzling, given what we expected and what was found in another seabird species (Kavelaars et al. 2019). This might be linked to the harsh (low ambient temperature) and unpredictable (varying foraging conditions) environment where little auks breed. Reciprocal behavior resulting in extended absence of the partner during the incubation period, imposing possibility of the egg abandonment might be risky in the Arctic conditions. The little auk egg must be consistently incubated to ensure good chick development and hatching (Stempniewicz 2001) and so prolonged absence of an incubating parent might

lead to breeding failure. Thus, in the conditions of the little auk environment there is not much room for behavioral adjustments of the partners, as retaliation or disagreement could be very costly. This conclusion is partly supported by another study in the same colony, showing that despite environmental conditions being different, there was no change in a way that little auk parents coordinated their activity of chick feeding (Grissot et al. 2019).

On the other hand, even in a limited space for negotiations, partners are likely to interact to ensure the continuous incubation. Our data clearly indicate that incubating little auks do wait for the return of their partner to leave the nest, and do so only after spending some time together. More interestingly, we found that partners vocally interact during the meeting. While duration of the meeting on its own did not seem to influence the following incubation bout, the duration of the vocal interaction occurring during this meeting seemed to play a role. The more parents vocalized and overlapped their vocalizations during a meeting, the longer was the subsequent incubation bout.

What exactly is being communicated during vocal interactions between the partners remains an open question, but apparently the proportion of time engaged in vocal activity is important. Perhaps the body condition of partners is established during such vocal interactions. Body condition seems to be of great importance for securing a continuous incubation in another seabird species (Gillies et al. 2022). Then, there is growing evidence that vocalizations may signal not



only general individual's quality (sex, body size) but also current body condition. This is well-established for chicks begging behavior (Gladbach et al. 2009; Reers and Jacot 2011), including in little auks (Kidawa et al. 2017), and there are studies showing that the same occurs in adults (Brunton et al. 2010; Favaro et al. 2017). For the little auk, it has been found that body size and affective state are somehow coded in bioacoustics properties of an individual's vocalization (Osiecka et al. 2023a, b). Thus, little auk parents might establish their mutual body condition (or simply motivation to take care for the egg) based on their vocal interaction while meeting at the nest. The departing partner, considering its own and/or its partner body condition/motivation, could then adjust its absence in a way to secure continuous egg incubation (e.g., better body condition of the incubating partner than the departing one may allow a longer foraging of the latter).

The fact that not only total vocalization time but also partners' vocal overlapping during the meeting was linked to the duration of the following incubation bout suggests an intriguing possibility of duetting in the little auk. Avian duets are mutual acoustic displays between two birds, most often breeding partners, which is temporally coordinated (Wachtmeister 2001; Hall 2004). So far only small numbers of species have been reported to duet (up to 4%) and most of them are in the tropics (Hall 2009). However, there is a great variety of duetting displays between the species (from complex coordinated performance to loosely overlapping bouts; Hall 2009; Mann et al. 2009) and its occurrence is widely dispersed across avian families (40% of bird families, both passerines and non-passerines; Farabaugh 1982; Hall 2009). Then, duetting seems to be very much important for monogamous species of slow life history traits (Hall 2009; Mann et al. 2009). Thus, one could expect it to be more prevalent than it is currently acknowledged. Whether the vocal interactions of little auk partners fulfill criteria of the duet requires a separated, more detailed study, absolutely worth to be considered.

The link between duration of the nest attendance and vocal interaction and between the incubating little auk partners is first evidence that vocal communication might play an active role in parental coordination in a pelagic seabird species. It is particularly valuable given that seabirds are greatly neglected in the studies looking at vocal negotiation over parental care, while being an ecological group with a great potential to tackle this question given that they are vociferous and exhibit long and extensive biparental care. Besides, they are known for turn-taking ceremony (Nelson and Baird 2002), where complex and synchronized movements between breeding partners signal a change of the incubating/brooding parent. These ceremonies have been suggested to serve as source of information on individuals body conditions (Takahashi et al. 2017), but also to transfer

information about foraging ground conditions, which could be used by the leaving partner to adjust its following activities (Courbin et al. 2020). However, when studying turntaking ceremony in seabirds, its acoustic aspect is often neglected, while it is the most studied one in passerines species.

If this work shows promising results, it also had several constraints that should be assessed and taken into consideration in further investigation. First, despite using a complex setting of audio and video recording to investigate the acoustic communication during turn-takings, our external video setting did not allow us to evaluate visual cues associated to the interactions happening inside the nest, while they could also be of importance. Second, our study is the first of its kind conducted on little auks and performed based on manual data processing, which is time-expensive. For these reasons, vocal signals were considered all together regardless of their type. Little auks have quite a rich vocal repertoire and each call may have its specific meaning, communicating various traits including body condition and emotional state of an individual (Osiecka et al. 2023a). Investigating this subtlety of the vocalization would be a fascinating research avenue in future. Third, not being able to distinguish individuals solely by their vocalizations, we had to constrain our study on the vocalizations made inside the nest, while we could observe that some birds started to vocally interact with their partner before entering the nest. This constraint means that we could in some cases underestimate the number of vocal signals exchanged between partners during a meeting. Finally, we decided to focus on relief meetings in this study (due to the study design and limited sample size), where turn-taking occurred, but we also recorded some meetings where one partner would just visit the nest without taking turn. For further investigation, it would be interesting to look at these visit meetings and compare their vocal activity with the turn-taking ones, as for example, some studies have identified specific calls signaling turn-taking in other birds species (Boucaud et al. 2016a, b, 2017).

Summing up, we found little auk breeding partners to equally share their incubation duty although duration of nest attendance is not fixed. Duration of incubation bouts varies and apparently the vocal interaction of breeding partners is linked to this variation—we found a positive relationship between the duration of the nest attendance and the vocal interaction between the partners. What the exact mechanisms are behind this relationship warrant further investigation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10336-024-02184-x.

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**Author contributions** MD, KW-J, DK, MAS: conceptualization. MD, KW-J and DK: funding acquisition. MD, KW-J, MAS, RLF, AG: data curation. MD, RLF: formal analysis. MD, KW-J, RLF, AG: investigation. MD: writing original draft. All co-authors: writing, review and editing.

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**Data availability** The data that support the findings of this study are made available as electronic supplementary material. Video and audio recordings from which these data are based will be made available from the authors upon request.

#### **Declarations**

**Conflict of interest** Disclosure of potential conflicts of interest: the authors declare they have no financial interests.

**Ethical approval** Research involving animals: the animal study was reviewed and approved by the Norwegian Animal Research Authority (NARA:19/32026) and the Governor of Svalbard (20/00373-2).

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