

“Coordination of male and female parental performance in the Little Auk, *Alle alle*”
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Contribution of male and female to parental care has been a hot topic in behavioural and evolutionary ecology for a long time. Bi-parental care, where both parents provide care to the offspring, is the most widely spread strategy among bird species (Cockburn, 2006), and as such has been extensively studied. Most studies, both theoretic and experimental, have been considering the issue from the perspective of sexual conflict (e.g., Houston *et al.*, 2005; McNamara & Wolf, 2015). They were also focusing on species of short-life history traits, in which sex differences in reproductive potential can obviously lead to strong sexual conflict over parental care. However, in species characterised by a long life and/or a long-term monogamy with strong pair bond, parental care can be expected to represent a cooperation between partners rather than a conflict (Griffith, 2019). Recently, such an alternative perspective to look at the parental care has been proposed, where both parents are considered as the owners of a ‘family firm’, and as such cooperate to maximize their fitness (Roughgarden, 2012; Griffith, 2019). When finding the right partner requires a lot of time and energy, and bi-parental care is needed to raise the offspring successfully, cooperation between the partners resulting in higher survival of the offspring and breeding adults should be favoured by selection.

The pair cooperation framework, being quite a recent concept of behavioural and evolutionary ecology, is not yet clearly defined but a promising and apparently fruitful approach is to study the coordination of parental activities between the partners (Griffith, 2019). A growing number of studies demonstrates that avian parents do coordinate their activity in respect to each other, either alternating or synchronizing their activities, with a focus switching from passerines to many other groups. The patterns and mechanisms of this parental coordination (and probably mechanisms behind) vary across species but its broad occurrence suggests its adaptive value.

Pelagic polar seabirds are a particularly interesting ecological group for studying parental care and coordination: they experience harsh environmental conditions in their breeding areas, which imposes bi-parental care, and high variability within and across breeding seasons, which promotes flexibility in parental involvement to secure breeding success. A growing number of studies examines their parental care in the context of cooperation, and coordination of the parental studies have been reported for several species (e.g., Tyson *et al.*, 2017, Gillies *et al.*, 2021). One of them, the Little Auk, *Alle alle*, a long-

lived, monogamous Arctic alcid, has also been reported to coordinate foraging trips during the chick-rearing period (Wojczulanis-Jakubas *et al.*, 2018). Little Auk parents adopt a bimodal foraging strategy (alternation of long trips with several short trips, see Welcker *et al.*, 2009), and avoid to perform long trips simultaneously, thus enabling a more even distribution of chick feeding through time. However, how this coordination varies in respect to environmental conditions and over the breeding season still remained open questions.

Aims and hypotheses

The aim of the present thesis was to investigate in details the parental coordination of the Little Auk, based on first evidence of its occurrence from Wojczulanis-Jakubas *et al.* (2018), with three specific objectives.

Potential effect of the environment on coordination of chick provisioning (*sensu* Wojczulanis-Jakubas *et al.*, 2018) was first investigated (*Objective 1*), to establish whether it is a fixed parental strategy or represent flexible response to current foraging conditions in this species. We hypothesised that if the former is the case, the coordination should be of similar level regardless of the circumstances. On the other hand, if the coordination is a flexible trait it should vary in respect to the environmental conditions in the foraging grounds.

In the second step (*Objective 2*) the work of Wojczulanis-Jakubas *et al.* (2018) was extended by investigating coordination of parental activities across the whole chick rearing period (previously limited to the mid phase) and also during the incubation period. We expected parental coordination during the incubation period to be even higher than during the chick rearing, as constant egg protection and thermoregulation may be even more crucial for reproductive success than parental coordination during the chick rearing. We further expected that coordination levels would overall increase within the course of the breeding season, and pairs more coordinated during the incubation would also exhibit a high coordination level in the chick rearing period.

Finally (*Objective 3*), a new methodology for investigating parental coordination in rock nesting seabirds (as the Little Auk) has been developed. All the previous studies on parental coordination of this species (and many other species) were based on either direct or video-recorded observations of birds in the field. These are adequate and quite accurate methods but also very time consuming, resulting in not continuous monitoring of birds behaviour over the time (i.e. birds are observed for a relatively short unit of time in given phase of breeding), which in turn, may limit comprehensive analysis of parental coordination. Methodology that would allow to continuously monitor birds behaviour, and so analyse parental coordination in a long time perspective is therefore very much desired. Thus, here we

proposed a method of continuous monitoring of bird behaviour based on data obtained from a small tracking device, the miniaturised light-based geolocator (GLS). While this device has never been used for this kind of studies, given broad usage of telemetry we expected it may be a powerful and reliable source of data for establishing breeding behavioural patterns and ultimately investigating coordination of parental performance.

Methods

This project was developed on existing data collected during the long-term monitoring of two Little Auk colonies located in the Svalbard Archipelago: Magdalenefjorden (NW Spitsbergen, 79°35' N, 11°05' E, in 2009 and 2010) and Hornsund (SW Spitsbergen, 77°00' N, 15°33' E in 2016 to 2018). Additional data were collected in the field in Hornsund colony in 2019 and 2020 (during the course of the PhD training). In each season, breeding phenology (mostly hatching and fledgling date, although egg laying was also established in some seasons) of known focal pairs was assessed by regularly inspecting the nest around an expected event. Adults were captured at least once per season and marked with colour signs dyed on breast feathers (waterproof markers, Sharpie USA) to ease individual identification. Patterns of behavioural activity during the breeding season of both partners in each monitored pairs was established using either direct observations or video recordings, and used to assess coordination of the parental performance in a similar way to Wojczulanis-Jakubas *et al.* (2018). This coordination was further explored in the context of Objectives 1 and 2. Additionally, in 2020 a group of 12 Little Auk pairs was deployed with GLS early in the breeding season, and collecting data since the moment of deployment, were retrieved during the next breeding season (this way, data on almost whole incubation and chick rearing period were collected, as well as data on migration although not considered here). The same pairs were also video-recorded (with the same methodology as for Objective 2). Video data and data extracted from the retrieved loggers were then used to investigate the ability of geolocators to provide reliable behavioural breeding patterns. The effect of the loggers deployment on breeding success and birds behaviour was also measured (Objective 3).

All statistical analyses were performed in R (R Core Team 2021). Specific statistical methods and relevant hypotheses were fully detailed in corresponding chapters.

Results

Chapter 1: Effect of environment on parental coordination. No inter-annual effect was found in coordination index of the mid phase of the chick rearing period, despite its high variability among pairs and high variation in experienced environmental conditions over the study seasons and locations. Nevertheless, we found that the energy density of food loads delivered

to chicks was associated with the level of parental coordination: when conditions were characterized by delivery of high-energy food loads, the level of coordination exhibited by the studied population was higher. These findings suggest that environmental conditions somehow affect parental coordination but the range of environmental variation handled in the study was probably still narrow enough to not cross a critical threshold. More extreme conditions could be expected to trigger more pronounced modifications of parental performance and coordination.

Chapter 2: Changes in coordination level over the course of the breeding season. We found that the level of coordination of parental performance is overall high and increasing during incubation period but decreases through the chick rearing phase. This suggests that coordination is not a fixed behaviour but temporally variable. Furthermore, we highlighted a relationship between the coordination at the chick rearing period, and that of the incubation period, suggesting some extent of temporal dependence of coordination within the breeding season.

Chapter 3: Investigating parental performance of the Little Auk with a new methodology. We proposed and validated a new method based on GLS data for the investigation of behavioural patterns during the breeding. We also examined the effect of logger deployment on breeding outcome of logged pairs. No apparent effect was found, although some behavioural changes in logged individuals (longer duration of incubation bouts and shorter foraging trips) could be observed. This suggests that the framework provided can be applied to investigate parental performance of crevice/burrow nesting seabirds (including the Little Auk), even though impact of the deployed device should always be taken into consideration.

Conclusions

The work carried out during my PhD training allowed to throw a light on cooperative aspects of parental performance in a species of specific (*sensu* relatively rarely studied in this context) life-history traits: long-lived, with long-term pair bonds, and long and extensive bi-parental care. The results presented in this thesis show that: (1) environmental conditions in the foraging grounds seem to have some influence on parental coordination, even though the investigated seasons were not characterised by differences in mid chick rearing coordination index; (2) the study species exhibits coordinated parental performance not only during the chick rearing period, but also during the incubation period, and that fine-scale changes within the breeding season can be noticed; (3) even though the traditional method based on video

recordings or direct observations is reliable, new technology in the form of miniaturised loggers can be used to acquire more data and establish breeding behavioural patterns reliably.

I. References

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