Faculty of Biology

University of Gdańsk

MSc. Antoine Grissot

“Coordination of male and female parental performance in the Little Auk, *Alle alle*”

Thesis presented to the
Biological Sciences Discipline Board of the University of Gdańsk
in order to obtain a doctoral degree
in the field of natural sciences
in the discipline of biological sciences

Supervisor: dr hab. Katarzyna Wojczulanis-Jakubas, prof. UG
Department of Vertebrate Zoology and Ecology

GDAŃSK 2022

Wydział Biologii
Uniwersytetu Gdańskiego

MSc. Antoine Grissot

“Koordynacja działań rodzicielskich samca i samicy alczyka, *Alle alle*”

Praca przedstawiona
Radzie Dyscypliny Nauki biologiczne Uniwersytetu Gdańskiego
celem uzyskania stopnia doktora
w dziedzinie nauk ścisłych i przyrodniczych
w dyscyplinie nauki biologiczne

Promotor: dr hab. Katarzyna Wojczulanis-Jakubas, prof. UG
Katedra Ekologii i Zoologii Kręgowców

GDAŃSK 2022

Summaries

I. English Summary

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 continous 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.

II. Streszczenie po Polsku

Udział samca i samicy w opiece rodzicielskiej jest od dawna gorącym tematem w ekologii behawioralnej i ewolucyjnej. Opieka dwurodzicielska, w której oboje rodzice opiekują się potomstwem, jest najbardziej rozpowszechnioną strategią wśród ptaków (Cockburn, 2006) i jako taka była szeroko badana. Większość badań, zarówno teoretycznych, jak i eksperymentalnych, rozpatrywała to zagadnienie z perspektywy konfliktu płciowego (np. Houston i in., 2005; McNamara i Wilk, 2015). Badania koncentrowały się również na gatunkach o krótkiej historii życia, u których różnice płciowe w potencjale reprodukcyjnym mogą w oczywisty sposób prowadzić do silnego konfliktu płciowego o opiekę rodzicielską. Jednak w przypadku gatunków charakteryzujących się długim życiem i/lub długotrwałą monogamią, z silną więzią w parze można oczekiwać, że opieka rodzicielska będzie reprezentować raczej współpracę między partnerami niż konflikt (Griffith, 2019). Ostatnio zaproponowano taką alternatywną perspektywę dla badania opieki rodzicielskiej, w której oboje rodzice są traktowani jako właściciele "firmy rodzinnej" i jako tacy współpracują w celu maksymalizacji swojego dostosowania (Roughgarden, 2012; Griffith, 2019). Gdy znalezienie odpowiedniego partnera wymaga dużo czasu i energii, a do pomyślnego wychowania potomstwa potrzebna jest opieka obojga rodziców, współpraca między partnerami skutkująca wyższą przeżywalnością potomstwa i przeżywaniem (w tym płodnością w przyszłości) osobników dorosłych powinna być faworyzowana przez selekcję.

Współpraca pary, będąca dość nowym pojęciem w ekologii behawioralnej i ewolucyjnej, nie została jeszcze jasno zdefiniowana, ale obiecującym i najwyraźniej owocnym podejściem do jej badania jest analiza koordynacji działań rodzicielskich między partnerami (Griffith, 2019). Rosnąca liczba badań pokazuje, że ptasi rodzice koordynują swoją aktywność względem siebie, wykonując różne czynności naprzemiennie lub też synchronizując swoje działania, przy czym rośnie liczba prac w których rozważa się inne gatunki ptaków niż te o krótkiej historii życia. Wzorce i mechanizmy tej rodzicielskiej koordynacji (i prawdopodobnie mechanizmy za nią stojące) różnią się u poszczególnych gatunków, ale jej powszechne występowanie sugeruje jej wartość adaptacyjną.

Pelagiczne ptaki polarne są szczególnie interesującą grupą ekologiczną do badania opieki i koordynacji rodzicielskiej: na obszarach lęgowych doświadczają surowych warunków środowiskowych, które wymuszają opiekę obojga rodziców, oraz dużej zmienności w obrębie i pomiędzy sezonami lęgowymi, co sprzyja elastyczności w zaangażowaniu rodziców w celu zapewnienia sukcesu lęgowego. Coraz więcej przeprowadzanych jest badań, gdzie opieka rodzicielska jest analizowana w kontekście współpracy, w tym często raportowana jest koordynacja działań rodzicielskich (np. Tyson i in., 2017, Gillies i in., 2021). Między innymi u alczyka *Alle alle*, długowiecznego, monogamicznego ptaka arktycznego, odnotowano koordynowanie lotów żerowiskowych w okresie wychowu piskląt (Wojczulanis-Jakubas i in., 2018). Alczyki przyjmując bimodalną strategię żerowania (naprzemienne długie loty żerowiskowe z kilkoma krótkimi, zob. Welcker i in., 2009), funkcjonując w parze unikają jednoczesnego odbywania długich lotów żerowiskowych, co skutkuje bardziej równomiernym rozłożeniem dostawy pokarmu dla pisklęcia. Jednak to, jak ta koordynacja zmienia się w zależności od warunków środowiskowych i w trakcie sezonu lęgowego, nadal pozostaje otwartą kwestią.

Cele i hipotezy

Celem niniejszej pracy było szczegółowe zbadanie koordynacji rodzicielskiej u alczyka, w oparciu o doniesienia o jej występowaniu, pochodzące z pracy Wojczulanis-Jakubas i in. (2018). Wyznaczono trzy cele szczegółowe.

W pierwszej kolejności zbadano potencjalny wpływ środowiska na koordynację rodzicielską, *sensu* Wojczulanis-Jakubas i in. (2018) (*Cel 1*), aby ustalić, czy jest ona stałą strategią, czy też stanowi elastyczną odpowiedź na aktualne warunki żerowania u tego gatunku. Postawiliśmy hipotezę, że jest to stała strategia, to koordynacja powinna być na podobnym poziomie niezależnie od okoliczności. Jeśli natomiast koordynacja jest cechą elastyczną, powinna się zmieniać w zależności od warunków środowiskowych panujących na żerowisku.

W drugim etapie (*Cel 2*) praca Wojczulanis-Jakubas i in. (2018) została rozszerzona o badanie koordynacji działań rodzicielskich w całym okresie wychowu piskląt (wcześniej ograniczonym do środkowej fazy), a także w okresie inkubacji. Oczekiwaliśmy, że koordynacja działań rodzicielskich w okresie inkubacji będzie jeszcze wyższa niż w okresie wychowu piskląt, ponieważ stała ochrona jaj i termoregulacja mogą być jeszcze bardziej kluczowe dla sukcesu reprodukcyjnego niż koordynacja działań rodzicielskich w okresie wychowu piskląt. Ponadto spodziewaliśmy się, że poziom koordynacji będzie wzrastał w trakcie sezonu lęgowego, a pary lepiej skoordynowane podczas inkubacji będą wykazywały wysoki poziom koordynacji także w okresie wychowu piskląt.

Wreszcie (*Cel 3*) opracowano nową metodologię badania koordynacji rodzicielskiej u ptaków morskich gniazdujących na skałach (takich jak alczyk). Wszystkie dotychczasowe badania nad koordynacją rodzicielską alczyka (i wielu innych gatunków) opierały się na bezpośrednich lub nagrywanych na wideo obserwacjach ptaków w terenie. Są to metody adekwatne i dość dokładne, ale jednocześnie bardzo czasochłonne, skutkujące brakiem ciągłego monitoringu zachowania ptaków w czasie (tj. ptaki są obserwowane przez stosunkowo krótką jednostkę czasu w danej fazie lęgu), co z kolei może ograniczać kompleksową analizę koordynacji rodzicielskiej. Dlatego bardzo pożądana jest metodologia, która pozwoliłaby na ciągłe monitorowanie zachowania ptaków, a tym samym na analizę koordynacji rodzicielskiej w dłuższej perspektywie czasowej. Dlatego też zaproponowaliśmy tutaj metodę ciągłego monitoringu zachowania ptaków opartą na danych uzyskanych z niewielkich urządzeń pasywnych, bazującego na pomiarach intensywności światła i zasolenia, gelokatorach (GLS). Chociaż urządzenia te nigdy nie było wykorzystywane do tego typu badań, to biorąc pod uwagę szerokie zastosowanie telemetrii, spodziewaliśmy się, że mogą one stanowić potężne i wiarygodne źródło danych do ustalania wzorców zachowań lęgowych i ostatecznie do badania koordynacji działań rodzicielskich.

Metody

Część danych wykorzystanych w projekcie została zebrana podczas długoterminowego monitoringu dwóch kolonii alczyka, zlokalizowanych w archipelagu Svalbard: Magdalenefjorden (NW Spitsbergen, 79°35' N, 11°05' E, w latach 2009 i 2010) oraz Hornsund (SW Spitsbergen, 77°00' N, 15°33' E w latach 2016-2018). Ponadto, dane zebrano w terenie w kolonii Hornsund w latach 2019 i 2020 (w trakcie doktoratu). W każdym sezonie oceniano fenologię lęgów (głównie datę wylęgu i lotu, choć w niektórych sezonach ustalono również składanie jaj) znanych par lęgowych, regularnie kontrolując ich gniazda w okolicy spodziewanego klucia/wylotu. Dorosłe osobniki chwytano co najmniej raz w sezonie i oznaczano kolorowymi znakami barwionymi na piórach piersi (wodoodporne markery, Sharpie USA), aby ułatwić identyfikację poszczególnych osobników. Wzorce aktywności behawioralnej w sezonie lęgowym obu partnerów w każdej monitorowanej parze ustalono za pomocą bezpośrednich obserwacji lub nagrań wideo i wykorzystano do oceny koordynacji działań rodzicielskich w sposób podobny do pracy Wojczulanis-Jakubas i in. (2018). Zebrane w ten sposów dane o koordynacji zostały dalej użyte do realizacji celów 1 i 2. Dodatkowo, w 2020 r. grupa 12 par alczyków została wyposażona w geolokatory na początku sezonu lęgowego, które to geolokatory zbierały dane od momentu założenia do odzyskania urządzeń w następnym sezonie lęgowym. W ten sposób zebrano dane prawie całej inkubacji i okresie pisklęcym (także dane o migracji, i zimowaniu, ale te nie były tutaj rozważane). Pary wyposażone w GLS były również nagrywane na wideo (z zastosowaniem tej samej metodyki, co w przypadku celu 2). Dane wideo i dane pobrane z odzyskanych loggerów wykorzystano do zbadania możliwości używania geolokatorów do dostarczania badania zachowań lęgowych. Zmierzono także wpływ instalowania loggerów na sukces lęgowy i zachowanie ptaków (Cel 3).

Wszystkie analizy statystyczne przeprowadzono w programie R (R Core Team 2021). Konkretne metody statystyczne i odpowiednie hipotezy zostały szczegółowo opisane w odpowiednich rozdziałach.

Wyniki

Rozdział 1: Wpływ środowiska na koordynację działań rodzicielskich. Badając poziom koordynacji rodziców w okresie pisklęcym w kontekście różnych warunków środowiskowych, pomimo dużej zmienności poziomu koordynacji wśród par i dużego zróżnicowania warunków środowiskowych w badanych sezonach i lokalizacjach badań, nie stwierdzono istotnego efektu środowiska. Stwierdzono jednak, że wartość energetyczna pokarmu dostarczanego pisklętom była związana z poziomem koordynacji rodzicielskiej: gdy warunki charakteryzowały się dostarczaniem wysokoenergetycznego pokarmu, poziom koordynacji wykazywany przez badaną populację był wyższy. Wyniki te sugerują, że warunki środowiskowe w sposób wpływają na koordynację rodzicielską, ale zakres zmienności środowiskowej w badaniu był prawdopodobnie na tyle wąski, że nie przekroczył pewnego progu krytycznego. Można oczekiwać, że bardziej ekstremalne warunki spowodują wyraźniejsze modyfikacje w funkcjonowaniu i koordynacji rodzicielskiej.

Rozdział 2: Zmiany w poziomie koordynacji rodzicielskiej w trakcie sezonu lęgowego. Badając zachowania rodzicielskie na przestrzeni całego sezonym, stwierdziliśmy, że poziom koordynacji działań rodzicielskich jest ogólnie wysoki i wzrasta w okresie inkubacji, ale spada w fazie odchowu piskląt. To sugeruje, że koordynacja nie jest zachowaniem stałym, ale zmiennym w czasie. Co więcej, stwierdziliśmy związek między koordynacją w okresie wychowu piskląt a koordynacją w okresie inkubacji, co sugeruje pewien zakres zależności czasowej koordynacji w sezonie lęgowym.

Rozdział 3: Badanie zachowań rodzicielskich alczyka za pomocą nowej metodyki. Zaproponowaliśmy i przetestowaliśmy nową metodę opartą na danych GLS do badania zachowań alczyków podczas okreu lęgowego. Zbadaliśmy również wpływ istalacji loggerów na zachowania lęgowe obiciążonych urządzeniami par. Nie stwierdziliśmy tutaj żadnego wyraźnego efektu, choć zaobserwowano pewne zmiany w zachowaniu osobników (dłuższy czas trwania okresów inkubacji i krótsze żerowanie), które powinny być uwzględniane w przyszłych badaniach. Wyniki sugerują, że zaproponowana metodologia może być zastosowane do badania zachowań rodzicielskich, w tym koordynacji rodzicielskiej właściwie wszystkich ptaków morskich gniazdujących w szczelinach/zagłębieniach (tak jak alczyk).

Wnioski

Prace prowadzone w ramach doktoratu pozwoliły rzucić światło na kooperacyjne aspekty funkcjonowania rodzicielskiego u gatunku o specyficznych (w sensie stosunkowo rzadko badanych w tym kontekście) cechach życiowych: długowiecznego, z długotrwałymi więzami w parach oraz długą i rozbudowaną opieką obojga rodziców. Wyniki przedstawione w tej pracy pokazują, że: (1) warunki środowiskowe na żerowiskach wydają się mieć pewien wpływ na koordynację działań rodzicielskich, mimo że badane sezony nie charakteryzowały się różnicami w indeksie koordynacji w połowie okresu wychowu piskląt; (2) badany gatunek wykazuje skoordynowane działania rodzicielskie nie tylko w okresie wychowu piskląt, ale także w okresie inkubacji, a także, że można zauważyć różne subtelne zmiany w obrębie sezonu lęgowego; (3) mimo że tradycyjna metoda oparta na nagraniach wideo lub bezpośrednich obserwacjach jest wiarygodna, nowa technologia w postaci zminiaturyzowanych loggerów może być wykorzystana do pozyskania większej ilości danych i wiarygodnego ustalenia wzorców zachowań lęgowych.

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Acknowledgments

This thesis was funded through the Polish National Science Centre (Narodowe Centrum Nauki; NCN, No: 2017/25/B/NZ8/01417) and the University of Gdańsk

All the fieldwork carried out during my PhD. training was performed under supervision of my PhD. supervisor, dr. hab Katarzyna Wojczulanis-Jakubas and/or prof. Dariusz Jakubas (both having the relevant qualifications and experience). All the required permission from the Norwegian Animal Research Committee, the Norwegian Food Safety Authority and the Governor of Svalbard were obtained for each fieldwork season, and reported accordingly in each of the main chapters.

I thank the members of the Discipline Council of Biological Sciences of the university of Gdansk for their support, and appointing the jury who will evaluate my work.

On a more personal note, I would like to start by thanking my family; tout particulièrement mes parents, Katty et Pascal pour leur soutien sous toutes ses formes et tout au long de mon parcours, et sans lesquels je n’aurais jamais pu accéder à et finir cette thèse. Je remercie également ma sœur; Julie et mes grands-parents Josette et Fernand, pour m’avoir toujours encouragé dans tout ce que j’ai pu entreprendre, même sans toujours complètement savoir ou comprendre à quoi ils m’encourageaient.

I would like to thank the people from the Department of Vertebrate Ecology and Zoology for welcoming their second foreign PhD. student so warmly, the people of Akcja Bałtycka and especially Magda and Krzysiek for always being so nice and making me so welcome to their conferences as well as their bird ringing camp; and the Little Auk team for being the best people I had the chance to work with. Obviously, the first person to thank within the team is Kasia, for being crazy enough to be willing to recruit me after meeting me for a few weeks in equatorial jungle conditions far from the polar conditions I was to be working in. You truly are the best PhD supervisor I ever had ! I have no doubts our friendship and scientific collaboration will endure the ending of this mere first step. Please keep being the nicest and warmest person ever, despite your bad habit of making bad jokes and tricks. I will never trust anything you say on a 1st of April ever again (and will always be careful on the other days as well). Darek, thank you for being my second unofficial supervisor, always so nice and cheerful, for the fascinating scientific discussion we had as well as the very peculiar Polish lessons. I thank Anne for being the first foreign PhD. student in the department and blazing a great trail for me to follow, I know your job was not easy, and I thank you for that and being a great team mate in general. Martyn(k)a, thank you for being part of the best Dream Team ever, no field season was ever as special as the first one we shared together. Of course your friendship and support lasted well after we left Svalbard and I also thank you for that and the hope it will last long. Thank you to all the interns who have been part of the team for a more or less long while: Clara, Dorian, Emilia, Lauraleen, Lea, Rozenn and Sofia. Among all of you, I would like to give particularly warm thanks to Clara and Lauraleen, I was very luck to supervise you during your master's internships; your contribution to this work is as valuable as the fun we had together. Latest addition to the team, but far from the least, Marty I am really glad that you joined us and thankful for your great ideas and motivation that boosted the team greatly. You are a great researcher and a good friend, and do not worry I will keep taking care of this friendship even after I leave, as I know you can't be bothered with it !

I would like to thank all my co-authors and collaborators in this work, including Dorota, Marcelo, Rafał, Kasia and everyone at the Institute of Oceanology, Hallvard, Malin and the great people of SEATRACK in general. Thank you for supporting me in my GLS project and welcoming me in the annual meetings. I would also like to thank all the persons I had the chance to meet at the Polish Polar Station, and especially the 43rd polar expedition for the special summer we had together, isolated even more than usual in the station amidst the pandemic. Flaku, Grucha, Łukasz Ola and Śliwka I am particularly grateful I met you and had the chance to spend time with you in two field seasons. Finally, thank you Janek for the sword fights and bow practice in the middle of the Arctic, I never thought I would ever do this kind of things there before meeting you. I know we are always busy or sick, but I hope we'll finally manage to come visit you in Poznań,

I greatly thank all of my friends, the ones I made along the way, the one I had before, the ones in France, Poland and beyond. Thank you Justyna and Ola, meeting you at this conference was decisive in my discovery of Polish culture and traditions, including Disco Polo. Thanks Jacek for being a good friend, a good Polish teacher as well as a good French student. Thank you Ala and Michał, seeing you quickly when you buy a car, visiting you in Białowieża and taking care of Rutka Malutka are always great experiences. Thank you Marta and Tomek, I had a great pleasure in discovering climbing again by your sides, and it was always a good excuse for spending time with you. Thank you to all my “friends from Toulouse”: Anais, tonton Artrhur, Benjam, Flo, Kloug, Niels, Veignie and of course Cecile and Darty (you two, our almost daily text conversation has been a great support during my PhD.). Thank you Alexandre for being such a great field assistant, and for being so annoyingly great at everything. Thank you Othilie and Seb for visiting us in Poland and for always being full of joy and adventurous plans. Thank you Luis for your patience, kindness and débilité. A big thank to La Mifa: Boisseau, Coco, Farlotti, Gloggy, Gourtay, HL, Matouf, Mehdi, Susette, Tisch, Toto, Valou and also all the new pièces rapportées ! I will never loose the hopes of being gathered all together like the good old times of the Campings Vendéens ! Finally, I would like to thank all the crazy people (most of them have already been mentioned before), who followed Mehdi in his crazy idea of helping me fund my last year of PhD. Your financial support obviously greatly helped me finishing this thesis (not only thanks to the brand new computer I am typing it on), but the associated moral support was a boost beyond anything you could have imagined. I am forever indebted to all of you.

Lastly, but definitely not least, I want to thank the one and only person who has been here absolutely every step of the long process this thesis was. Without you, Marion, not a word of this thesis could have been written, and not a day would have been as enjoyable. You are not only a great partner in life, but the best work partner I could ever ask for. I also thank your family: Babette, Thierry, Pierre, Nolwen, Alphonse and all the others for supporting us crazy people living in Poland, and welcoming us when in France. I can’t wait to see where our next step will take us, together.

Table of contents

General introduction

Providing parental care to progeny is a quite common behavioural strategy, observed in a variety of animal taxa (Gonzalez-Voyer & Kolm, 2010; Fromhage, 2017). Mechanisms and patterns of care can vary widely between groups, species and sometimes individuals, but its broad occurrence and stability suggest its great adaptative value (Hamilton, 1964; Trivers, 1972). Despite obvious costs associated with parental care (e.g., time, energy, sometimes decreased chance of parent survival), caring for offspring instead of solely producing and leaving them fend for themselves, does not only ensure a better chance for their survival, but is also beneficial for the parent, increasing directly its fitness.

During my Ph.D. training, I studied parental performance in an emblematic seabird species of the Arctic ecosystem, the Little Auk, *Alle alle*, where bi-parental care is exhibited and crucial for successfully raising an offspring. I focused on the cooperative aspect of bi-parental care, despite it being traditionally seen through the context of sexual conflict. I explored some effect of environment on the coordination of parental perfromance (see **Chapter 1**), investigated how the coordination changes within the span of the breeding season (see **Chapter 2**), and developed a new method, based on GLS technology, to facilitate further investigation (see **Chapter 3**).

In this introduction, I will review the current knowledge on parental performance, and the key notions needed for contextualisation and better understanding of the work carried on and presented in this thesis. First I will focus on general knowledge on parental care (see I.), then more particularly on bi-parental care in birds, and how research focus shifted from sexual conflict to cooperation (See II.).

The general discussion following the main chapters of the thesis will give the opportunity to bring these separate part of the present work together, and back within a broader context.

I. Parental care and parental performance

A. To care or not to care?

Parental care can be defined as any behaviour exhibited by a parent that increases the fitness of the offspring (Clutton-Brock, 1991; Smiseth, 2012). Some studies narrow it down to behaviour happening after fertilisation and directly addressed to the offspring. In its broader acceptation, however, parental care includes choice of the breeding site, preparation of nests or burrows, production and care of eggs or young inside or outside the parent's body, provisioning of young before and after birth and care of the offspring after nutritional independence (Fromhage, 2017). Parental investment, on the other hand represents any expenditure that a parent dedicates to an individual offspring in order to increase its fitness, at the cost of any other offspring (current or future) and/or the parent itself. Given that most of the aforementioned aspects of parental care are indeed costly (Trivers, 1972), they usually represent a parental investment, and raise the question of why care is provided.

Many species, including the vast majority of invertebrates, do not provide extensive care, instead producing offspring along with an initial input of resources, and ultimately leaving them to fend for themselves (Trumbo, 2012). This strategy that does not involve the parent any further in the increase of their offspring fitness, nonetheless leads to successful reproduction and passing of parental genes to the next generation. Additionally, given the investment that care represents, and natural limitations in time and resources, parents are faced with a trade-off between allocating resources to offspring and themselves. Consequently, one can question how parental care came to be a so widespread and apparently beneficial strategy? To evolve and remain an evolutionary stable strategy, parental care has to benefit not only the offspring, but the parent providing it as well (Hamilton, 1964). Naturally, an increase in offspring fitness often coincides with an increase in parental fitness, as a failure to raise progeny results in a loss of fitness to the parent. However, in some situations the costs of care may exceed its benefits, or the mere presence of care may lead to dependence on it (Fromhage, 2017), either honest (e.g., naked and blind offspring at earliest stage) or faked by the offspring (e.g., begging not representing the actual offspring needs). Care provided in such situations is not beneficial for the parent, and should therefore be curtailed.

To care or not to care remains therefore a crucial question, that the study of parental performance aims to elucidate, by studying parental care and investment in various contexts. This greatly helps in comprehending evolutionary processes, mechanisms and factors influencing parental care.

B. When to care and how much to provide ?

Presence and amount of parental care depend on many factors, both biotic and abiotic, and disentangling their effect and directions can be challenging in many cases, but needed for a better understanding of what shapes observed behavioural patterns of activity, and assess the parental performance of the study subjects. To ease the challenge, most of the factors can be apprehended easily through how they are influencing the balance between cost and benefit of care.

Life-history traits have a major impact on how much care should be invested by a parent, as the balance between cost and benefit is well reflected in the trade-off between current and future reproduction (Silver *et al.*, 1985; Martin, 1987; Fontaine & Martin, 2006; Klug & Bonsall, 2010; Klug *et al.*, 2012). Since care provided to a given offspring is an investment that is made at the expense of a potential future offspring, a parent is expected to act in a way that optimises this investment. Consequently, long-lived species tend to have less offspring and/or tend to be more restrictive in their allocation of care in a given breeding attempt compared to species of shorter life, or greater predation risk. Ghalambor and Martin (2001) illustrated how parental care affect the trade-off between current and future reproduction by comparing how two closely related bird species exposed to different predation pressure, leading to different life expectancy, would react to a dummy predator representing a greater threat to either the parent or the offspring. In every cases, parents reduced their number of visits to the nest, which was interpreted as a way to reduce the risk to be detected by the predator. However, individuals of the species with short life expectancy tended to respond more to threat toward their offspring (placing higher value on current reproduction), whereas individuals of the species with long life expectancy did put their own survival first (placing higher value on future reproduction).

Environmental conditions are also expected to influence the presence and amount of provided care, via the means (e.g., good quality sites, food and other resources) available to parents to increase their offspring’s fitness (Martin, 1987). At the evolutionary scale, environments characterised by mild and/or predictable conditions are generally associated with lower amount of care, compared to environments with harsher conditions, that seem to require a higher parental involvement in order to raise offspring successfully (Wilson, 1975; Clutton-Brock, 1991; Cockburn, 2006). Inversely, Stearns (1976) suggested that stable and predictable environment would be associated with more care than variable environment, but more recent theoretical work highlighted the importance of interactions between environmental variability, life-history traits and cost of parental care (Bonsall & Klug, 2011).

According to this model, resource variability does not directly affect the likelihood of care. Instead, the way environmental variability affects parent or offspring mortality can lead to changes in the fitness benefit associated with providing care.

Complex interactions between needs and fitness of parent and offspring, can also have an effect on the presence and amount of provided care. Providing parents can rely on cues and signalling from the offspring (e.g., strength of colouration, body condition or vigour of vocalisation; see Kilner, 2002), to know when and how much to care for them. The information transmitted through these signals can be used by offspring as an honest or exaggerated signal, therefore parents need to account for it and adjust their care accordingly. Like mentioned before, offspring signalling can interact with other factors, such as environmental conditions (Caro *et al.*, 2016). In birds species exhibiting begging as a vocal signal and gape colouration as a body condition signal, parents can preferentially use one or the other signal depending on environmental conditions. Stable environments are associated with restrictive number of offspring, and parents preferentially feed the ones begging more, reflecting their higher need. In contrast, in species living in unpredictable environments, parents ignore begging as it can be an exaggerated signal, and instead rely on gape colouration and size to choose which offspring to feed in priority, avoiding the waste of resources on weaker offspring that are likely to die anyway (Caro *et al.*, 2016). Consequently, some extent of conflict between providing parent and demanding offspring can arise, and many studies on parental performance investigated extensively its dynamics.

C. Who should provide care?

The matter of factors influencing the presence and amount of care provided by a parent can be transposed easily from the scale of one individual to the scale of a pair or a social group, and therefore a wide variety of patterns of parental care evolved from the complexity of interactions between factors and individuals involved.

The first pattern of parental care is the lack thereof, exhibited in many invertebrate species for instance (Trumbo, 2012), but also some fish, reptiles and amphibians (Balshine, 2012). When care is present, it raises the question of who should provide it. Some species tipped the balance between cost and benefit of parental care by discharging it on other individuals, through the evolution of parasitism, allowing to keep the benefits of fitness increase without investing in costly parental care themselves (Rothstein, 1990). In most species, however, such cost-cutting behaviour is not exhibited, and the question of who should provide care remains. Early studies on this matter focused on a sex difference in parental care, based on the obvious tendency of female biased care in mammals (Clutton-Brock, 1991). Patterns of male-only care, bi-parental or even cooperative breeding have since been highlighted and extensively studied (Balshine, 2012; Trumbo, 2012).

Sex differences in parental care can arise from the difference in the size and the number of their gametes (Kokko & Jennions, 2012). Dimorphism in gametes (anisogamy) usually leads to production in greater number of smaller gametes, and early studies suggested that the sex with smaller gametes (i.e., males) would show greater readiness for reproduction than the sex with larger gametes (i.e., females). Nonetheless, it does not always predict which sex will provide more parental investment, as other factors are involved, such as sex differences in costs and benefits of care. For instance, parents can differ in benefits provided by parental care if relatedness to the offspring is uncertain or if one sex is less effective at caring. Another source of sex differences in the costs of parental care may be related with competitive traits. If one sex is competing more for access to mates and reproduction, more energy must be allocated to exhibit traits that are attractive to potential mates. Investing in care is then conflicting with investing in attractiveness, therefore more costly and leading to overall reduction in fitness. Consequently, sex differences in costs and benefits can create a conflict between parents over care.

II. Avian bi-parental care, from sexual conflict to cooperation

A. Sexual selection and sexual conflict over parental care

Some of the earliest work on sexual selection focused on birds, and considered it not in the light of conflict between the sexes, but giving credits to cooperation between reproductive partners (Huxley, 1914; 1923). Huxley for instance focused on pair displays of Great-Crested Grebes, *Podiceps cristatus,* and Red-Throated Diver, *Gavia stellate,* and noticed that highly coordinated vocal and physical displays performed by male and female together were more prevalent after, rather than before pair formation, suggesting that their function was to strengthen the partnership and improve the fitness of the pair together (Huxley, 1914; 1923). However, the focus of sexual selection, especially in birds, quickly shifted to mate choice and was then considered within the context of sexual conflict (Campbell, 1972; Symes & Price, 2015). Very spectacular sex differences in ornamentation, mating and reproduction, embodied by the Peacock, *Pavo cristatus*, may be a good example of this perspective. Outside of the extreme Peacock example, some extent of sexual conflict derived from sexual selection does exist in various avian species, manifesting itself over mate choice (Arnqvist &

Kirkpatrick, 2005) or parental care (Horváthová, 2012). Sexual conflict can be driven by overall sex differences in costs and benefits associated with parental care, and has been the framework for many studies on parental care over the last four decades (e.g., Houston *et al.*, 2005; McNamara & Wolf, 2015), especially concerning bi-parental care, the most widespread strategy among bird species (Cockburn, 2006).

Indeed, when two parents are actively involved, each invests in costly care, but both benefit not only from own investment but also from the partner's. Therefore, a given parent could find an advantage in leaving a greater share of the duty to the other, shifting the cost while keeping the benefits. For this reason, bi-parental care has long been viewed as a constant tug-of-war between two parents (Wojczulanis-Jakubas, 2021), and its evolutionary stability has been discussed and modelled based on how the apparent conflict is being handled. Theoretical models initially suggested that parents invest in care independently from each other, each providing care at a fixed level that maximises its fitness ("sealed bids" hypothesis, Chase, 1980; Houston & Davies, 1985). Later models started to incorporate some behavioural negotiation to the "sealed bid", to account for the observation that a parent takes its partner's parental investment into consideration in the optimisation of its own care (McNamara *et al.*, 1999). However, all the models consider this behavioural negotiation as part of the conflict, and predict that the reduction of care by one individual should not be fully compensated by the other, as this will eventually lead to uniparental care (Chase, 1980; Houston & Davies, 1985; McNamara *et al.*, 1999).

Recent empirical and theoretical work started to question the importance of the conflict in the evolutionary stability of bi-parental care (Wojczulanis-Jakubas, 2021), and Griffith (2019) argued that it is often overestimated and that cooperation between partners is therefore underestimated, if not entirely overlooked.

B. Cooperation as a way to minimise conflict

Although some work followed the direction initiated by Huxley and focused on understanding partnership, through the study of greeting ceremonies, duetting (Odom *et al.*, 2014), allopreening (Kenny *et al.*, 2017), and ritualized copulation (reviewed in Wachtmeister, 2001), the majority of studies on parental care until recently focused on sexual conflict and neglected the value of a good partnership to evolutionary fitness. It has been proposed that sexual selection alone cannot explain the evolution of all traits and is emphasising too much on conflict, whereas social selection firstly proposed by West-Eberhard (1983) acknowledges some elements of sexual conflict between individuals, but places greater emphasis on social negotiation to ensure the successful production of offspring. Social selection suggests that, for partners and offspring as well, having and maintaining a good partnership is more beneficial fitness-wise than choosing a mate based on sexual selection of traits that indicate “good genes” and conflicting over care (Roughgarden, 2012). A good partnership can be attained when parents cooperate, and for instance exhibit coordination in the way they provide parental care.

Cooperating with the partner for the production of offspring can be advantageous, but its benefit might depend on ecological and environmental conditions. The life-history trade-off between current and future reproduction, for instance, is equally important as a driver of care and in the dynamics of cooperation between parents. Species of short life-history tend to place higher value in current reproduction (Ghalambor and Martin, 2001). When both parents of such species are involved in care, each should try to maximise their fitness in the current reproduction event, for instance by providing care independently of partner’s performance, or by shifting cost of care on to the partner and benefiting from the care it provided. Given the low chance to reproduce again with the same individual, acting independently or burdening the partner might be more valuable than tending to a partnership that will not bring any long-term benefits. Inversely, long-lived species that have the opportunity to produce offspring during several attempts might consider the benefit of mating for several times with the same partner (Griffith, 2019), and therefore cooperation can be expressed by the coordination of parental care. Long-term studies suggest that pairs breeding together for a long time are significantly more successful even after accounting for individual age and breeding experience (van de Pol *et al.*, 2006; Sanchez-Macouzet *et al.*, 2014). Additionally, when finding the right partner requires a lot of time and energy, tending to the partnership can be a way to prolong it and reduce the costs associated with courtship and mating at every new breeding event. Another advantage of cooperation between parents, is to compensate for reduced performance of one another, for instance when experimentally handicapped (Gillies *et al.*, 2021), that usually results in a successful breeding, as well as an increase in body condition, survival and fitness of both partners (Sanchez-Macouzet *et al.*, 2014).

Similarly, environmental conditions can play a major role in the added benefits of cooperation over conflict, and therefore the former’s set up and maintenance. Harsh environment is generally associated with higher amounts of parental care (Wilson, 1975; Clutton-Brock, 1991). In birds, this is reflected by the higher proportion of bi-parental care in harsher environments (Cockburn, 2006). Consistently, higher cooperation can also be expected in extreme ecological conditions. A good example is the Kentish Plover, *Charadrius alexandrines*, where coordinated incubation between parents is essential for egg survival in the hot desert where it is breeding and also helps the parents to cope with their own heat stress (AlRashidi *et al.*, 2010). Similarly, the environment where pelagic seabirds are breeding is particularly harsh, and additionally sometimes characterised by a very short time-window dedicated to breeding. Consequently, all the pelagic seabirds exhibit an obligatory bi-parental care system (Schreiber & Burger, 2002), and some species have been found to coordinate their parental care, in a way that increases their breeding success (Congdon *et al.*, 2005; Tyson *et al.*, 2017; Wojczulanis-Jakubas *et al.*, 2018, Gillies *et al.*, *2021*).

C. Patterns of cooperation

Interactions between life-history traits and environmental conditions led to the evolution of multiple strategies for cooperation between partners and the coordination of parental care (Griffith, 2019). Patterns can thus vary between groups, species and sometimes within individuals, as well as temporally, for instance between stages of breeding (i.e., incubation and chick rearing in birds species).

A recent review on the cooperative aspects of bi-parental care by Savage and Hinde (2019) identified four patterns of partners interaction that lead to the coordination of care: *Negotiation*, *Alternation*, *Synchrony* and *Task specialisation*. They are based on theoretical and empirical work, and likely to be highly system-specific. *Negotiation* is built on early theoretical work, and consists in individuals in biparental species responding to changes in the contributions of their partner by incompletely compensating (Houston and Davies, 1985; McNamara *et al.*, 1999). It suggests some extent of independence of parental performance from partners, but mediated through behavioural negotiation and compensation. In *Alternation*, carers exhibit a “turn-taking” by alternating their contribution, and therefore resolve sexual conflict efficiently through reciprocity of care provided by both partners (Johnstone *et al.*, 2014), without having to monitor each other perfectly (Johnstone and Savage, 2019). Inversely, *Synchrony* consists in both partners performing the same activity at the same time. Consequently, parents visit the offspring simultaneously, which can help decrease predation risk associated with nest visit (Martin et al., 2000), as well as a more even distribution of resources between offspring (Shen et al., 2010). *Task specialisation* is exhibited when care can be simultaneously needed across multiple behavioural dimensions, e.g., shortly after hatching most avian offspring need to be both fed and brooded (Iserbyt *et al.*, 2017).

The patterns presented above can be challenging to identify, but they are easily apprehended through how they maximise fitness in a given situation. Therefore, taking into account specificity of a given species and a given temporality (i.e., stage of the breeding), studies investigating parental performance with a cooperative perspective, in species exhibiting bi-parental care, need to identify what decisions parents can take together to satisfy offspring needs as well as their own, and reduce potential intra-family conflicts (summarised by Parker *et al.* (2002), and presented in Figure 1. below). Any pattern of parental care satisfying the needs of both parents and offspring, reducing conflict and leading to an increase in fitness for all parties involved can therefore be considered as cooperation and coordinated parental performance.

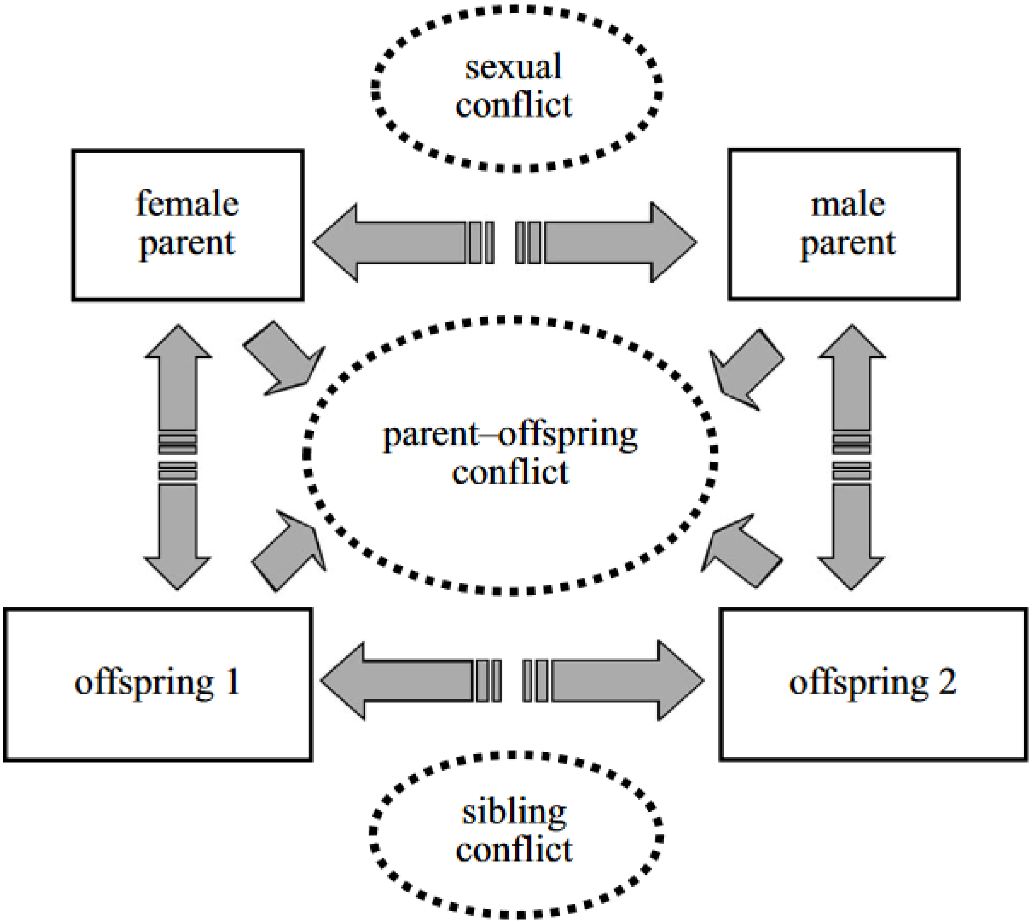

Figure 1. Intrafamilial conflict over parental care. Siblings compete between each other over the investment from parents (sibling conflict). Offspring have different interests from their parents over investment (parent–offspring conflict). Parents are in conflict over the amount each should give (sexual conflict). From Parker *et al.* (2002).

Conclusion

Parental care remains a hot topic in evolutionary and behavioural ecology. Evolutionary context of bi-parental care, most widespread strategy among avian species, is particularly intriguing. For a long time bi-parental care has been considered in the context of sexual conflict and only recently research focus has shifted towards partners cooperation. I performed my Ph.D. training in the spirit of partners cooperation, focusing on the reproductive system represented by the Little Auk – monomorphic species, socially and genetically monogamous, with long and extensive bi-parental care. I studied how Little Auk partners cooperate, to raise their offspring successfully. Using the framework of coordination of parental performance, I examined how breeding partners perform their parental activities in respect to each other, how that is related to their harsh and variable environment, and varies during the course of the breeding season.

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Chapter 1: Effect of environment on Parental Coordination of Chick Provisioning

I. Research paper n°1 - Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds

Antoine Grissot[1*], Marcelo Araya-Salas[2,3], Dariusz Jakubas[1], Dorota Kidawa[1], Rafał Boehnke[4], Katarzyna Błachowiak-Samołyk[4], Katarzyna Wojczulanis-Jakubas[1]

[1] *University of Gdańsk, Faculty of Biology, Dept of Vertebrate Ecology and Zoology, Gdańsk, Poland*
[2] *Laboratory of Ornithology, Cornell University, Ithaca, New York, United States of America*
[3] *Escuela de Biología, Universidad de Costa Rica, San Pedro, San José, Costa Rica*
[4] *Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland*

*Corresponding author: antoine.grissot@gmail.com

Published in *Frontiers in Ecology and Evolution*:
http://doi.org/10.3389/fevo.2019.00349.

Abstract

An increasing number of studies report coordinated chick provisioning by avian parents. Although the pattern of parental coordination varies across species, broad occurrence of this coordination suggests that it has an adaptive value: it may increase individual fitness via higher offspring survival, faster offspring growth rate and/or higher body reserves of the parents. However, to what extent the pattern of coordinated provisioning in a species represents a flexible response to current foraging conditions remains an open question. Here, we examined coordination of chick provisioning in the Little Auk (*Alle alle*), a planktivorous seabird species that breeds in the Arctic. Harsh environmental conditions impose bi-parental care on this species, and high variability within and across breeding seasons promotes flexibility in parental involvement to secure breeding success. During the chick rearing period, parents exhibit a dual-foraging strategy (i.e. alternating long foraging trips, serving to maintain the adults' body reserves, with several short trips aimed to provision the chick). We examined coordination of parental provisioning across five breeding seasons varying in terms of environmental conditions and found that the parents indeed coordinate their provisioning, avoiding performing long trips simultaneously and thus enabling a more even distribution of feeding through time. We also examined chick body condition in relation to the level of parental coordination to test the potential adaptive value of coordination, but we found no significant relationship between these two parameters. We found high variability in the level of the coordination between pairs, and this variability was similar across all study seasons, which represented a wide range of experienced environmental conditions. Nevertheless, we found that the energy density of food loads delivered to chicks was associated with the level of parental coordination: when conditions were characterised by the delivery of higher-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 the environmental variation could be still below a critical threshold of extreme conditions that would trigger more pronounced modifications of parental foraging patterns and coordination.

Keywords: coordinated provisioning, environmental effect, Little Auk (Dovekie), seabird, parental care

Introduction

Ecological conditions associated with food availability and predatory pressure are among the most important determinants of benefits and costs of parental care in birds and are therefore thought to play an important role in the evolution of avian breeding systems (Silver *et al.,* 1985; Martin, 1987; Arnold & Duvall, 2002; Fontaine & Martin, 2006; but see Olson *et al.,* 2008; Remeš *et al.,* 2015). At the evolutionary scale, environments characterised by mild and/or predictable conditions are associated with the system of uniparental care (8% of avian species) while environments with harsher or unpredictable conditions seem to require the involvement of both parents, and sometimes even help from other individuals, in order to raise the offspring successfully (81 and 9% of species, respectively representing bi-parental and cooperative breeding systems; see Cockburn, 2006). Ecological constraints or hazards faced by parents may also operate at a narrower scale, for instance shaping the extent of each parent's engagement and the manner in which they perform their care.

A growing number of studies highlight the importance of subtle partner inter-play in the form of coordinated parental performance (Hinde, 2006; Johnstone & Hinde, 2006; Elliot *et al.,* 2010; Raihani *et al.,* 2010; Massoni *et al.,* 2012; van Rooij & Griffith, 2013; Johnstone *et al.,* 2014; Bebbington & Hatchwell, 2016; Mariette & Griffith, 2015; Tyson *et al.,* 2017; Wojczulanis-Jakubas *et al.,* 2018). Patterns of parental coordination may vary across groups, species and even breeding stages (e.g. alternated vs intermittent incubation, alternated vs overlapped feeding patterns, etc), but overall, coordination of efforts by both breeding partners may substantially increase their reproductive success (e.g. Davis, 1988; Raihani *et al.,* 2010; Mariette & Griffith, 2015). This seems to be particularly important in extreme ecological conditions. A good example is the Kentish Plover, *Charadrius alexandrines,* which breeds in a hot desert where coordinated incubation between parents is essential for egg survival and also helps the parents to cope with their own heat stress (AlRashidi *et al.,* 2010). However, coordination *per se* is relatively rarely examined, and studies examining the issue in the context of environmental constraints are even more scarce.

Life-history traits of pelagic polar seabirds make them a particularly interesting ecological group in terms of parental care on the background of environmental conditions. Their harsh and highly variable environment poses a great challenge during the breeding period when, in addition to self-maintenance, the parents need to satiate the needs of their offspring. Many species are known to exhibit flexible strategies to buffer environmental variability until conditions reach a critical threshold beyond which they are unable to buffer suboptimal conditions without visible changes in their survival and/or breeding success. As such, seabirds are often used as binary bio-indicators of environmental conditions (Piatt *et al.*, 2007). In addition, foraging on distant marine resources, which are often patchily distributed (Schreiber & Burger, 2002), forces seabird parents to spend prolonged periods of time away from the nest (for hours or even days, e.g., Congdon *et al.*, 2005; Welcker *et al.*, 2009). Low ambient temperature imposes additional constraints for the parents, as embryos or young can be exposed to risks of death from hypothermia if left unattended for too long. All of these factors promote parental cooperation in seabirds and indeed, all the pelagic seabirds exhibit an obligatory bi-parental care system (Schreiber & Burger, 2002). Importantly, seabirds have been found to coordinate their food provisioning in a way that may potentially increase their breeding success (Congdon *et al.*, 2005; Tyson *et al.*, 2017; Wojczulanis-Jakubas *et al.*, 2018). Nevertheless, substantial variation in the level of coordinated provisioning has been observed in these seabirds, and it raises the interesting question of the extent to which this coordination is a plastic response of parents to foraging conditions. If the coordination is a flexible trait, it should vary with regard to the current foraging context, with two possible scenarios. First, unfavourable foraging conditions could hamper the coordination as each parent faces the challenge of self-maintenance in a way that causes coordination to fail. Alternatively, unfavourable conditions could enhance the coordination if the coordination only has an adaptive value under such challenging circumstances (e.g., regularly provisioning the offspring may compensate for low food quality; Jones *et al.*, 2002). The question about the relationship between the coordination and environmental conditions is particularly valid in the context of ongoing global warming, when dramatic changes in distribution of ocean currents impose additional constraints on entire marine ecosystems, including seabirds (e.g., Wassmann *et al.*, 2011; Frederiksen *et al.*, 2013).

Here, we examine foraging patterns and food provisioning schemes of breeding partners in the Little Auk (or Dovekie, *Alle alle*) in two breeding colonies across five breeding seasons. The Little Auk is a small pelagic seabird, breeding exclusively in the High Arctic zone. It is long-lived, with long-term pair bonds and long and extensive bi-parental care of a single egg/chick annually (Stempniewicz, 2001). Parents equally share their incubation duty for four weeks (Wojczulanis-Jakubas *et al.*, 2009) and both brood and feed the chick at a similar rate for 3–4 weeks (Harding *et al.*, 2004). Importantly, the Little Auk exhibits a dual-foraging strategy during the chick-rearing period, regularly alternating a few short trips in a row (up to 8 hours each, serving solely to provision the offspring) with a long foraging trip (> 8 hours up to 28 hours, primarily serving adult self-maintenance, even though some food is also brought to the chick; see Welcker *et al.,* 2009, 2012; Wojczulanis-Jakubas *et al.,* 2010; Jakubas *et al.,* 2012). This pattern seems to be universal as no evidence of birds performing only one type of trip was found in five colonies located across the whole breeding range (Welcker *et al.,* 2009). Thus, with both parents performing this bi-modal foraging strategy, a mismatch between partners can have consequences for breeding success, as long trips by adults represent extended periods of waiting for food by the chick. In the worst-case scenario, when both parents make their long trips simultaneously, the chick may face a periodic risk of starvation. Even if an extended wait for food is not lethal, it may lead to energy allocation switching from growth to thermoregulation, resulting in prolonged growth (Ricklefs, 1990; Schreiber & Burger, 2002). Combined with life-history traits demonstrating the importance of both parents' role in successful breeding, the dual foraging strategy makes the Little Auk a good model species for investigating coordinated efforts of breeding partners.

A recent study revealed that Little Auks indeed coordinate chick provisioning, avoiding simultaneous performance of long trips (Wojczulanis-Jakubas *et al.,* 2018). A potential benefit of the coordination has also been demonstrated, as parents provisioning the chicks in a coordinated manner reduced the variation in the duration of periods when the chick is waiting for food (i.e. an even distribution of feedings through time). This study, however, was performed in a single breeding colony located at a relatively long distance from optimal foraging grounds, and thus the role of specific environmental conditions in shaping the coordinated provisioning remains unknown. It is known that the foraging patterns of the Little Auk depend on oceanographic conditions, with unfavourable conditions being associated with extension of the overall duration of foraging trips (Welcker *et al.,* 2009; Jakubas *et al.,* 2013; Hovinen *et al.,* 2014; Kidawa *et al.,* 2015). Therefore it is possible that coordination performance may be different in another ecological context. Wojczulanis-Jakubas *et al.* (2018) also examined the effect of coordination on chick body condition but found no significant relationship. Why the coordination was not related to chick body condition, despite apparently favourable pattern of food delivery (i.e. reduced variation in duration of inter-feeding intervals), and whether coordination is associated with given environmental conditions, remains unclear.

The aim of the present study was two-fold. Firstly, we verified the results from the previous study (Wojczulanis-Jakubas *et al.,* 2018) by extending the earlier dataset by adding new records from another large breeding colony and subsequent seasons. Furthermore, using a different approach to measure chick body condition, we also re-examined the relationship between parental coordination and chick growth rate. We expected to find a positive correlation, which would show another benefit of coordination and give insights into the adaptive value of coordinated provisioning. Secondly, we analysed the parental coordination in regard to relevant environmental conditions. If coordination is a flexible trait varying in relation to foraging conditions, we expected to find variation in coordination level somehow associated with differences in environmental conditions.

Methods

Study area

We carried out the study in two breeding colonies: Hornsund (SW Spitsbergen, 77°00’ N, 15°33’ E) and Magdalenefjorden (NW Spitsbergen, 79°35’ N, 11°05’ E; Fig. 1). These two colonies constitute the core of the Little Auk breeding population on Svalbard (ca 590 000 breeding pairs in Hornsund and 18 000 in Magdalenefjorden; Keslinka *et al.,* 2019). Given high gene flow between these two colonies, they could be treated as a single panmictic population (Wojczulanis-Jakubas *et al.,* 2014). However, owing to their different location on the Svalbard archipelago, birds from these two colonies are exposed to different oceanographic conditions. Thus, examining the provisioning schemes in these two locations expands the range of environmental conditions. The sea shelf in the vicinity of Hornsund constitutes the main foraging area of the Little Auks from this colony (Jakubas *et al.,* 2013, 2014; and see Fig. 1). This area is typically under the influence of two currents: the coastal Sørkapp Current, which carries cold, less saline Arctic water, and the West Spitsbergen Current (an extension of the Norwegian Atlantic Current), which transports warmer, more saline Atlantic water (Piechura *et al.,* 2001; Cottier *et al.,* 2005). The contribution of the two currents varies among years with greater or smaller contribution from Arctic waters, which in turn creates more or less favourable foraging conditions for the local population of the Little Auk. The nearby sea shelf area in Magdalenefjorden (one of the foraging areas of Little Auks from Magdalenefjorden; Jakubas *et al.,* 2013) is primarily supplied with warm Atlantic waters from the West Spitsbergen Current. The aforementioned area is also under the partial influence of Arctic waters from the Sørkapp Current (Cottier *et al.,* 2005; Piechura & Walczowski, 2009) but the influx of cold waters varies greatly between years, creating in comparison with Hornsund generally less favourable foraging conditions and a greater challenge for the local population of the Little Auk (Jakubas *et al.,* 2013; Kidawa *et al.,* 2015). For these reasons, birds from Magdalenefjorden may also forage in the marginal ice zone despite its distance from the breeding grounds, as it seems to be more profitable foraging grounds than the waters in the close vicinity of the colony (Fig. 1).

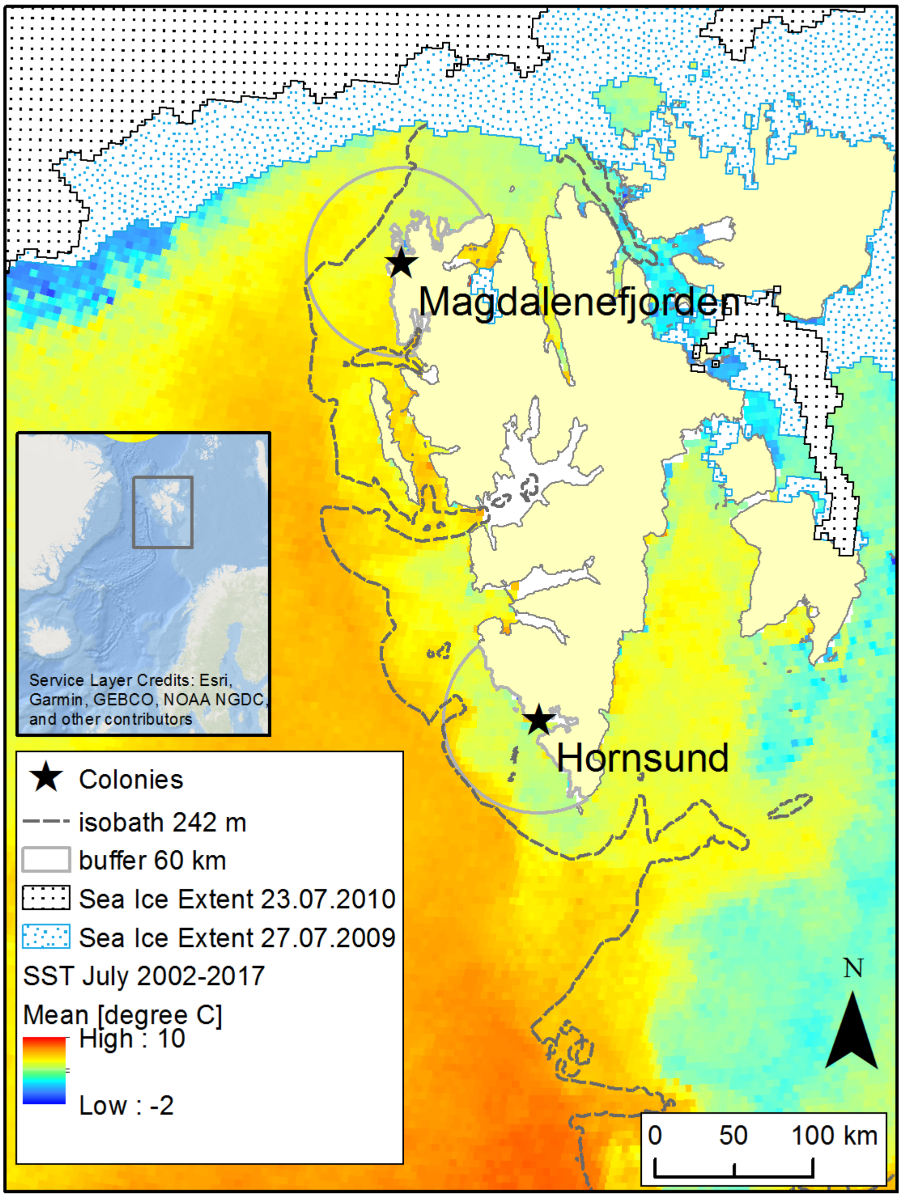

Figure 1. Study area. Mean sea surface temperature (SST) values for July 2002-2017; the 242-m isobath represents the shelf break and boundary of the Arctic zooplankton community (Kwaśniewski *et al.*, 2012), and the 60-km buffers around the studied colonies represent close foraging grounds of Little Auks (Jakubas *et al.*, 2017). Two example sea ice extents are shown for the dates when Little Auks were food sampled in both colonies. Data sources: SST: MODIS Aqua SST data (NASA Goddard Space Flight Center, 2014); sea ice extent: Multisensor Analyzed Sea Ice Extent - Northern Hemisphere (MASIE-NH), Version 1 with 4 215 km grid cell size (National Ice Center & NSIDC, 2010); bathymetry: a 500 m global relief model of Earth's surface IBCAO ver. 3 (Jakobsson *et al.*, 2012).

Behavioural observations

We collected data during three breeding seasons in the Little Auk colony at Hornsund (2016 to 2018) and two seasons in the colony at Magdalenefjorden (2009 and 2010). Data from Magdalenefjorden have been already used in Wojczulanis-Jakubas *et al.* (2018). Here, however, they are restricted to specific chick age, and analysed along with data from Hornsund. The data from Hornsund are considered in this context for the first time.

To establish bird presence/absence in the colony (and later to obtain duration and time distribution of foraging trips needed to determine the coordination level) we used one of the two following bird monitoring systems: direct observation or video-recording, carried out in three and two seasons, respectively (Table 1). The system of monitoring depended on field logistics and had slightly different accuracy. Nevertheless, obtained data were standardised in a way that ensured the two systems were comparable (see details below). To identify individuals, two weeks before the onset of the monitoring we marked both breeding partners from focal nests with a unique code using colour combinations of leg-rings and colour signs dyed on breast feathers (waterproof markers, Sharpie USA). The breast-signs usually faded away slightly throughout the monitoring period but were still clearly visible at the critical time, allowing quick and reliable individual identification in combination with the permanent coloured leg-rings. In both systems we monitored nests of focal birds continuously for 48 hours, and we could establish presence and absence of focal parents in the nest and its vicinity during this period with sufficient precision, owing to the nest site ‘fidelity’ of Little Auks when at the colony (personal observations). The 48-hour sessions (both observations and video recordings) were divided into 10-minute bouts (assigned with presence or absence of focal birds) due to respective methodological constraints of both observation methods and to allow comparison of data originated from the two systems. In both systems, arrival of the parent at the colony with a food load for the chick was evident (indicated by fullness of the gular pouch). Consequently, we considered a sequence of the 10-min periods of absence of a focal bird in the colony, followed by its appearance with a full gular pouch, as a foraging trip.

During the direct observations, pairs of observers (changing every 6 - 8 hours) watched the colony plot with the group of focal nests. The observations were carried out from a blind situated ca 20 m from the colony edge (ensuring minimal disturbance and securing identification of individually marked birds). The observers used binoculars (10 x 35) to confirm the birds’ identity, if necessary. It was possible to follow all marked birds because all the focal nests were located relatively close to each other, and marked individuals were never all simultaneously on the plot. The nest areas were observed continuously and presence/absence of parents at a given nest and fullness of their gular pouch were noted every 10 minutes (owing to uncertainty of exact departure time and securing acceptable accuracy).

For automatic video recording, we set a video camera (in total four types, commercial HD models, with 1-sec time lapse mode) at each focal nest separately. The cameras recorded the situation in a 3 m radius of the focal nest entrance. Thus, as for the direct observations, we were able to register presence/absence of parents at a given nest and fullness of their gular pouch. Despite the greater time-precision (1 second) of arrival at the nest, this system was less precise concerning arrival at the colony, due to spatial limitations of the camera frame. Presence/absence in the colony was assigned to every 10-min time-window because the birds returning from foraging trips usually enter the nest within the first 10 minutes after arrival at the colony (average latency = 7 min; unpublished data). Video material was processed using VLC software (VideoLAN, France) and QuickTime player (Apple Inc. USA).

To establish hatching date, nests under monitoring were checked every 2 days for the last week of the incubation, so we were able to adjust the timing of observation and video-recording to the chick's age. Although dates of the observations/video recordings varied between the colonies and seasons, focal birds were phenologically all in the same phase of the chick rearing period, i.e. "mid" chick rearing period (7 - 18 days old chicks; Table 1). Parental coordination may possibly change with age, and homogeneity in chick age among study nests minimises the variation within this confounding variable.

Table 1. Detailed sample sizes across the five seasons.

Colony	Season	System	N pairs	Chicks age [d] (mean; min-max)
Hornsund	2016	Observation	16	12; 9-16
	2017	Video recording	14	12; 8-14
	2018	Video recording	16	13; 10-17
Magdalenefjorden	2009	Observation	16	12; 9-17
	2010	Observation	19	13;10-17

Determination of coordination levels

To establish coordination level within a pair, every 10-min time-window for each individual was assigned to one of four categories: ST – short trip, LT – long trip, CO – presence in the colony, X - unknown. We classified foraging trips as short trip (ST) or long trip (LT) following the method previously used by Welcker *et al.* (2009), where the best cut-off value to separate the trips is the one that minimises the sum of variances of both trip types, given their log-normal distribution. We calculated the cut-off value separately for every season and obtained a mean cut-off value of 6.75 hours (range: 5.85 – 7.1 hours). At least one 10-min time-window classified as presence at the colony (CO) was always between two foraging trips. As some trips started or ended beyond the fixed 48 h observation/recording period, their duration could not be calculated, and we assigned such trips to the fourth category, unknown whereabouts (X), to avoid losing information when the partner's status was known at the same time.

In total, we obtained data for 81 pair-sessions, balanced between the 5 seasons and with a few repeated pairs across two seasons, and no pair repeated for more than two seasons (Table 1). To establish and test the coordination of provisioning, we followed the procedure applied in Wojczulanis-Jakubas *et al.* (2018). Thus, for each pair-session we first calculated the frequency of 10-min time windows in which one pair member was on ST while the other was on LT. Then we tested significance of this frequency using a Monte Carlo randomisation approach (i.e., randomisation that does not necessarily generate all possible combinations; see Wojczulanis *et al.,* 2018 for detailed information). This way we obtained a single p-value for every pair-observation. To obtain an overall p-value for the given data set, we used the Z-method using the R package *metap* (Dewey, 2019). Finally, we calculated the coordination index for every pair-observation as the proportional difference between the observed (obs) and expected (exp) proportion of 10-min time-windows in which one pair member was on ST while the other was on LT according to the respective randomisation procedure ($[\text{obs-exp}] \times \text{exp}^{-1}$). The obtained index varied between -1.00 and 1.42, with positive values associated with apparent coordination in the sense we consider in the present study (i.e. avoiding overlap of LTs by the two partners), and values equal to 0 or negative corresponding to an absence of this type of coordination.

Coordination and inter-feeding intervals

To verify the relationship found by Wojczulanis-Jakubas *et al.* (2018) between coordination and the variation in duration of time-intervals between the feedings, we first calculated the coefficient of variation in the duration of inter-feeding intervals ($CV = \sigma_{duration} - \mu_{duration}$). Then we fitted a linear mixed model with maximum likelihood using the R package *lme4* (Bates *et al.,* 2015), in which coordination index (calculated as described above) was the explanatory variable and CV was the response variable. Identity of the pair was also included in the model as a random effect (random intercept). The significance of the explanatory variable was tested with the *Anova* function using type III Wald Chi-square tests from the R package *car* (Fox & Weisberg, 2011).

Influence of environmental factors on coordination levels

To characterise environmental conditions for each season, we considered both biotic and abiotic parameters that are known to be important for foraging Little Auks: (1) total energy density of average food load brought to the chick [in kJ.g^{-1} dry weight (hereafter dw)]; a proxy of overall efficiency in chick provisioning, being a combination of food availability and parental foraging effort (see Kwaśniewski *et al.,* 2010); (2) the ratio of abundance of the two food items which are considered crucial for the chick diet, i.e. *Calanus glacialis* being associated with cold Arctic waters (considered as the preferred food item), and its warm-water Atlantic counterpart *Calanus finmarchicus*; a proxy of efficiency in foraging on preferred food item (Kwaśniewski *et al.,* 2010; Jakubas *et al.*, 2011); (3) the Simpson Diversity Index of the food provided; another proxy of efficiency in foraging on preferred food items (Kwaśniewski *et al.,* 2010); (4) sea surface temperature in the foraging areas (hereafter SST); a proxy of contribution of warm and cold waters, and thus availability of preferred zooplankton items associated with cold waters (Kwaśniewski *et al.*, 2010, 2012).

We established diet parameters based on food samples (on average 41 samples per season; range: 20-65 samples) collected from gular pouches of adults arriving at the colony from a foraging trip during mid chick rearing period (see Wojczulanis *et al.,* 2006; Kwaśniewski *et al.,* 2010 for all the methods related to sample preservation and analysis). We calculated zooplankton dry weight and energy density according to Wojczulanis *et al.* (2006), Kwaśniewski *et al.* (2010) and literature therein. To avoid disturbing provisioning schemes of birds under observation/recording, the food samples were collected from different individuals, meaning that diet composition cannot be linked directly to coordination but may serve as a proxy of overall foraging efficiency in a given season. Therefore, we calculated average diet parameters per season, which were used for further analysis. Dates of diet samples collection are provided in Table S1.

We collected SST data for 60 km marine buffers around the studied colonies (after Jakubas *et al.*, 2017) for the period when diet samples were collected from parental birds. We extracted data from the Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua satellite data. We used Level 3 daytime SST data derived from 11 μm thermal IR infrared (IR) bands with a 4 km spatial resolution (see NASA Goddard Space Flight Center, 2014). We mainly used 8-day products from periods corresponding to the dates when we collected diet samples from Little Auks. However, in some cases, due to cloudy conditions, we used monthly composites for July or August (see details in Table S1). Therefore, an average value per season was then calculated and used for further analysis. We extracted all abiotic data from GIS data using ArcGIS software 10.3.1 (Redlands, CA, USA: Environmental Systems Research Institute).

Due to inherent limitations in obtaining biotic and abiotic environmental factors, parameters were averaged per season and were at a very different scale from coordination data (i.e. we had up to five different values for environmental parameters and 81 pair-level calculated coordination indices, thus all pairs from the same season had the same value of each predictor). Thus, we were not able to use those parameters directly in a linear model to explain variation in coordination index as such an approach would lead to artificial data multiplication for predictors. Instead, we chose to use the season as a proxy for environmental conditions. To do so, we needed to first verify whether the five seasons were truly different considering the chosen environmental parameters. For this purpose, we tested each of the environmental parameters separately, using raw values collected for each season, and applied Kruskal-Wallis non-parametric test with season as a grouping variable. As a post-hoc test, we used Mann-Whitney U tests for all the pairwise comparisons. Then we modelled the previously calculated coordination index against the five seasons investigated, using a linear mixed model fitted with maximum likelihood including the identity of the pair as a random effect. Significance of the explanatory variable was tested using the *Anova* function. Following this analysis, multiple comparison post-hoc Tukey tests were performed to assess specific differences within the five studied seasons, using the *glht* function from the R package *multcomp* (Bretz & Westfall, 2008).

We also investigated the influence of environmental conditions on parental coordination by constructing a regression tree based on recursive partitioning using the R package *rpart* (Therneau & Atkinson, 2019). Recursive partitioning is a statistical method that examines the relationship between multiple explanatory variables and a single response variable using a recursive binary-partitioning process. It is particularly useful for identifying particular thresholds affecting the degree of response to variation of parameters when this response is expected to be more binary than linear. In this analysis, we used the pair-level coordination index as a response variable, and the seasonal average values of the four environmental parameters presented above were used as explanatory variables. These environmental parameters are thus used as general proxies for foraging conditions in each season. *Rpart* creates a decision tree classifying members of a given statistical population by splitting it into sub-populations based on the explanatory variables. The process is recursive because each sub-population may in turn be split an indefinite number of times until the subgroups either reach a minimum size or until no improvement can be made. The aim of splitting the data at each step is to establish groups that have a between-variation as large, and a within-variation as small, as possible. The second stage of the procedure consists of using cross-validation to trim back the full tree, based on a number of statistics calculated during the first step. Model outputs produce an 'inverted tree', in which the root at the top contains all observations, which is divided into two branches at the node. These branches can further be split into two subsequent nodes and so on. The nodes provide information about the explanatory variable name used for the split, and the value used for the split is represented on the branches. Each terminal node shows the size of the formed group (n) and the mean of the response variable for this group. Then we tested the significance of the differences between the groups created by each split using Mann-Whitney U tests. To evaluate to what extent the tree splits along colony lines, we calculated the proportion of cases from the two colonies in each final group.

Effect of coordination on chick body condition

The previous paper on parental coordination in the Little Auk also examined the effect of coordination on chick body condition (Wojczulanis-Jakubas *et al.,* 2018); however, the parameters describing body condition that were used in that study had some limitations, i.e. body mass was measured at several time-points during the second half of the chick rearing period, whereas coordination level was calculated for a restricted period of time. Thus, difference in time scales could blur the effect (see Wojczulanis-Jakubas *et al.,* 2018 for more details). We used a different approach to examine the effect of parental coordination on chick body condition. We evaluated the relative change in chick body mass between the onset (m_{start}) and end of the observation/recording session (m_{end}). For that purpose, we weighed the focal chicks in these two time-points ($d_{start,}$ and d_{end}) using an electronic balance (0.1 g accuracy; OHAUS, China) and calculated the daily relative change in chick body mass as

$[(m_{end} – m_{start}) \times m_{start}^{-1} \times 100] / [d_{end} - d_{start}]$. The chosen age stage (7 - 18 days) corresponds to a phase of linear growth of the Little Auk chick (Konarzewski & Taylor, 1989), which should allow detection of changes during 48 hours. In this analysis, we considered only data from Hornsund, the only location in which chicks were weighed in a systematic manner before and after observations. We used the daily relative change in chick body mass as a response variable in a linear mixed model fitted with maximum likelihood, with coordination index as an explanatory variable and the identity of the pair as a random effect. The statistical significance of the model was assessed using a type III Wald Chi-square test, as described above.

All analyses were carried out with R version 3.5.1 (R Core Team, 2018) and statistical significance was taken to be $P < 0.05$.

Results

Coordination level and inter-feeding intervals

We found that the frequency of 10-min time windows in which one pair member was on ST while the other was on LT was significantly greater than expected by chance according to the combined p-value from our Monte-Carlo randomisation tests ($Z = 2.47$, $P = 0.007$), indicating coordinated provisioning. The mean proportion of 10-min time windows in which one pair member was on ST while the other was on LT was 22.7% (Interquartile range: 11.5% - 32.3%). Nevertheless, high variability could be observed between the pairs (Fig. 2). We found a significant relationship between the coordination index and the variation of inter-feeding intervals (LMM, $\chi^2 = 14.44$, $P = 0.0001$), with a higher coordination being linked to a more even distribution of feedings through time (Fig. 3).

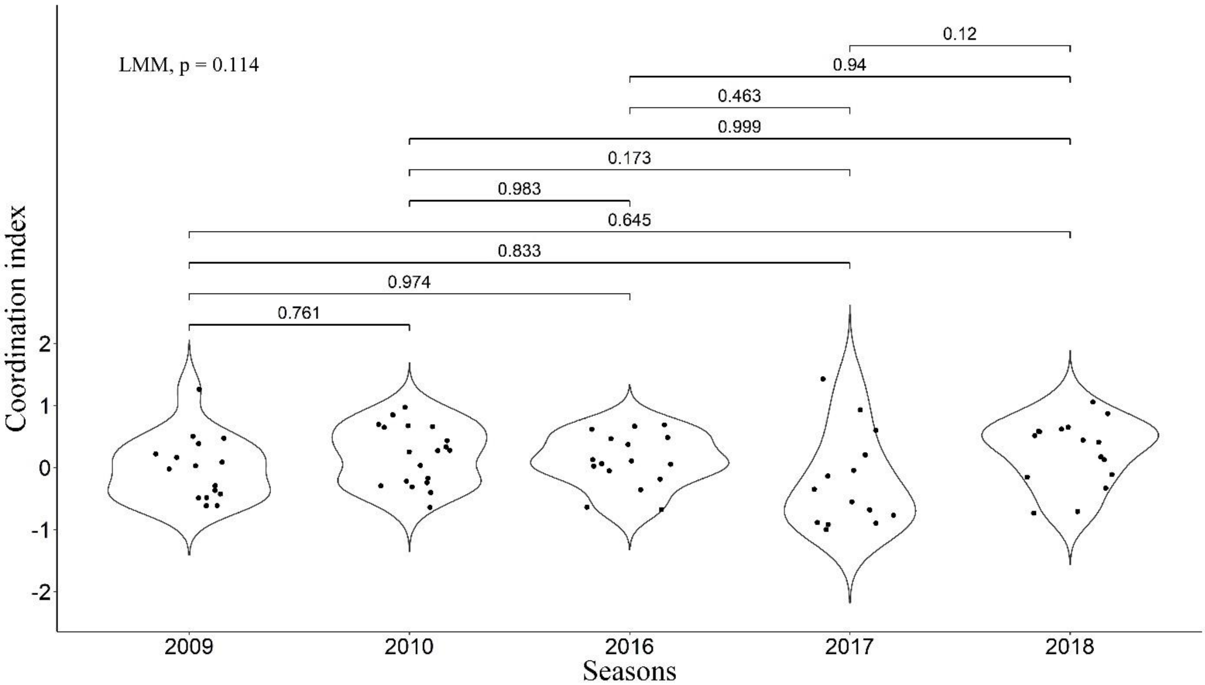

Figure 2. Coordinated index for all five seasons. Violin plots represent the distribution. P-values from inter-season comparisons made with Tukey tests are presented above the lines. Overall differences were statistically tested with linear mixed modeling. Positive values are associated with apparent coordination in the sense we consider in the present study (i.e. avoiding overlap of LTs by the two partners), and values equal to 0 or negative correspond to an absence of this type of coordination.

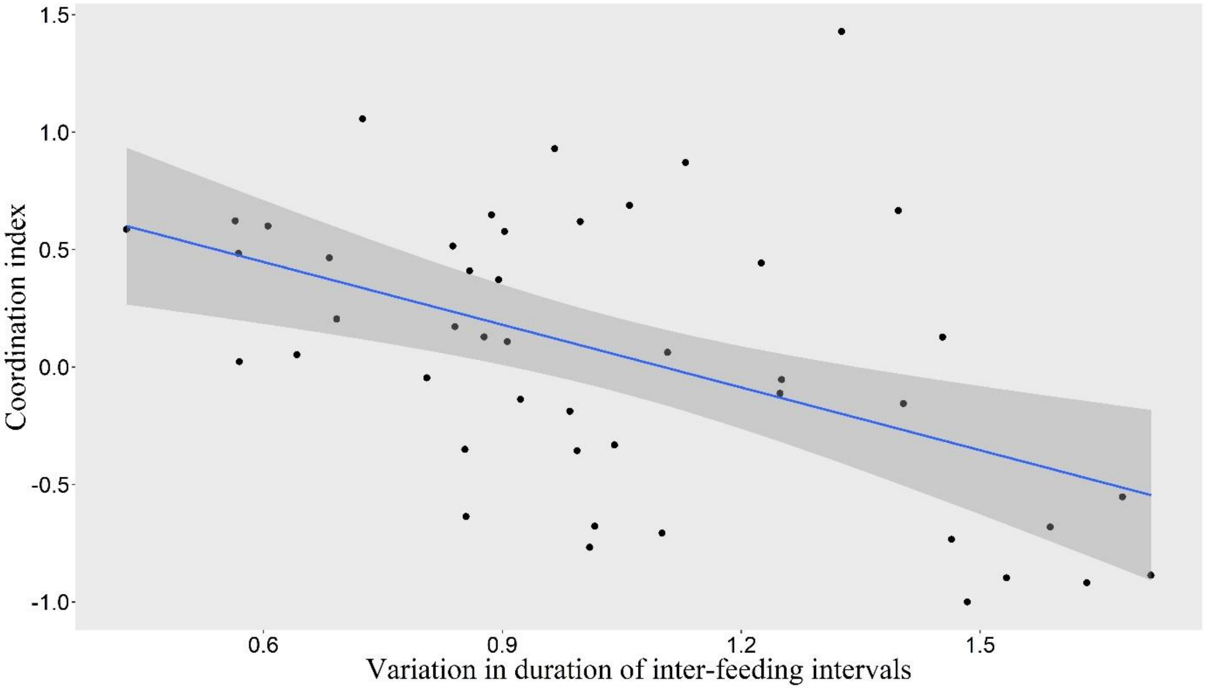

Figure 3. Relationship between coordination index and variation in duration of inter-feeding intervals. Scatterplot with linear regression line (in blue) and 95% Confidence Interval (in shaded grey).

Environmental conditions and coordination level

As assumed, all the five seasons were different in regard to the considered environmental parameters (Kruskal-Wallis tests, Total energy density: $P = 0.0008$; Ratio between abundance of *Calanus glacialis* and *Calanus finmarchicus*: $P < 2.2e^{-16}$; Simpson's Diversity Index: $P = 9.6e^{-12}$; SST: $P < 2.2e^{-16}$; see Fig 4 for detailed U test post-hoc comparisons concerning Total energy density [highlighted as most important in further recursive partitioning analysis]; and Fig S1 for other parameters). However, no significant effect of the season was found on the coordination index (LMM, $\chi^2 = 7.44$, $P = 0.11$; Tukey test, $P > 0.05$ for every possible combination), and only trends could be observed on the distribution of coordination index between the seasons (Fig. 2).

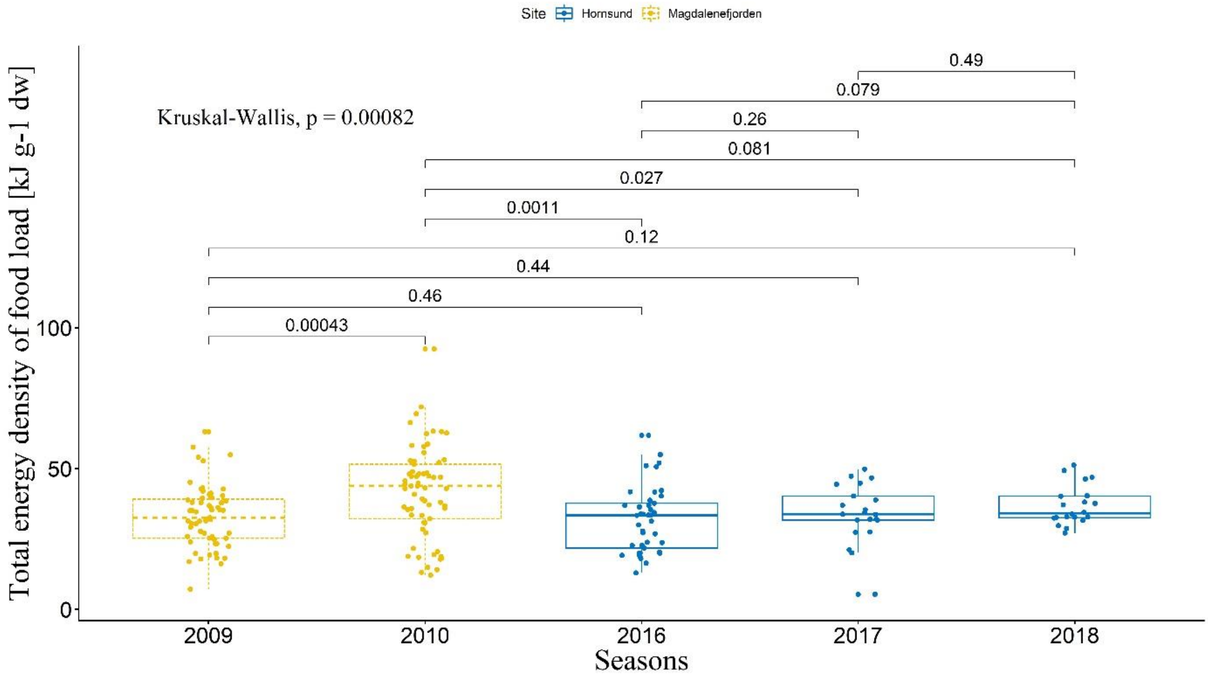

Figure 4. Total energy density of food loads delivered to the chicks during the studied breeding seasons. The boxes depict interquartile range, with median as a bold line inside the box. Whiskers indicate variability outside the upper and lower quartiles. Dots represents the raw data points. Inter-season comparisons were made with a Mann-Whitney U test, and overall difference was statistically tested with a non-parametric Kruskal-Wallis test. Only Total energy density is presented here as it was highlighted as most important in recursive partitioning analysis (see Fig S1 for other parameters).

Recursive partitioning analysis revealed that, of all the environmental parameters investigated, the mean total energy density of food load in a given season had the highest relative importance in shaping the coordination index. This analysis created a regression tree with two splits based on the total energy density of the food load (Fig. 5), resulting in three groups with different foraging conditions regarding this parameter. The first split divided our data set into two significantly different groups (U test, *P* = 0.026, and balanced between the two colonies, Fig. 5) and identified that when the foraging conditions are characterised by a total energy density of food load ≥ 35 kJ g^{-1} dw, the coordination index is the highest (mean = 0.22, n = 35), compared to the group characterised by foraging conditions of total energy density of food load < 35 kJ g^{-1} dw (mean coordination index = -0.033, n = 46). A second split was then applied to the latter group and divided it into two sub-groups that were not significantly different (U test, *P* = 0.071, Fig. 5). When the total energy density of food load is between 34 and 35 kJ g^{-1} dw, the coordination index is the lowest (mean = -0.22, n = 14), indicating that parents are not coordinated and even have a high chance of performing a LT at the same time. When the total energy density of food load is < 34 kJ g^{-1} dw, the coordination level is close to what is expected by chance (mean = 0.048, n = 32), meaning that parents are not coordinating their provisioning.

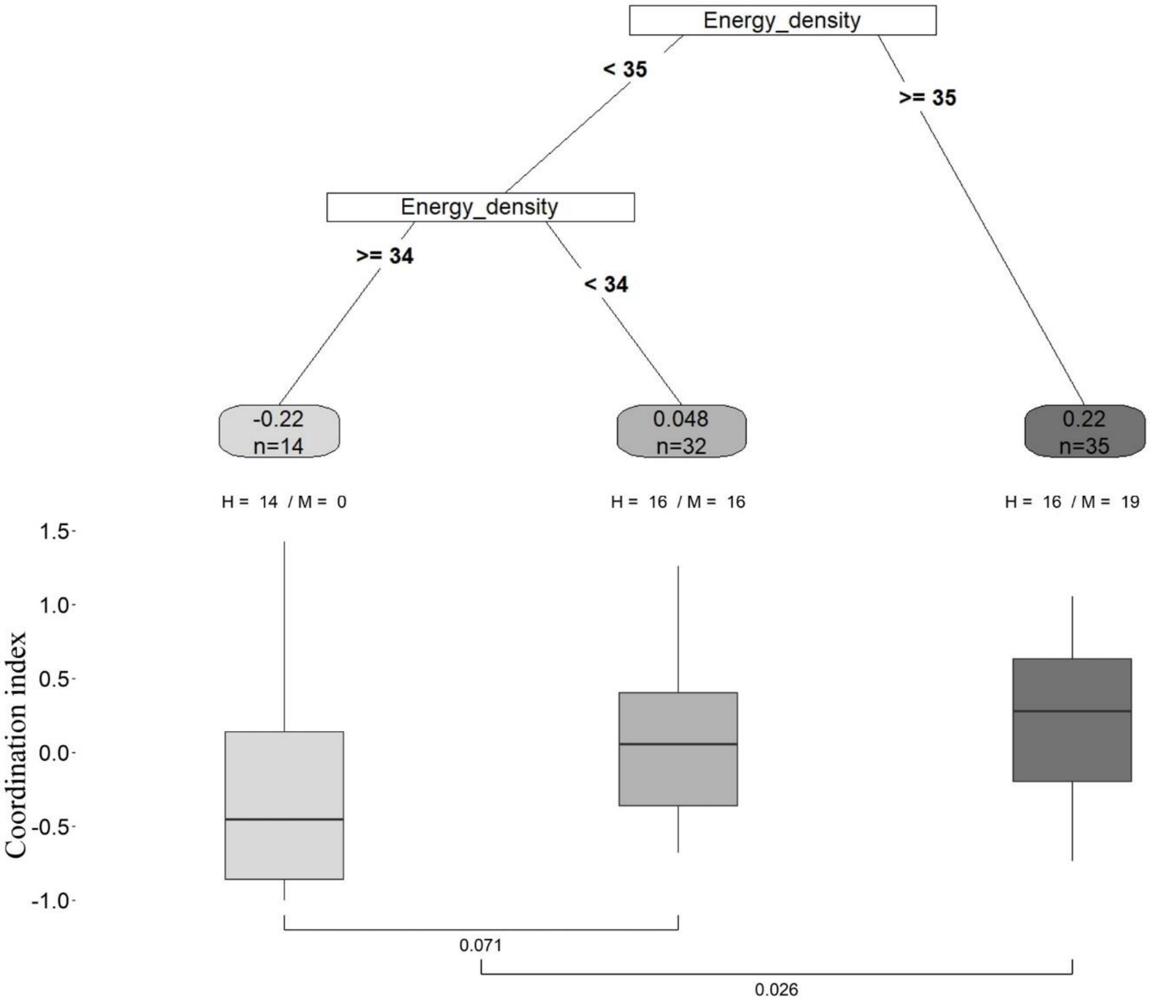

Figure 5. Regression tree obtained with recursive partitioning analysis. The 'inverted tree' presents the nodes and branches found by the analysis. The root at the top contains all observations, and is divided into two branches at the node. The group on the left is further split into two subsequent groups. The nodes provide information about the explanatory variable name (in a box) used for the split, and the value used for the split is represented on the branches. Each terminal node (in an oval) is showing the mean of the coordination index and the sample size (n) for the formed group. Proportion of cases from the two colonies in each final group is indicated (H = Hornsund; M = Magdalenefjorden). Boxplots for particular nodes depict the interquartile range of coordination indices of each group, with the median as a bold line and whiskers indicating variability outside the upper and lower quartiles. Inter-group comparisons were made with Mann-Whitney U tests. Energy_density: Mean total energy density of food load in a given season (in kJ.g^{-1} dw).

Effect of coordination on chick body condition

The 48-hour period between the onset and end of the observation was characterised by an overall gain in chick body mass. On average, a chick gained 10% of its initial body mass per day during the 48-hour period (interquartile range: 6.4 – 14.2%). However, we found no significant effect of the coordination index on body mass gain (LMM, $\chi^2 = 0.31$, $P = 0.58$).

Discussion

Our results showed that Little Auk parents coordinate chick provisioning, adjusting the timing of ST and LT to those of the partner, thereby reducing the variation in the duration of inter-feeding intervals. Our findings are consistent with the previous study on coordinated provisioning by the Little Auk parents (Wojczulanis-Jakubas *et al.*, 2018). Since the previous study, was performed in a colony located at a relatively long distance from the optimal foraging grounds, it imposed the question of how colony-specific the observed pattern is. Present findings, obtained using a broader spatial and environmental context, showed coordinated provisioning with a similar variability regardless of environmental conditions, suggesting that current foraging conditions have no notable effect on coordination. Nevertheless, we also found that the energy density of food loads delivered to chicks was associated with parental coordination: when conditions were characterised by the delivery of higher-energy food loads, the level of coordination exhibited by the studied population was higher. Thus, the coordination is not entirely independent from environmental conditions. We also examined whether chick body condition is related to the level of parental coordination to test potential adaptive value of the coordination. However, we did not find any significant effect, at least within the observed range of environmental conditions.

Although Little Auks are known to change foraging flight duration in response to environmental conditions (Welcker *et al.,* 2009; Kwaśniewski *et al.,* 2010; Jakubas *et al.,* 2011; Grémillet *et al.,* 2012; Jakubas *et al.,* 2013; Hovinen *et al.,* 2014; Kidawa *et al.,* 2015), the pattern of dual-foraging strategy (alternated ST and LT) seems to be fixed regardless of the environmental circumstances (Steen *et al.,* 2007; Welcker *et al.,* 2009; Wojczulanis-Jakubas *et al.,* 2010; Jakubas *et al.,* 2016). It has also been suggested that the dual foraging strategy could be a fixed trait due to its adaptive value. Foraging parents gained weight when returning from LT and lost an equivalent amount of mass during subsequent ST. Thus, the bimodal foraging allows adults to regularly restore their body mass after intensive chick provisioning (Welcker *et al.,* 2012). Therefore, if dual foraging is a fixed and adaptive trait in the Little Auk, the coordination of foraging trips between partners could be relatively easy to achieve, regardless of the foraging conditions.

As argued in the Introduction, the coordinated provisioning is expected to have an adaptive value. If so, why Little Auk parents coordinate the chick provisioning if it does not influence chick growth rate remains an intriguing question. However, although a positive relationship between coordination and chick body condition has been demonstrated in some species (Mariette & Griffith, 2015), some other studies have also failed to demonstrate a direct effect of parental coordination on nestling growth rate (van Rooij & Griffith, 2013; Bebbington & Hatchwell, 2016). One explanation of this apparent paradox in the Little Auk could be that coordination also aims to improve the parents’ condition and thus increases the fitness of the whole family. As body mass of adult Little Auks increases after the long trip and decreases after subsequent short trips (Welcker *et al.,* 2012), coordination between partners could be used to minimise this body mass decrease while assuring regular chick provisioning. This could be a mechanism to secure both present and future breeding success of the two partners. If the participation of both parents is necessary to raise the offspring successfully, and partners are paired for multiple seasons, as is the case in the Little Auk (Stempniewicz, 2001; Kidawa *et al.,* 2012), not only body condition of the current offspring but current and future condition of both partners are expected to be under strong evolutionary selection (Jones *et al.,* 2002). The lack of association between parental coordination and chick condition could also be a result of methodological constraints, which could operate at two levels. First, we performed the study during the mid-chick rearing period, when Little Auk chicks are already thermally independent and may be quite resistant to a prolonged fasting period (Taylor & Konarzewski, 1989; Konarzewski *et al.*, 1993). Taylor and Konarzewski (1989) found that the estimated fat reserves of 99.7% of chicks are sufficient to support them for longer than the maximum recorded interval between feedings. Another study on parental coordination in seabirds (Tyson *et al.*, 2017) suggests that the propensity for pairs to coordinate declines across the chick-rearing period. Thus, at the beginning of the chick-rearing period, when chicks' parental care requirements (food and brooding) are higher, the level of coordinated provisioning would probably be higher and could also have a more visible effect on chick body condition. The second methodological issue is that our measure of chick body condition in the form of body mass change may not be an ideal predictor. Although more accurate than that applied in Wojczulanis-Jakubas *et al.* (2018), it still presents some limitations: some events potentially happening before the measurement (e.g., feeding, defecation, wings training) could have considerably affected chick body mass but were not accounted for in our study. In addition, some studies suggest that increased parental provisioning does not necessarily result in greater chick body mass (Titulaer *et al.*, 2012). A future study could consider examining the effect of parental coordination on other parameters of chick body conditions, e.g., immunological or haematological parameters.

Another intriguing question raised by our study and worth examining in future is the mechanism behind the parental coordination. We have assumed an active foraging coordination of the partners as a response to the feeding needs of growing offspring. However, we cannot exclude the possibility that the observed coordination is a result of selection for different behaviours, diet and/or foraging specialisations of the breeding adults. For example, sex-specific provisioning behaviour has been observed in another alcid species, the Common Guillemot (*Uria lomvia*), where males fed on 'risk-averse' and females on 'risk-prone' prey items. Importantly, availability of the prey types may vary across the day, creating the pattern of males foraging during the night and females foraging during the day (Elliot *et al.*, 2010). Such a sex-specific niche partitioning may lead to a coordinated pattern of provisioning resulting from constraints other than those investigated in our study. However, no sex difference in the diel distribution of feedings has been observed in the Little Auk (unpublished data), suggesting that sex specific foraging specialisations might not play a role in the observed coordination. Nevertheless, other scenarios related to foraging, individual specialisation, and assortative/disassortative mating are possible in the Little Auk and could potentially create a misleading coordinated manner of chick provisioning.

Although environmental conditions are considered important in the evolution of avian breeding systems, with numerous examples of direct effects of environment on reproductive success (harsh environment hypothesis; Silver *et al.*, 1985; Martin, 1987; Arnold & Duvall, 2002; Fontaine & Martin, 2006; AlRashidi *et al.*, 2010), the two existing meta-analyses on this topic have not found a significant link between environmental conditions and parental cooperation (Olson *et al.*, 2008; Remeš *et al.*, 2015). Both meta-analyses support the view that the major correlates of parental cooperation are lack of mating opportunities for both sexes and mode of offspring development, rather than the breeding environment. Our results demonstrate a similar level of coordinated provisioning regardless of ecological conditions and also question the importance of environmental parameters in parental cooperative behaviour. Nevertheless, we cannot entirely reject the harsh environment hypothesis. First, our findings could suffer from methodological constraints, as we tested for differences in coordination between years and assumed that these differences were driven by differences in the measured environmental parameters. Other environmental parameters not accounted for in our study, or variability in followed pairs could drive the difference, thus we cannot make a causative link between environmental variability and coordination. This approach was chosen due to the unavailability of finer-scale parameters, and measured parameters were carefully chosen from relevant literature, but we cannot exclude the role played by unexpected parameters. Second, it is possible that despite considerable variation in environmental conditions across the studied seasons, the conditions were still within a tolerable range of variation and consequently did not affect parents' provisioning behaviour. Third, we found that the level of coordination seemed to be related to the energy value of food, as revealed by our recursive partitioning analysis: seasons characterised by a higher energy density of food were associated with a higher level of coordination. This finding suggests that environmental conditions do affect the coordination of parents but that the relationship may not be straightforward to explain due to the complex nature of the examined parameter, i.e. energy value of the food load. This is because the composition of food load was not obtained from focal pairs but from other birds from the same colony; therefore it is a proxy for energetic value of the food delivered to chicks at the colony scale and is also a combination of environmental conditions and parental effort. Moreover, high energetic value of food may indicate either good foraging conditions on foraging grounds, or high parental efficiency in foraging regardless of conditions on the foraging areas, or a combination of both. Hence, our results could mean that partners better coordinate their foraging trips in good conditions, i.e. high availability of energetic food in close vicinity of the colony. Only in this situation would pair members be able to adjust foraging flights in regard to each other and optimise use of good foraging conditions as much as possible in order to increase the fitness of both parents and chick. Alternatively, however, it could also mean that parents coordinate better in poor conditions i.e. low availability of energy-rich food in close vicinity of the colony. These circumstances would force them to increase energy expenditure allocated to chick provisioning. In consequence, they would need to coordinate their provisioning with each other, as only then could they feed their chick and secure an acceptable body condition for current and future breeding success.

The present study brings insight into the role of one environmental parameter (energy value of the food load) in shaping variability of parental coordination, suggesting that environmental conditions might affect the coordination of Little Auk parents. However, further studies investigating the full extent of the relationship are needed, to fully comprehend the mechanisms behind the parental coordination. They could take advantage of the recent improvements in tracking devices to establish very precise foraging areas and extract finer scale environmental parameters.

Acknowledgments

We thank Mateusz Barcikowski, Lech M. Iliszko, Małgorzata Jakimiak, Magdalena Hadwiczak and Katarzyna Pińska for their help in the field. We also thank Marion Devogel for her help with video processing and editing of earlier versions of the manuscript. Final version of the manuscript was proof-read by Carissa Ganong, as a native English speaker and specialist in ecology, and we particularly thank her for the improvements she made.

Ethical note

All the fieldwork was performed under supervision of KWJ and DJ (both having the relevant qualifications and experience). We handled all the birds for no more than ca 10 minutes and released them unharmed. We observed and handled the birds under permission of the Norwegian Animal Research Committee and the Governor of Svalbard (2007/00150-9, 2007/00150-11, 17/00663-2, 17/00663-7).

Data availability

Data provided in Supplementary Material Table S2. contains already calculated coordination indices but allow to repeat the analyses presented in the present paper. A script and relevant data to calculate a coordination index *per se* have been presented in the previous paper (Wojczulanis-Jakubas *et al.*, 2018). Raw data used in the present paper can be made available without undue reservation, to any qualified researcher.

Funding

The study was supported by Norway through the Norwegian Financial Mechanism (grant number: ALKEKONGE, PNRF-234-AI-1/07), by Poland through National Science Centre (no: 2017/25/B/NZ8/01417 to KWJ, and no: 2017/26/D/NZ8/00005 to DK), and received additional support from Polish Ministry of Science and Higher Education co-funded project (3605/SEAPOP/2016/2).

Author Contributions

Conceptualisation: AG, KWJ, DJ, MAS
Data curation: KWJ, KBS
Formal analysis: AG
Funding acquisition: KWJ, DK, KBS
Investigation: KWJ, DJ, DK, RB
Writing – original draft: AG
Writing – review & editing: all co-authors

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II. Supplementary Materials

Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds

Antoine Grissot[1*], Marcelo Araya-Salas[2,3], Dariusz Jakubas[1], Dorota Kidawa[1], Rafał Boehnke[4], Katarzyna Błachowiak-Samołyk[4], Katarzyna Wojczulanis-Jakubas[1]

Table S1. Detailed information on abiotic data used in analyses, and dates of data collection

Colony	Year	Date of diet sampling		Distance to the ice edge [km]	SST Data	
		day-month	Julian date		Period – Julian dates	Data Type
Magdalenefjorden	2009	27-Jul	208	81	209-216	8 d composite
		04-Aug	216	80		
	2010	23-Jul	204	111	201-208	
		01-Aug	213	101	209-216	
		06-Aug	218	103		
Hornsund	2016	21-Jul	203	480	201-208	8 d composite
		27-Jul	209	458		
	2017	22-Jul	203	290	182-212	monthly for July
		25-Jul	206	282		
		27-Jul	208	288		
		29-Jul	210	290	209-216	8 d composite
		30-Jul	211	320		
		01-Aug	213	305		
		04-Aug	216	355		
	2018	21-Jul	202	440	213-243	monthly for August

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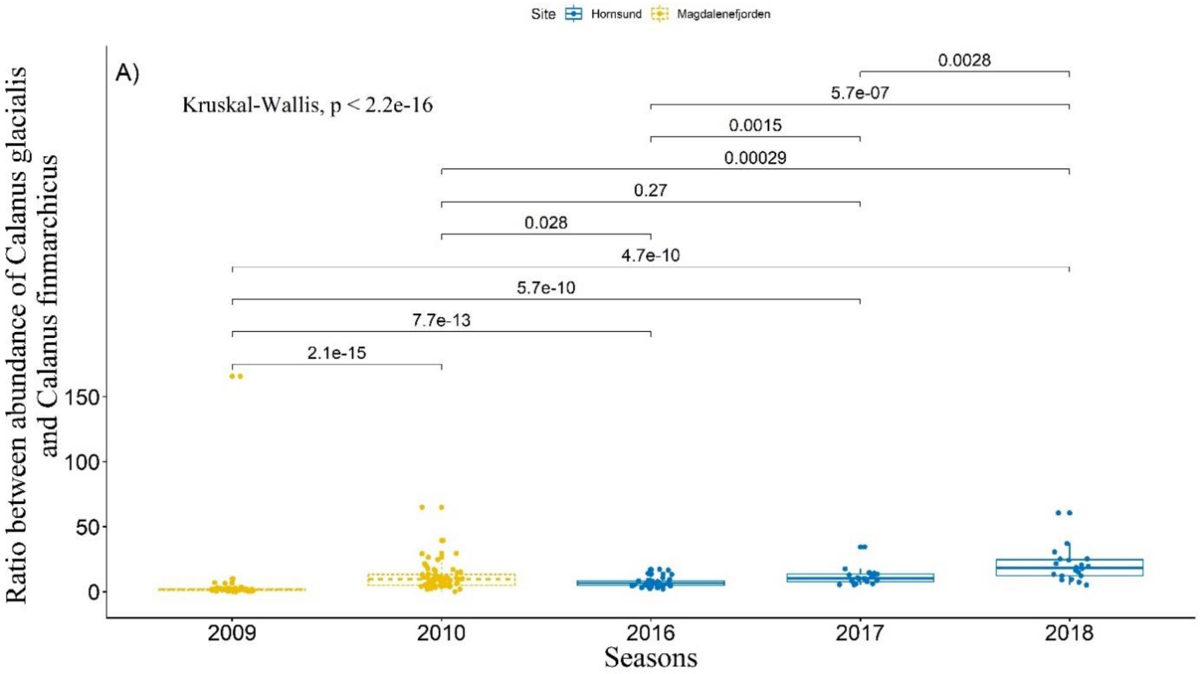
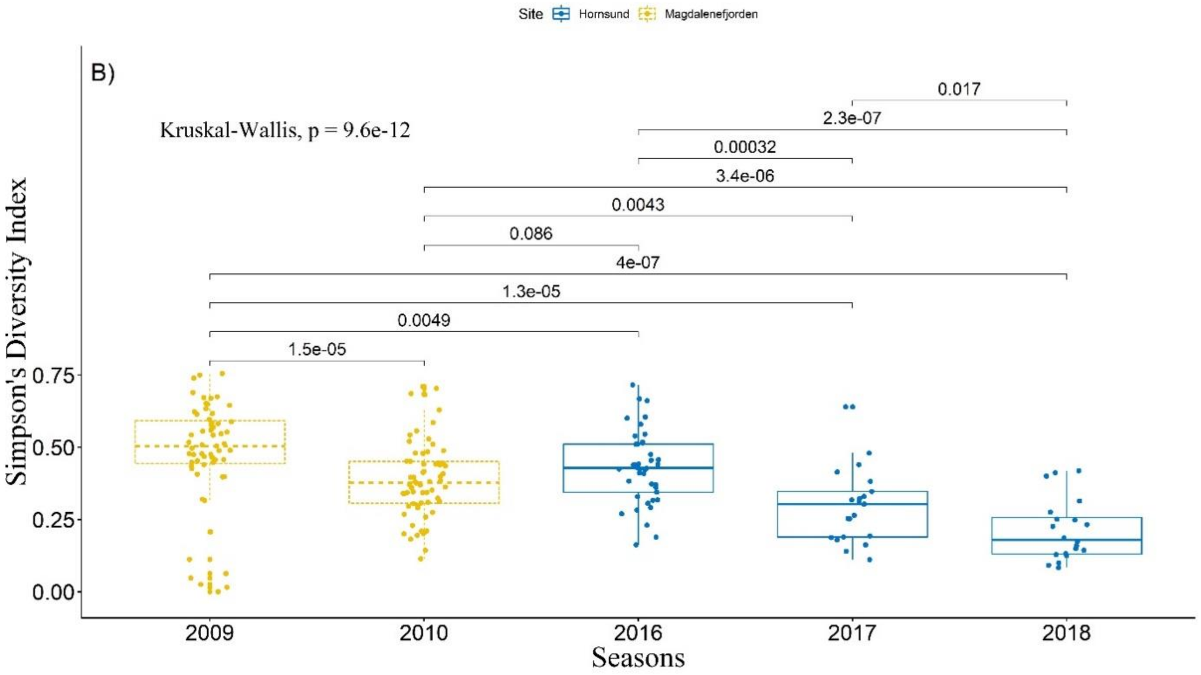
Table S2. Coordination and environmental data.

Nest	Colony	Season	Pair_ring	Coordination data			Feeding data		Relative change in chick body mass	Diet data			Mean SST
				pvalue randomisation	Overlap ST-LT	Coordination index	Number of feedings	CV inter-feeding		Mean energy density	Mean ratio of abundance CgV-CfV	Mean Simson Diversity index	
M.M23	Magdalenefjorden	2009	41164_41158	0,862	0,177083333	-0,369295057	23	0,946762973		33,0433122	5,146313718	0,481755919	1,905153645
M.M41	Magdalenefjorden	2009	41186_41191	0,7534	0,038194444	-0,61555533	10	1,130444702		33,0433122	5,146313718	0,481755919	1,905153645
M.F23	Magdalenefjorden	2009	41439_41427	0,2393	0,204861111	0,385301714	16	0,599136891		33,0433122	5,146313718	0,481755919	1,905153645
M.M31	Magdalenefjorden	2009	41189_41163	0,3589	0,232638889	0,165189021	15	0,733637404		33,0433122	5,146313718	0,481755919	1,905153645
M.F11	Magdalenefjorden	2009	41411_41425	0,808	0,0625	-0,491498131	14	1,448006367		33,0433122	5,146313718	0,481755919	1,905153645
M.M42	Magdalenefjorden	2009	41453_41444	0,8085	0,100694444	-0,485598533	13	1,012523781		33,0433122	5,146313718	0,481755919	1,905153645
M.M25	Magdalenefjorden	2009	41423_41414	0,7435	0,15625	-0,291756837	18	1,099922731		33,0433122	5,146313718	0,481755919	1,905153645
M.M35	Magdalenefjorden	2009	41166_41172	0,0002	0,350694444	1,261425235	20	0,592401307		33,0433122	5,146313718	0,481755919	1,905153645
M.F33	Magdalenefjorden	2009	41456_41461	0,3287	0,350694444	0,221318661	26	0,653478222		33,0433122	5,146313718	0,481755919	1,905153645
M.M29	Magdalenefjorden	2009	41162_41443	0,4602	0,15625	0,086764894	19	0,905584596		33,0433122	5,146313718	0,481755919	1,905153645
M.M39	Magdalenefjorden	2009	41181_41431	0,1926	0,097222222	0,503581747	16	1,028113479		33,0433122	5,146313718	0,481755919	1,905153645
M.F22	Magdalenefjorden	2009	41173_41185	0,4469	0,173611111	0,027246691	20	0,774270786		33,0433122	5,146313718	0,481755919	1,905153645
M.M44	Magdalenefjorden	2009	41308_41438	0,115	0,53125	0,472708687	23	0,707122137		33,0433122	5,146313718	0,481755919	1,905153645
M.M24	Magdalenefjorden	2009	41413_41430	0,5579	0,270833333	-0,023525524	15	0,772889153	0,438596491	33,0433122	5,146313718	0,481755919	1,905153645
M.M34	Magdalenefjorden	2009	41412_41424	0,801	0,15625	-0,425362947	23	1,291312409		33,0433122	5,146313718	0,481755919	1,905153645
M.F20	Magdalenefjorden	2009	41434_41426	0,9379	0,086805556	-0,615574462	22	1,182655892		33,0433122	5,146313718	0,481755919	1,905153645
M.M25	Magdalenefjorden	2010	41423_41414	0,6447	0,118055556	-0,312087632	13	1,21830783		41,8756473	11,50641664	0,387829603	2,228777799
M.F47	Magdalenefjorden	2010	41881_41880	0,7578	0,184027778	-0,218126484	19	0,98034602		41,8756473	11,50641664	0,387829603	2,228777799
M.M35	Magdalenefjorden	2010	41166_41434	0,7146	0,180555556	-0,242819159	19	1,389500364		41,8756473	11,50641664	0,387829603	2,228777799
M.M24	Magdalenefjorden	2010	41413_41430	0,2422	0,399305556	0,33376323	18	1,320282299		41,8756473	11,50641664	0,387829603	2,228777799
M.M25a	Magdalenefjorden	2010	41884_41883	0,0609	0,315972222	0,660847616	16	0,677964982		41,8756473	11,50641664	0,387829603	2,228777799
M.M41	Magdalenefjorden	2010	41186_41191	0,9311	0,090277778	-0,641270949	18	1,419672294		41,8756473	11,50641664	0,387829603	2,228777799
M.M39	Magdalenefjorden	2010	41431_41181	0,1936	0,371527778	0,673056596	20	0,556942713		41,8756473	11,50641664	0,387829603	2,228777799
M.M44	Magdalenefjorden	2010	41438_41308	0,0197	0,520833333	0,848264849	19	0,558469063		41,8756473	11,50641664	0,387829603	2,228777799
M.M29	Magdalenefjorden	2010	41443_41162	0,4133	0,260416667	0,033146081	19	1,033538934		41,8756473	11,50641664	0,387829603	2,228777799
M.M31	Magdalenefjorden	2010	41163_41189	0,5335	0,197916667	-0,173024944	18	0,866581743		41,8756473	11,50641664	0,387829603	2,228777799
M.M23	Magdalenefjorden	2010	41158_41164	0,2865	0,368055556	0,250783214	25	0,802804348		41,8756473	11,50641664	0,387829603	2,228777799
M.F31	Magdalenefjorden	2010	41306_41875	0,0213	0,409722222	0,97228439	16	0,687367368		41,8756473	11,50641664	0,387829603	2,228777799
M.M20a	Magdalenefjorden	2010	41890_41150	0,3505	0,305555556	0,278419409	21	0,473492561		41,8756473	11,50641664	0,387829603	2,228777799
M.F33	Magdalenefjorden	2010	41456_41882	0,0001	0,458333333	0,648217864	15	0,960294352		41,8756473	11,50641664	0,387829603	2,228777799
M.M43	Magdalenefjorden	2010	41446_41194	0,1615	0,392361111	0,431929493	24	0,558748768		41,8756473	11,50641664	0,387829603	2,228777799
M.M34	Magdalenefjorden	2010	41425_41424	0,0677	0,444444444	0,694060597	23	0,585744154		41,8756473	11,50641664	0,387829603	2,228777799
M.M28	Magdalenefjorden	2010	41161_41429	0,2801	0,354166667	0,272542402	20	0,983112772		41,8756473	11,50641664	0,387829603	2,228777799
M.F11	Magdalenefjorden	2010	41411_44022	0,7922	0,121527778	-0,401761556	14	1,349317288		41,8756473	11,50641664	0,387829603	2,228777799
M.F22	Magdalenefjorden	2010	41173_44021	0,7331	0,25	-0,295543825	19	0,991669696		41,8756473	11,50641664	0,387829603	2,228777799
101	Hornsund	2016	48567_48575	0,4255	0,184027778	-0,054262155	18	1,250754196	6,52173913	31,83356455	7,429870342	0,429269699	6,440323813
11_58	Hornsund	2016	26937_26859	0,4635	0,204861111	0,023046285	16	0,569683366		31,83356455	7,429870342	0,429269699	6,440323813
12_16	Hornsund	2016	50259_50301	0,1901	0,607638889	0,052107582	20	0,641974703	13,79310345	31,83356455	7,429870342	0,429269699	6,440323813

Table S2. cont.

12_26	Hornsund	2016	48545_48566	0,0226	0,239583333	0,482844138	21	0,568587083		31,83356455	7,429870342	0,429269699	6,440323813
14_10M	Hornsund	2016	48546_48568	0,4353	0,319444444	0,062106689	15	1,107556616	6,896551724	31,83356455	7,429870342	0,429269699	6,440323813
14_12M	Hornsund	2016	50096_48556	0,2335	0,25	0,370431419	18	0,8955756	8,888888889	31,83356455	7,429870342	0,429269699	6,440323813
D15_11	Hornsund	2016	50070_50230	0,2739	0,079861111	0,664905245	8	1,397419281	-1,53256705	31,83356455	7,429870342	0,429269699	6,440323813
D15_13	Hornsund	2016	50033_35945	0,3332	0,368055556	0,10834026	19	0,906270282	14,35185185	31,83356455	7,429870342	0,429269699	6,440323813
D15_13G	Hornsund	2016	43812_50225	0,9045	0,059027778	-0,678370207	18	1,016236972	10,98901099	31,83356455	7,429870342	0,429269699	6,440323813
D15_5	Hornsund	2016	26555_26557	0,3852	0,305555556	0,127465049	19	0,877104728	18,71345029	31,83356455	7,429870342	0,429269699	6,440323813
D15_8	Hornsund	2016	46021_31277	0,629	0,131944444	-0,188696406	14	0,984914094	6,140350877	31,83356455	7,429870342	0,429269699	6,440323813
D16_1	Hornsund	2016	48455_50303	0,2267	0,190972222	0,687339128	16	1,059660614	8,547008547	31,83356455	7,429870342	0,429269699	6,440323813
K16_4	Hornsund	2016	50302_50097	0,8756	0,059027778	-0,636885589	14	0,854472586	6,060606061	31,83356455	7,429870342	0,429269699	6,440323813
K4	Hornsund	2016	46030_50093	0,1428	0,444444444	0,464143916	20	0,683021125		31,83356455	7,429870342	0,429269699	6,440323813
K8	Hornsund	2016	44931_50217	0,01	0,215277778	0,618494696	19	0,997829291	4,166666667	31,83356455	7,429870342	0,429269699	6,440323813
W6(D15_6)	Hornsund	2016	50099_50088	0,8412	0,114583333	-0,356805389	12	0,993984172	8,169934641	31,83356455	7,429870342	0,429269699	6,440323813
D15_13G	Hornsund	2017	43812_50225	0,0293	0,315972222	0,928816088	19	0,965950169	24,24651372	34,10806634	11,48629921	0,296556058	5,594883103
W6	Hornsund	2017	50088_50099	0,5216	0,20979021	-0,046420262	20	0,805117985	9,812409812	34,10806634	11,48629921	0,296556058	5,594883103
D17_14	Hornsund	2017	50491_50500	0,8506	0,052631579	-0,767941237	20	1,009800126	8,815088151	34,10806634	11,48629921	0,296556058	5,594883103
W39	Hornsund	2017	46028_50152	0,4216	0,246527778	0,203626476	17	0,691946735	9,552845528	34,10806634	11,48629921	0,296556058	5,594883103
D17_16	Hornsund	2017	50165_50172	0,1744	0,181184669	0,600009846	17	0,605632852	10,01451379	34,10806634	11,48629921	0,296556058	5,594883103
W38A	Hornsund	2017	46025_46070	0,6343	0,09375	-0,3511643	16	0,853062511	15,47816473	34,10806634	11,48629921	0,296556058	5,594883103
W40	Hornsund	2017	41260_43817	0,5585	0,125	-0,137730747	23	0,922958207	12,28558183	34,10806634	11,48629921	0,296556058	5,594883103
K17_25	Hornsund	2017	43761_50494	0,9613	0,020833333	-0,89823195	23	1,53343685		34,10806634	11,48629921	0,296556058	5,594883103
11_36	Hornsund	2017	50499_43841	0,9825	0	-1	22	1,484033365	18,24324324	34,10806634	11,48629921	0,296556058	5,594883103
D16_10	Hornsund	2017	43873_48559	0,7318	0,045138889	-0,553533099	12	1,678976944	9,780092593	34,10806634	11,48629921	0,296556058	5,594883103
11_58	Hornsund	2017	26937_26859	0,9307	0,013888889	-0,918096061	19	1,634177175	15,51094891	34,10806634	11,48629921	0,296556058	5,594883103
W39B	Hornsund	2017	50167_50327	0,0001	0,208333333	1,427518348	11	1,326100485	14,99672561	34,10806634	11,48629921	0,296556058	5,594883103
D15_5	Hornsund	2017	26555_26557	0,9144	0,065972222	-0,682121687	19	1,588373971	26,79324895	34,10806634	11,48629921	0,296556058	5,594883103
W49	Hornsund	2017	43858_50492	0,8603	0,013888889	-0,887058292	13	1,714755112	21,4953271	34,10806634	11,48629921	0,296556058	5,594883103
D17_15	Hornsund	2018	55407_50173	0,4185	0,163194444	0,127003729	17	1,452980161	7,136279926	36,85819285	20,1351419	0,212604447	5,358536336
K8	Hornsund	2018	44931_55404	0,1885	0,21875	0,576821229	15	0,902867353	11,78045515	36,85819285	20,1351419	0,212604447	5,358536336
D16_1	Hornsund	2018	50303_48455	0,0076	0,472222222	1,056284747	21	0,724565536	7,4204947	36,85819285	20,1351419	0,212604447	5,358536336
11_58	Hornsund	2018	55405_26937	0,8893	0,21875	-0,332930974	25	1,04087892	6,869918699	36,85819285	20,1351419	0,212604447	5,358536336
D17_8	Hornsund	2018	50290_48597	0,0923	0,409722222	0,585906399	21	0,428076833	7,499102978	36,85819285	20,1351419	0,212604447	5,358536336
101	Hornsund	2018	50161_48567	0,6432	0,270833333	-0,112610824	22	1,248845704	3,212851406	36,85819285	20,1351419	0,212604447	5,358536336
K17_15	Hornsund	2018	50498_50153	0,6107	0,197916667	-0,156324238	23	1,403699198	4,026217228	36,85819285	20,1351419	0,212604447	5,358536336
113_10	Hornsund	2018	50135_50495	0,1667	0,232638889	0,408589875	19	0,858807494	14,16526138	36,85819285	20,1351419	0,212604447	5,358536336
113_41	Hornsund	2018	44892_46155	0,0929	0,402777778	0,621268811	22	0,564648805	5,829903978	36,85819285	20,1351419	0,212604447	5,358536336
14_18K	Hornsund	2018	50468_43004	0,0137	0,388888889	0,869679968	19	1,130402282	4,217054264	36,85819285	20,1351419	0,212604447	5,358536336
14_6K	Hornsund	2018	48518_50154	0,1161	0,378472222	0,64750871	22	0,886493767	6,574500768	36,85819285	20,1351419	0,212604447	5,358536336
D17_14	Hornsund	2018	50491_50500	0,8596	0,065972222	-0,707776378	19	1,10077423	6,086956522	36,85819285	20,1351419	0,212604447	5,358536336
12_16	Hornsund	2018	50259_50138	0,7972	0,03125	-0,7342742	19	1,464329959	5,310457516	36,85819285	20,1351419	0,212604447	5,358536336
D15_5	Hornsund	2018	26555_55401	0,1529	0,322916667	0,514174628	17	0,837860786		36,85819285	20,1351419	0,212604447	5,358536336
NI	Hornsund	2018	50150_55408	0,3609	0,069444444	0,4417116	8	1,225344352	30,6122449	36,85819285	20,1351419	0,212604447	5,358536336
11_75	Hornsund	2018	55403_10905	0,3297	0,284722222	0,171930827	14	0,840492604		36,85819285	20,1351419	0,212604447	5,358536336


Site Hornsund Magdalenefjorden
A)
Kruskal-Wallis, p < 2.2e-16
0.0028
5.7e-07
0.0015
0.00029
0.27
0.028
4.7e-10
5.7e-10
7.7e-13
2.1e-15
Ratio between abundance of Calanus glacialis and Calanus finmarchicus
150
100
50
0
2009
2010
2016
2017
2018
Seasons


Site Hornsund Magdalenefjorden
B)
Kruskal-Wallis, p = 9.6e-12
0.017
2.3e-07
0.00032
3.4e-06
0.0043
0.086
4e-07
1.3e-05
0.0049
1.5e-05
Simpson's Diversity Index
0.75
0.50
0.25
0.00
2009
2010
2016
2017
2018
Seasons

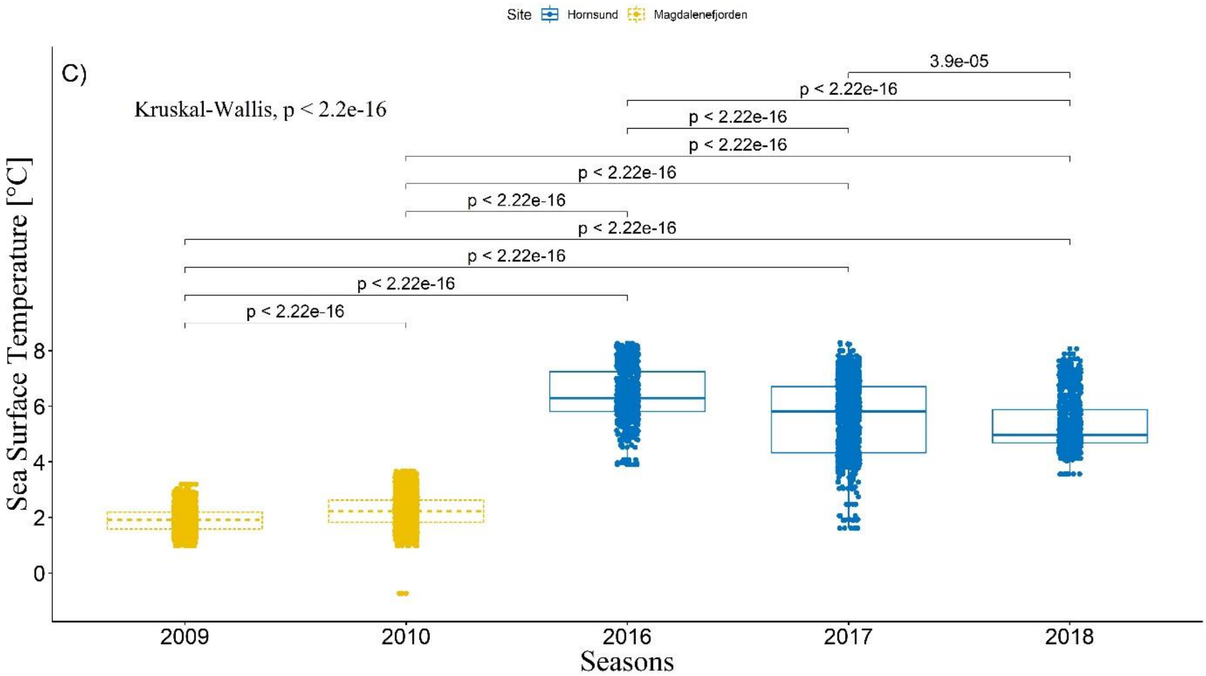


Figure S1. Environmental conditions during the studied breeding seasons (A: *Calanus glacialis/Calanus finmarchicus* ratio; B: Simpson's Diversity Index; C: Sea Surface Temperature [SST]). Values above the lines represent p values from t-tests comparing particular pairs of seasons. Boxplots show the median (bold line inside the box), the first (25%) and third (75%) quartile (box), and the lowest and highest values within 1.5 interquartile range (whiskers). Dots represent the raw data points.

Chapter 2: Coordination of Parental performance Through the Whole Breeding Season

I. Research paper n°2 - Breeding phase-dependant coordination of parental performance in a pelagic Arctic seabird

Antoine Grissot[1*], Lauraleen Altmeyer [1,2,3], Marion Devogel[1], Emilia Zalewska[1], Clara Borrel[1,2,3], Dorota Kidawa[1], Dariusz Jakubas[1], Katarzyna Wojczulanis-Jakubas[1]

[1] University of Gdańsk, Faculty of Biology, Dept of Vertebrate Ecology and Zoology, Wita Stwosza 59, 80-308 Gdańsk, Poland

[2] Université de Rennes 1, 2 rue du Thabor - CS 46510, 35065 Rennes CEDEX, France

*Corresponding author: antoine.grissot@gmail.com

Manuscript to be submitted in a scientific journal

Abstract

Currently parental care is becoming increasingly perceived as male and female cooperation, instead of being driven by a potential sexual conflict. Nevertheless, we are still far from understanding mechanisms of cooperative performance of breeding partners in birds, as many studies focus on a short time-window including only one stage of breeding (i.e. incubation or chick rearing period). Here, we investigated coordination of parental performance in a long-lived seabird with long and extensive bi-parental care, the Little Auk, *Alle alle,* throughout the whole breeding season. Previous studies on this species revealed coordinated chick provisioning, but parental coordination during incubation remained unstudied. Using video recordings collected over the course of two breeding seasons, we investigated the coordination of parental activities in both breeding stages, tested whether it was subject to small scale changes within each stages, and whether there was a relationship between coordination levels in both stages. We found that the level of parental coordination is overall high and increasing with the phases of the incubation period but decreases through the chick rearing phases, suggesting coordination is not a fixed behaviour but breeding phase-dependent. Furthermore, we highlighted a relationship between coordination levels during chick rearing and incubation periods, suggesting some extent of temporal dependence of parental performance coordination within the breeding season.

Keywords: Little Auk, Breeding, Behaviour, Parental Care

Introduction

Parental care is widely spread among animals, allowing a parent to increase its inclusive fitness through successful reproduction (Kokko & Jennions, 2008; Fromhage, 2017). However, investing in care is costly (Trivers, 1972; Ghalambor & Martin, 2001), and therefore a parent has to balance resources allocation between own maintenance and offspring care (Stearns 1992).When biparental care is involved, as is the case in 81% of avian species (Cockburn, 2006), another player is added in the equation, hence complexity of the interactions increases. Numerous theoretical and behavioural studies consider this tripartite equation (i.e., two parents and one/several offspring) to lead to a conflict. Indeed, the partners could both benefit from burdening the other with a greater proportion of parental care (Trivers, 1972; Houston & Davies, 1985; Westneat & Sargent, 1996; Arnqvist & Rowe, 2005; Wedell *et al.*, 2006). However, cooperation between parents expressed by coordination in parental activities was recently proposed as a solution minimising the sexual conflict between parents (Johnstone and Hinde, 2006; Wojczulanis-Jakubas, 2021; and reviewed in Griffith, 2019). An increasing number of studies suggests that the coordination of parental performance not only ensures a successful breeding but also an increase of fitness of both parents (Raihani et al., 2010; van Rooij & Griffith, 2013; Bebbington & Hatchwell, 2016; Mariette & Griffith, 2015; Gillies *et al.*, 2021). Furthermore, it may allow the maintenance of good body condition of both partners, essential for future reproduction (Tyson et al., 2017; Wojczulanis-Jakubas et al., 2018a; Grissot *et al.*, 2019a), which is particularly relevant in species of long-term pair bond (Mariette & Griffith, 2015). Most studies initially focused on passerines (e.g. Hinde, 2006; Raihani *et al.*, 2010; van Rooij & Griffith, 2013), but recently a greater variety of species and stages of breeding (i.e. incubation and chick rearing) are investigated, revealing a very broad range of species-specific behavioural patterns and mechanisms (e.g., Tyson *et al.*, 2017).

Many studies on parental coordination focus on a short time-window of a single breeding stage rather than considering it over its whole time span. Even when a full breeding stage is considered (Tyson *et al.*, 2017; Kavelaars *et al.*, 2021), how coordination is changing over its course is often overlooked. Given that the breeding period is characterised by many fine-scale changes, e.g., in parental behaviour (Fattah *et al.*, 2021; Morandini *et al.*, 2021), metabolic rate (Rønning *et al.*, 2008; Kulaszewicz *et al.*, 2018), hormonal levels (Wojczulanis-Jakubas *et al.*, 2018b; Fattah *et al.*, 2021) or body conditions parameters

(Wojczulanis-Jakubas *et al.*, 2012), one could expect that these changes influence the coordination of parental performance over the course of the breeding season.

Similarly, because coordination of parental activities is often investigated during a single breeding stage, the interconnection between the coordination at different breeding stages is understudied. Due to different behavioural and coordination patterns, as well as levels of parental investment and associated costs between the incubation and chick rearing periods, one could expect some extent of interconnection between these breeding stages. Similar interplay have been mostly identified in respect to seasonality, e.g. between non-breeding and breeding periods (Reudink *et al.*, 2009; Briedis *et al.*, 2018) or *vice-versa* (Yahkat *et al.*, 2011; Grissot *et al.*, 2019b) as well as between consecutive breeding seasons (Reed *et al.*, 2015; Shoji *et al.*, 2015). However, within season interconnection between breeding stages is poorly understood, especially in regard to the coordination of parental care, while important for understanding the mechanisms beyond the observed patterns.

Pelagic seabirds are top marine predators with life-history traits that make them ideal model species for investigating cooperation in parental care. Most species are long-lived, socially and genetically monogamous with long term pair bond, and long and extensive bi-parental care (Schreiber & Burger, 2002). In such a system, parental cooperation is likely to be favoured by selection (Griffith, 2019). Besides, as seabirds forage on food resources unpredictable in space and time (e.g. Jakubas *et al.*, 2020), raising the offspring may be particularly costly, therefore both parents' contribution is essential for successful breeding (Schreiber & Burger, 2002). Thus, coordination of parental activities in seabirds is thought to be a key adaptation for coping with the harsh and variable environment they breed in. Indeed, it has been already repetitively demonstrated that seabird parents do coordinate their parental performance (e.g. Tyson et al., 2017; Wojczulanis-Jakubas et al., 2018a; Grissot *et al.*, 2019a; Gillies *et al.*, 2021).

In this study, we focus on the Little Auk, *Alle alle*, to study changes in parental coordination across the whole breeding season, and a potential interconnection between levels of coordination during the incubation and chick rearing stages. This small seabird, breeding exclusively in the High Arctic, exhibits life-history traits making it a good model species for this purpose (e.g., long-lived socially monogamous with long-term pair bond and long and extensive bi-parental care; reviewed in Wojczulanis-Jakubas *et al.*, 2021). The coordination of parental duties in this species has been demonstrated, although, solely focusing on coordinated chick provisioning during the mid phase of the chick rearing period (Wojczulanis-Jakubas et al., 2018a; Grissot *et al.*, 2019a). We aim to fill in the remaining gaps and extend previous work on Little Auk parental coordination, by investigating it both during incubation and chick rearing periods. We expect a high level of coordination during the incubation period, as constant egg protection and thermoregulation may be crucial for reproductive success (Stempniewicz, 2001), and a positive progression of this coordination over the course of the incubation period. We also expect a similar progression of the coordination during the chick rearing period, and that coordination established during the incubation may affect coordination at the later phases of breeding with pairs highly coordinated during incubation sustaining high level of coordination also during the chick rearing period.

Methods

Study site and video recordings

We performed the fieldwork in two consecutive breeding seasons, 2019 and 2020 (June to August) in the Little Auk colony at Ariekammen slope (77˚00′ N, 15˚33′ E) in Hornsund, SW Spitsbergen. This very well-studied colony is located in one of the densest breeding concentration of Little Auks in Svalbard (ca 590 000 breeding pairs; Keslinka *et al.*, 2019). We monitored 23 breeding pairs in 2019, and 20 in 2020, with 20 pairs being monitored for the two consecutive seasons. We established phenology (egg laying, hatching and fledgling date) by controlling nests every day for a week around an expected event. In 2020, egg laying events could not be monitored, thus for both seasons hatching date will hereafter be used as a reference point of bird phenology. We established breeding success based on whether or not the breeding attempt led to a successful chick fledging, and included in further analysis only successful pairs, resulting in 18 pairs in 2019, and 16 in 2020 (with 13 pairs monitored and successful in both studied seasons).

Each parent in each pair was ringed in the previous seasons (with blood sampling for the sex analyses), and marked by a unique combination of colour rings and a colour mark on the breast’s feathers (waterproof markers, Sharpie USA). The surrounding area of the nesting burrow of monitored pairs was video-recorded using a separate video camera (commercial HD model of JVC, Japan) placed in front of its entrance. Chosen settings allowed to record presence and behaviour of focal parents within a 3 m radius from their nest entrance. This is the principal area where the birds spent their time when in the colony (based on own direct observations of bird behaviour in the study colony). All recordings were in a time-lapse mode

(1 frame per sec), which allowed to capture all the birds presence and behaviours of interest, while economizing memory space and battery usage.

Each pair was video-recorded for several continuous 48 hours sessions, aimed to be distributed equally over the whole breeding period. Throughout the incubation, we aimed for recording three sessions per pair representing the early, mid and late phases of incubation. However, due to the aforementioned lack of egg laying data for 2020, the recordings were performed in a slightly different way for the two years: in accordance with egg laying date of each pair in 2019 (i.e. adjusted to pair phenology), and on fixed calendar days for all pairs in 2020 (i.e. unknown phenology) with the incubation phase being back-calculated using the hatching date. Little Auks are highly synchronised in breeding phenology at the population scale (Stempniewicz 1995), and hatching dates are usually distributed over a week (personal observation). As a consequence, in 2020 the first session (supposed to be representing the early incubation phase) started when pairs were on average in 20th day before hatching (min-max: 16-27 d), when it was 26th day before hatching (min-max: 24-27 d) in 2019. The second session (mid incubation phase) on average started at 12th day before hatching (min-max: 8-19 d) in 2020, whereas it was 15th day before hatching (min-max: 13-17 d) in 2019. The third session (late incubation phase) in 2020 started at 4th day before hatching (min-max: 2-11 d), against 5th day before hatching (min-max: 4-7 d) in 2019 (see supplementary material Table S1). Given the wider range of incubation phases present in each type of recording session in 2020, it was not comparable with 2019, and therefore for further analyses including both years we will use the relative days before hatching date as a measure of the incubation phase. During the chick rearing period in both studied years, in contrats, we performed two recording sessions per pair well-adjusted to respective phenology, representing the early (session started when chick was in average 4 days after hatching; min-max: 3-5 d) and mid chick rearing (11 days after hatching; min-max: 11-12 d).

The video material was then processed using VLC software (VideoLAN, France) or QuickTime player (Apple Inc. USA). While watching the videos, we noted the time (with 1 sec accuracy) when focal individuals were appearing/disappearing on the frame and when they were entering/exiting the nest. We also noted the presence/absence of food in adult bird gular pouch (established by evaluating its size). Due to camera failure and/or bad quality of the framing around the nest entrance, some sessions had to be discarded, and so sample size varied slightly among the analyses. We extracted from the video material continuous time-intervals for each focal bird for each recording session, with three behavioural modalities: (1) “nest” – the time interval between a focal individual entered and exited the nest; (2) “colony”

– the time interval between a focal individual was visible in the nest vicinity but not in the nest (i.e. seen repetitively in the frame, with < 1 h gap in between each at-frame presence); and (3) “foraging” – the time interval a focal individual disappeared for > 1 h, or the time interval between a focal individual left the frame and came back with a full gular pouch. We choose the threshold of 1 h for the foraging trip based on previous studies on foraging durations (Welcker *et al.*, 2009; Brown *et al.*, 2012; Jakubas *et al.*, 2012, 2016, 2020) and personal observations. Each of the behavioural modalities were then further explored or modified to adjust to specificity of breeding stages and the purpose of each further analyses described below.

All data manipulations and statistical analyses were performed in R environment version 4.1.2 (R Core Team 2021), using custom made functions or existing packages, specified in the relevant context. Statistical significance was taken to be $P < 0.05$.

Coordination of parental care during the incubation period.

To investigate parental coordination during the incubation period, we focused on the three behavioural modalities described above: “nest”, “colony” and “foraging”. They represent quite faithfully Little Auk parental activities and constraints of parental care during the incubation period. Indeed, to ensure successful development of embryo resulting in hatching, the egg needs to be incubated continuously, i.e. cannot be left unattended for a long period of time (Stempniewicz, 2001). Thus, each parent is faced with a trade-off between the need to incubate the egg (represented here by “nest” modality, i.e. the time they spend in the nest) and its own need to maintain their body reserves (“foraging” modality, i.e. the time they spend in foraging). When considering the Little Auk pair, then sexual conflict could be raised from both partners addressing the trade-off independently from each other (e.g. foraging at the same time and leaving the egg unattended, or simultaneously present at the colony and risking depletion of their body reserves). However, this conflict could be reduced by coordination, i.e. partners doing the opposite activity in respect to each other (“nest” vs “foraging” or *vice versa*). To establish whether sexual conflict is apparent or solved by coordination we calculated the amount of time when one partner was in the nest, while the other partner was foraging, and tested its significance by comparison with what could be expected by chance. We used a Monte Carlo randomization approach, following Wojczulanis-Jakubas *et al.* (2018a) and Grissot *et al.* (2019a), where this procedure was used for the investigation of coordinated chick-provisioning. During the randomization procedure, we shuffled 10,000 times the observed continuous pattern of the three activity categories (“nest”, “colony” and “foraging”) for both male and female of each pair in each incubation session, with specific constraints (e.g. a “colony” activity always present before and after each “nest” and “foraging” activities), and then we compared the obtained randomised patterns with the originally observed pattern. We calculated the p-values as the proportion of expected random values that were higher than the observed value, separately for each pairs in each session, and then produced a single p-value for the whole incubation, using the Z-method from the R package *metap* (Dewey, 2022), to see if incubation patterns are coordinated at the level of our monitored population of Little Auk pairs.

Changes in parental coordination throughout the incubation period.

For further analyses, the amount of time when partners performed opposite activities (i.e., one partner in the nest, while the other is foraging) was used as a proxy for their coordination, given the results of the randomisation procedure (see **Results**). We chose to use the duration *per se* instead of calculating an index based on our randomisation procedure (see Wojczulanis-Jakubas *et al.*, 2018a, Grissot *et al.*, 2019a and below), to account for the amount of time one partner was in the nest and the other was foraging that can arise by chance, given the length of incubation bouts. Furthermore, our recordings lasting all strictly 48 h, the time spent performing opposite activities represents well the coordination of parental performance, and not a potential increase in duration of incubation bouts and/or foraging trips. Given that time considered is finite (48 h), and that each parent can perform three behavioural activities (“nest”, “colony” and “foraging”), with two of them representing the needs of offspring (“nest”) and themselves (“foraging”), the more they perform opposite activities satisfying one or the other need, in regard to each other, the more they are coordinating.

To further explore changes in coordination of parental activities during the incubation period, we consequently constructed a generalised linear mixed model with the amount of time partners performed opposite activities during a recording session as the response variable, and the phase of incubation (represented by the number of days before hatching, taken as continuous) as well as the year and their interaction as explanatory variables. Given the distribution of our response variable, we used a gamma distribution with an inverse link function within the *glmer()* function from the *lme4* package (Bates *et al.*, 2015). To account for pseudoreplication associated with multiple representation of the same pairs in data set, we also included pair identity as a random effect.

We tested significance of explanatory variables with the *Anova()* function, using type III Wald Chi-square tests from the package *car* (Fox & Weisberg, 2011), and removed from the model the variables that were not significant. Then, we confirmed the better fit of the candidate model using the Akaike information criterion, corrected for small sample size, with the functions *AICc()* and *Weights()* from the *MuMIn* package (Bartoń, 2020), with lowest AICc and highest weight indicating the best model (see Table 1). Assumptions of homoscedasticity and normal distribution of residuals were verified in the candidate model.

Parental coordination throughout the chick rearing period.

Following Grissot *et al.* (2019a) and the process detailed above for the incubation, we investigated the coordination of chick provisioning using an activity pattern obtained by combining the aforementioned “nest” and “colony” activities. During the chick rearing period the time spent in the nest is mainly dedicated to chick provisioning and therefore consists in quick visits. Besides, Little Auks adopt unimodal foraging trip duration strategy during the incubation period performing all flights of similar duration, in contrast with the chick rearing period during which they perform two types of flight differing in duration (Jakubas *et al.,* 2014). Thus, during the chick rearing period, we split the “foraging” activity in “short trips” and “long trips”, following the method proposed by Welcker *et al.* (2009). We then calculated the observed within-pair amount of time with one individual performing a short foraging trip, and its partner performing a long foraging trip, as it well represents the constraints of parental care during the chick rearing. Indeed, each parent needs to satisfy the need of its chick (mainly by performing short trips) while maintaining its body reserves (during the long trips; see Welcker *et al.,* 2012). It has been previously shown that during the mid chick rearing, the potential conflict generated by this situation can be avoided through coordination, by effectively avoiding to perform the long trips of both parents at the same time (Wojczulanis-Jakubas *et al.*, 2018a; Grissot *et al.*, 2019a), and we reproduced the same procedure for both the early and mid chick rearing phases. To do so, we shuffled the activity patterns of partners 10,000 times and compared the obtained chick provisioning pattern with the originally observed one. As previously, for each pairs in each session we calculated p-values as the proportion of expected random values that were higher than the observed value. We then produced a single p-value for all the chick rearing sessions, using the Z-method to see if the coordination of chick provisioning previously identified in our population of Little Auk pairs would still be present when including the so far non-investigated early phase of the chick rearing period.

We then calculated the coordinated index coined by Wojczulanis-Jakubas *et al.* (2018a) using the formula: [*obs* - *exp*] x exp^{-1}, where *obs* is the observed amount of time with one partner performing a short trip and the other on a long trip and *exp* is the mean of all the values obtained during the randomisation procedure. Because foraging events were categorised in short and long trips to reflect the bi-modal strategy of Little Auks, and the cut-off value distinguishing the two categories was decided by the method proposed by Welcker *et al.* (2009), some amount of time one partner was performing a short foraging trip, while its partner was performing a long foraging trip, could arise from said method. Therefore, we decided to reduce the noise created by chance by calculating this index instead of using the amount of time *per se*. We explored the changes of coordination index over the course of the chick rearing period by fitting a linear mixed model using the *lmer()* function of the package *lme4*, with the coordination index as the response variable, and the phase of the chick rearing period (represented by the session: early or mid) as well as the year and their interaction as explanatory variables. To account for pseudoreplication (multiple representation of given pairs), we also included pair identity as a random effect. Significance of explanatory variables was established as mentioned above, and we likewise performed model selection based on AICc differences (see Table 1). Whenever we found qualitative explanatory variables or their interactions to be significant, we performed post-hoc Tukey tests to assess specific differences, using the *emmeans()* function from the *emmeans* package (Length, 2022). Assumptions of homoscedasticity and normal distribution of residuals were also verified in the candidate model.

Relationship between the coordination of the two breeding stages

We investigated a potential relationship between the coordination of the two breeding stages (i.e. incubation and chick rearing) by fitting a linear model with coordination index in the chick rearing period as a response variable, and coordination during the incubation period (i.e., amount of time partners are performing opposite activities) as explanatory. In order to account for differences between phases of the chick rearing period, we fitted two separate linear models, one with the coordination index of the early phase of the chick rearing as the response variable, and the other with the coordination index of the mid chick rearing as a response variable. To account for similar differences within incubation period, we selected in our dataset only the year 2019, for which the three recording sessions represent well the early, mid and late phases of the incubation period, and included the values of coordination in each phases (early, mid and late) as three explanatory variables. We included in this analysis only the pairs for which we had three incubation recording sessions successfully performed, as well as two full chick rearing recording sessions (early and mid chick rearing), resulting in a sample size of 15 pairs. Like previously, we tested their significance with type III Wald Chi-square, and removed non-significant variables, checking for the best fitted model using differences in the Akaike information criterion, correcting for small sample size. Assumptions of homoscedasticity and normal distribution of residuals were verified in the candidate model.

Results

Coordinated parental care during the incubation period

During the incubation period, the amount of time when one partner was incubating in the nest while the other was foraging at sea was overall high and on average represented 88% (interquartile range: 79-98 %) of the time of a given recording session. Such an amount of time was greater than expected by chance (Z-method, $Z = 31.5$, $P < 0.001$) indicating that partners spend more time than expected by chance performing opposite activities. This amount of time will hereafter be used as a proxy for active parental coordination, as it results in almost equal alternation of incubation duty between the two partners.

The amount of time when partners performed opposite activities (i.e., incubation coordination) was significantly affected by the incubation phase (GLMM, gamma family, $\chi^2 = 19.25$, $P < 0.001$) and its interaction with the year (GLMM, gamma family, $\chi^2 = 6.33$, $P = 0.012$). The amount of time partners performed opposite activities was increasing the closer the session was performed to the hatching date (Fig. 1), meaning that the incubation coordination increased throughout the incubation period. This increase was more accentuated in the year 2020, compared to 2019 (Fig. 1).

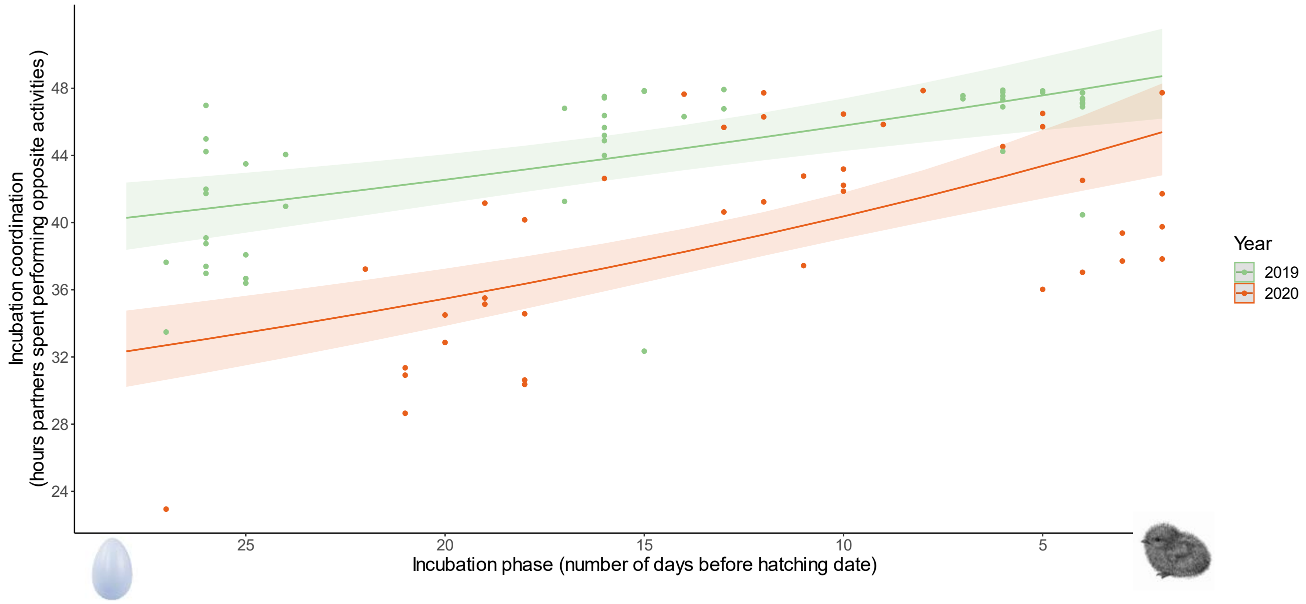


Figure 1. Changes in the coordination of parental performance between partners during the incubation period. The dots represent a given 48 h recording session for one focal pair. The incubation coordination is the amount of time from this session that partners spent performing opposite activities (i.e., one partner incubating in the nest, while the other was foraging at sea). Incubation phase is the number of days before the hatching date of the given pair the recording sessions was performed (i.e. the lower the number, the closer to the hatching date, illustrated by an egg to the left side and a chick to the left). Lines represent the regression obtained from the candidate GLMM, with shaded areas representing 95% confidence intervals.

Parental coordination throughout the chick rearing

During the chick rearing period, the amount of time one partner was performing a long trip while the other was performing a short trip was relatively high and in average represented 27% (Interquartile range: 16-36 %) of the time of a given recording session. Such an amount of time was greater than expected by chance (Z-method, Z = 3.35, P < 0.001) indicating an active coordination of the foraging pattern, leading to an avoidance of both partners performing long trips at the same time.

The coordination index was significantly affected by the chick rearing phase (LMM, χ^2 = 9.12, P = 0.002), as well as by the year (LMM, χ^2 = 13.02, P < 0.001), and their interaction (LMM, χ^2 = 8.94, P = 0.003). Early chick rearing was on average characterised by a higher coordination index (LMM, t = -3.02), with in particular the coordination index of the early phase of the chick rearing in 2019 being significantly higher compared to the mid chick rearing of the same year (*post-hoc* Tukey test, P < 0.05, t = 3.02; Fig. 2). The coordination index of the early chick rearing period was also significantly different between the two years investigated (*post-hoc* Tukey test, P < 0.01, t = 3.59; Fig. 2), with a higher coordination during the year 2019. No difference could be found between the years in the coordination index of the mid chick rearing period (*post-hoc* Tukey test, P > 0.05, t = -0.62; Fig. 2).

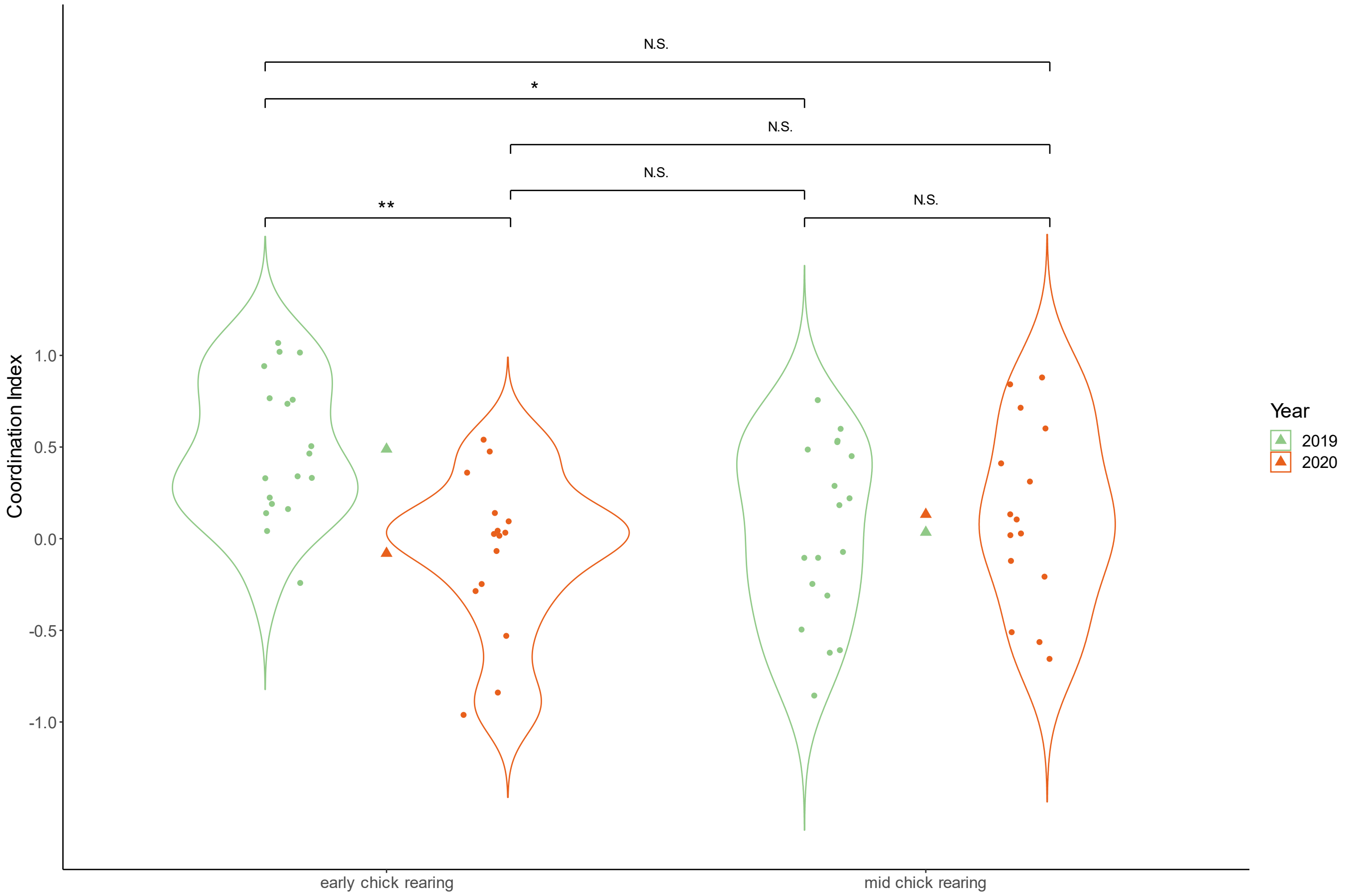


Figure 2. Differences in coordination index during early and mid phases of the chick rearing periods in two consecutive years. Violin plots represent the distribution, dots the real values, and triangles the mean. Difference between every combination was tested with pair-wise *post-hoc* Tukey test performed on the candidate LMM, and significance is indicated at the top. (N.S. : P > 0.05; * : P < 0.05; ** : P < 0.01; *** : P < 0.001).

Link between the coordination of breeding stages

The coordination index of the early phase of the chick rearing period was not significantly related to the way partners coordinate their activities during any of the incubation phases (LM, F = 3.81, P = 0.07 for early incubation, resp. F = 0.99, P > 0.05 and F = 1.02, P > 0.05 for the mid and late incubation phases). During the mid phase of the chick rearing period, however, the coordination index was significantly related to the coordination during the early (LM, F = 6.91, P = 0.02) and mid phases of the incubation (LM, F = 10.95, P < 0.01). The direction of the relationship was the opposite for the two significant phases (see Fig. 3), with a higher amount of coordination during the early incubation associated with a lower mid chick rearing coordination index, while a higher amount of coordination during the mid phase of the incubation was linked with a higher mid chick rearing coordination index (Fig. 3).

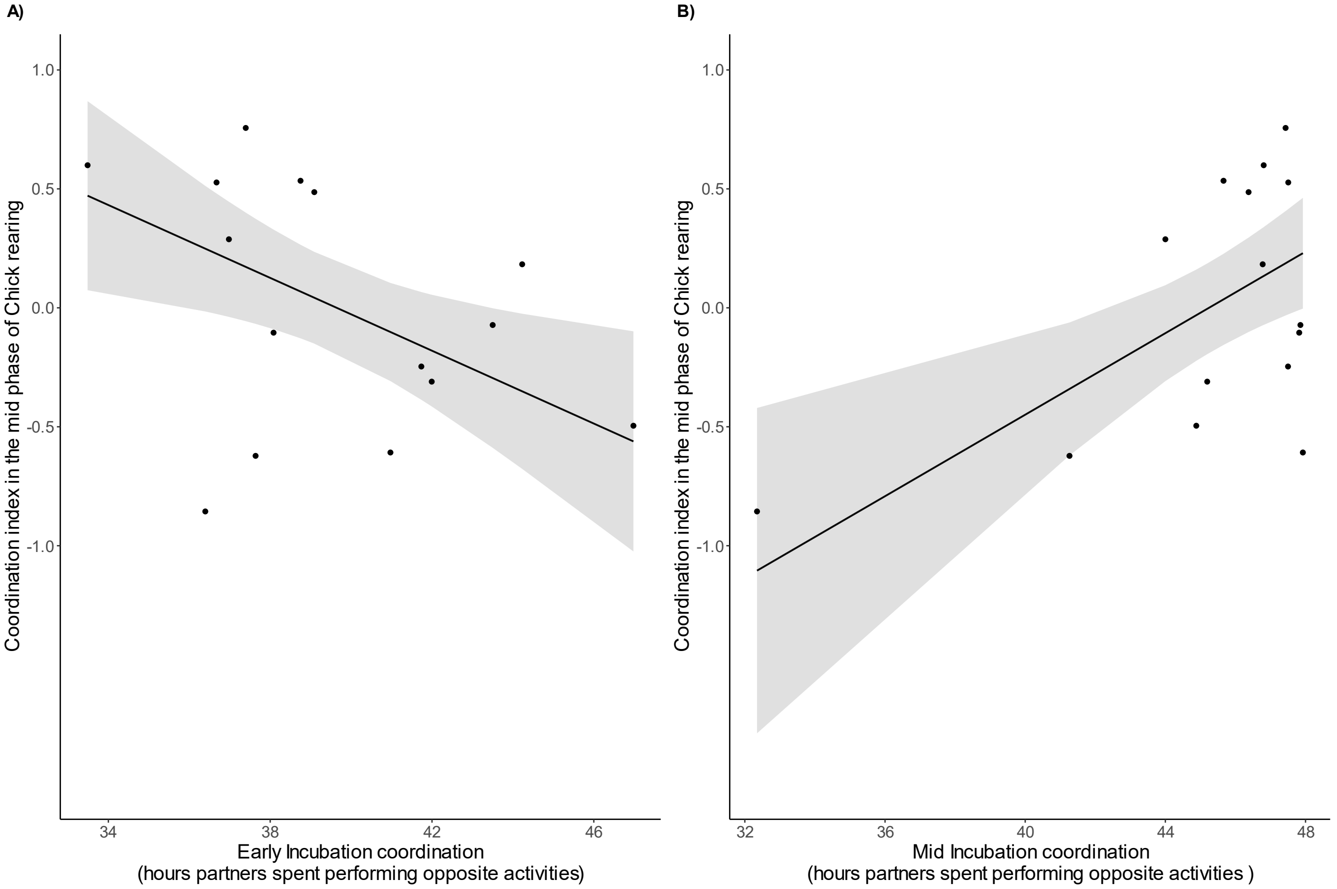


Figure 3. Relationship between coordination during the incubation and coordination index during the mid phase of the chick rearing period. The dots represent a focal pair. The incubation coordination is the amount of time from the early (A) or mid phase of incubation (B) that partners spent performing opposite activities (i.e. one partner incubating in the nest, while the other was foraging at sea). Lines represent the regressions obtained from the candidate LM, with shaded areas representing the 95% Confidence intervals.

Table 1. Model selection based on Akaike Information Criterion (ΔAIC: differences in AIC; wAIC: AIC weights) for the four models. Significant explanatory variables are highlighted in grey. The best-fitting model is represented between the dotted lines

Response variable		Explanatory variable 1	Explanatory variable 2	Explanatory variable 3	Interaction	Random factor	ΔAICc	wAICc
Incubation coordination	~	days_before_hatching	year		days_before_hatching:year	pair	0	0.87
		days_before_hatching	year			pair	3.81	0.13
		days_before_hatching				pair	31.64	0
						pair	49.20	0
Chick rearing coordination index	~	session_type	year		session_type:year	pair	0	0.47
		session_type	year			pair	4.89	0.04
			year			pair	1.74	0.2
						pair	0.91	0.3
Early chick rearing coordination index	~	coord_inc1	coord_inc2	coord_inc3			6.72	0.02
		coord_inc1		coord_inc3			2.62	0.13
		coord_inc1					0	0.5
							0.67	0.35
Mid chick rearing coordination index	~	coord_inc1	coord_inc2	coord_inc3			1.98	0.22
		coord_inc1	coord_inc2				0	0.59
			coord_inc2				3.00	0.13
							4.85	0.05

Discussion

We showed that Little Auk partners coordinate their performance in respect to each other throughout the incubation and chick-rearing periods, with specific patterns in each breeding stages corresponding to the different constraints imposed on the reproduction attempt. Such results reveal further insights into the way parents in this long-lived monogamous seabird resolve the tripartite equation involving two adults and an offspring, each with their own specific needs. Furthermore, our results revealed changes in coordination within the course of each studied breeding stage, and a relation between the coordination of both stages, highlighting that bi-parental care is not a fixed behaviour or a “sealed bid” as previously thought (Houston & Davies, 1985), but something that is temporally variable. Studies like this one, investigating coordination of parental care in more and more species and contexts are needed to further understand how parental care evolved to be a widespread behavioural strategy and the implications of such a strategy.

Cooperation in parental care is receiving a growing and well deserved attention, but few studies take into consideration more than one breeding stage at a time. Here, our study species was already known for its coordination of the chick provisioning (Wojczulanis-Jakubas *et al.*, 2018; Grissot *et al.*, 2019a), but the incubation period remained unstudied in the same context. We bridged this gap by showing that indeed, Little Auk parents spend more time than expected by chance performing opposite activities during the incubation period (i.e., one partner incubating the egg, and the other foraging), revealing coordination of their parental activity. Similarly, we confirmed in this study, using a different dataset never used in this context, the pattern initially highlighted by Wojczulanis-Jakubas *et al.* (2018) of an avoidance of partners performing simultaneously their long self-maintaining trips during the chick rearing period. The fact that coordination of parental care is exhibited during both stages of the breeding season highlights that, in this species, both stages present their own kind of constraints that seem to be overcome by cooperation between parents, in order to ensure a successful outcome of the breeding attempt. Such cooperation throughout the whole breeding season is not surprising, given high Little Auks energy requirements (Gabrielsen *et al,*. 1991; Konarzewski *et al.*, 1993), very harsh breeding environment (Stempniewicz, 2001), and unpredictable foraging conditions (Grissot *et al.*, 2019a; Jakubas *et al.*, 2020).

We also showed that Little Auk pairs exhibit changes in coordination levels within both breeding stages that constitute their breeding season. Those changes seem to be going in opposite directions, as coordination during the incubation (in the sense of partners performing opposite activities and alternating incubation duty) is in average increasing over the course of this breeding stage (Fig. 1), whereas coordination during the chick rearing period (in the sense of avoidance of simultaneous long trips) is in average decreasing between the early and mid phases of this breeding stage (Fig. 2), which contrasts with our initial hypothesis. Further investigation of the factors influencing such changes is needed to disentangle the observed patterns, and we can only suggest some abiotic (e.g. changes in environmental conditions) and biotic factors (e.g. hormonal and behavioural changes during the breeding season) as main directions for the investigation of factors influencing the within-season changes in coordination of the parental performance.

Grissot *et al.* (2019a) suggested some effects of environmental conditions on parental coordination even though no clear year differences could be highlighted in their study. Here, we investigated the effect of the season and its interaction with the different phases of breeding stages and, interestingly, we found contrasting results compared to the aforementioned study. In the present study, we found a significant year difference on the chick rearing coordination index (see Table 1 and Fig. 2), and a significant interaction of the year with the phases of both breeding stages (see Table 1 and Fig. 1, 2). Such contrast between the two studies, using the same population and very similar methodology, could come from the different years investigated. Grissot *et al.* (2019a) suggested that the range of environmental conditions was not extreme enough to highlight changes in coordination strategy, so we could hypothesize that years investigated in the present study represent a greater range of environmental conditions. Another explanation for the present year differences in coordination could come from the greater range of temporal scale used here. Grissot *et al.* (2019a) focused solely on the coordination index during the mid phase of the chick rearing period, which seems to be the least subject to year difference in the present study (Fig. 2). Given that coordination of parental performance during the chick rearing is decreasing between the early and mid phases, we could assume coordination of chick provisioning is set up early after the hatching date, where the breeding constraints (e.g., chick thermoregulation and feeding) are at their highest in this breeding stage (Stempniewicz, 2001). Therefore, mid chick rearing coordination may be less crucial for the breeding outcome, which is supported by the absence of effect of coordination on the chick growth rate highlighted by Wojczulanis-Jakubas *et al.* (2018a) and Grissot *et al.* (2019a). All this could explain why environmental conditions do not have such a strong effect on coordination during this particular phase of the chick rearing period (at least within the range of observed inter-annual variability). Expanding the knowledge about seabird coordination during different breeding stages and different phases within breeding stages therefore allows a better understanding of fine scale changes in coordination, and will be needed in future studies of factors influencing parental cooperation.

Our results indicated a relationship between the parental coordination during the incubation stage and the chick rearing stage (Fig. 3). However, given the opposite directions of relationships highlighted, and the fact that such relationship between breeding stages has been understudied, present results are hard to interpret. We found no effect of incubation coordination on the coordination index of the early phase of the chick rearing, but the coordination index of the mid chick rearing was significantly affected by both the early and mid incubation coordination. This could suggest that the late incubation is the phase having the least impact on how Little Auk parents coordinate their activities during the chick rearing period, despite being the temporally closest incubation phase to the chick rearing period. This could be explained by the very high amount of incubation coordination reached by all the pairs monitored here during the late incubation, and the low variation between pairs (93% of the time of a given recording session, interquartile range: 88-99 %). Further investigation on the highlighted relationship between coordination of parental performance during the mid phase of the chick rearing period, and coordination at the incubation stage is needed to further understand the temporal dependence between the two stages.

To conclude, our study highlights the importance of considering coordination not only during a short time-window of a specific breeding stage, but using a broader temporal scale. Indeed, coordination of Little Auk parental performance is exhibited all throughout the breeding season, but small-scale changes could be noticed and therefore it seems that coordination is a temporally dependant trait. The drivers of such temporal changes remain to be identified, but any study investigating the drivers of coordination should take the fine-scale changes highlighted here and importance of temporal scale into consideration.

Acknowledgments

We thank Martyna Cendrowska for her help in the field, the Polish Polar Station for hosting us even in pandemic times, and Łukasz Pracki for his precious IT help in the field.

Ethical note

All the fieldwork was performed under supervision of KWJ and DK (having the relevant qualifications and experience). We handled all the birds for no more than ca 10 minutes and released them unharmed. We recorded and handled the birds under permission of the

Norwegian Animal Research Committee and the Governor of Svalbard (2007/00150-9, 2007/00150-11, 17/00663-2, 17/00663-7).

Disclosure statement

The authors have no potential conflict of interests with respect to the research, authorship, and/or publication of this article.

Data availability

All data will be made available on a Dryad Digital Repository during submission process

Funding

The study was supported by Poland through National Science Centre (no: 2017/25/B/NZ8/01417 to KWJ, and no: 2017/26/D/NZ8/00005 to DK), and received additional support from Polish Ministry of Science and Higher Education co-funded project (3605/SEAPOP/2016/2).

Author Contributions

Antoine Grissot (AG), Katarzyna Wojczulanis-Jakubas (KWJ), Dariusz Jakubas (DJ) and Lauraleen Altmeyer (LA) conceived the ideas and designed methodology; KWJ, DJ and Dorota Kidawa (DK) provided the resources and material; AG, KWJ, LA, Emilia Zalewska (EZ), Clara Borrel (CB), and Marion Devogel (MD) collected the data; AG and LA analysed the data; KWJ, DK and DJ acquired the financial support, AG led the writing of the original draft. All authors contributed critically to the following drafts and gave final approval for publication.

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II. Supplementary Materials

Breeding phase-dependant coordination of parental performance in a pelagic Arctic seabird

Antoine Grissot[1*], Lauraleen Altmeyer [1,2,3], Marion Devogel[1], Emilia Zalewska[1], Clara Borrel[1,2,3], Dorota Kidawa[1], Dariusz Jakubas[1], Katarzyna Wojczulanis-Jakubas[1]

Table S1. Egg development phases and age of the chick. Values are expressed in number of days before (resp. after hatching date), at the beginning of the recording session.

Recording Session	Year	Mean age (in days)	Min age (in days)	Max age (in days)
early incubation	2019	26	24	27
	2020	20	16	27
	combined	23	16	27
mid incubation	2019	15	13	17
	2020	12	8	19
	combined	14	8	19
late incubation	2019	5	4	7
	2020	4	2	11
	combined	5	2	11
early chick rearing	2019	3	3	4
	2020	4	4	5
	combined	4	3	5
mid chick rearing	2019	11	11	12
	2020	12	12	12
	combined	11	11	12

Chapter 3: Development Of A New Method To Look At Parental Investment And Coordination Using Miniaturised Light-Based Geolocators (gls)

I. Research paper n°3 - Use of geolocators for investigating breeding ecology of a rock crevice-nesting seabird: method validation and impact assessment

Antoine Grissot[1*], Clara Borrel[1,2,3], Marion Devogel[1], Lauraleen Altmeyer[1,2,3], Malin Kjellstadli Johansen[4], Hallvard Strøm[4], Katarzyna Wojczulanis-Jakubas[1]

[1] *University of Gdańsk, Dept of Vertebrate Ecology and Zoology, Wita Stwosza 59, 80-308 Gdańsk, Poland*

[2] *Université de Rennes 1, 2 rue du Thabor - CS 46510, 35065 Rennes Cedex, France*

[3] *L'institut Agro (AgroCampus Ouest Rennes), 65 rue de Saint-Brieuc - CS 84215, 35042 Rennes Cedex, France*

[4] *Norwegian Polar Institute, Fram Centre, 9296 Tromsø, Norway*

*Corresponding author: antoine.grissot@gmail.com

Manuscript submitted in a scientific journal

Abstract

1: Investigating ecology of marine animals, including seabirds, imposes a continuous challenge due to their temporal and/or spatial unavailability. Light-based geolocators (GLS) are animal-borne devices that provide a cheap and efficient method to track seabird movement and is now commonly used to study their migration. Here we explore the potential of GLS data to establish individual behaviour during the breeding period in a rock crevice-nesting seabird, the Little Auk.

2: By deploying GLS on 12 Little Auk pairs, we developed a methodological workflow through which to extract birds' behaviour from GLS data (nest attendance, colony attendance and foraging activity), and validated its accuracy using behaviour extracted from a well-established method based on video recordings. We also compared breeding outcome (hatching success, chick growth rate), as well as behavioural patterns of logged individuals with a control group that was treated similarly in all aspects except the deployment of a logger, to assess short-term logger effect on fitness and behaviour.

3: We found a high accuracy of GLS-established behavioural patterns, especially during the incubation and early chick rearing period (when birds spend relatively long time in the nest). We observed no apparent effect of logger deployment on breeding outcome of logged pairs. However, we recorded some behavioural changes in logged individuals (longer duration of incubation bouts and shorter foraging trips).

4: Our study provides a useful framework for establishing basic behavioural patterns (nest attendance and foraging) of a crevice-nesting seabird from GLS data (light and conductivity) that is especially efficient during incubation and early chick rearing period. Given that GLS deployment does not seem to affect the breeding outcome of logged individuals, our framework is likely to be applicable to a variety of crevice/burrow nesting seabirds. However, our results revealed some behavioural changes in logged individuals and, because each species may have its own specificity, we recommend performing a pilot study before implementing the method to a new study system.

Keywords: Little Auk, breeding, behaviour, geolocator, method validation, impact assessment

Introduction

Study of animal ecology is often confronted to temporal and/or spatial unavailability of a target species. This is related to species-specific behaviour and/or environment, as well as a variety of researchers constraints. Obviously, limitations must be accepted in many cases, but sometimes the issue creates gaps in our understanding of species ecology that can, in worst-cases, lead to misunderstandings and to inadequate usage of the knowledge, including unsuitable and/or lack of conservation management. Any effort to fill these gaps is therefore worth performing.

Seabirds are a great example of animals that, for the majority of time, are beyond the reach of researchers, and thus studies of their ecology often exhibit a large caveats in the overall understanding of their annual cycles. Many species spend their non-breeding period at sea where they are inaccessible for study. As a consequence, this part of their annual cycle is poorly documented and only recently, through the application of modern technology, has this picture started to change (Fauchald *et al.*, 2021; Strøm *et al.*, 2021). In contrast, all seabirds are associated with land during the breeding period resulting in this part of their annual cycle being most extensively studied (e.g. Le Corre, 1996; Frederiksen *et al.*, 2004; Moe *et al.*, 2019; Merkel *et al.*, 2019; Carr *et al.*, 2020). Nevertheless, even during the breeding, researchers are sometimes faced with a temporal unavailability of the study species and/or difficulties in monitoring their movement and behaviour. For instance, all pelagic species alternate between periods spent on/in the nest (i.e. taking care of eggs or chicks) and periods spent at sea (foraging for themselves and/or their offspring). While absences at sea obviously represent spatial unavailability of the study species to the researcher, periods spent on/in the nest are also sometimes difficult to establish at a reliable temporal and/or spatial scale as disturbance of breeding birds should be kept to a minimum.

The breeding ecology of seabirds is of great scientific interest for many reasons. Primarily, they are often a key component of both marine and terrestrial ecosystems as a crucial vector of organic matter and nutrients from sea to land (Erskine *et al.*, 1998; Ellis, 2005; Zmudczyńska *et al.*, 2012; Zwolicki *et al*,, 2016) and as such are sentinels of ongoing environmental changes (e.g. Parson *et al.*, 2008; Gonzales-Carman *et al.*, 2021; Wojczulanis-Jakubas *et al.*, 2021). Furthermore, their specific life-history traits (i.e., long-lived, socially monogamous with long and extensive parental care, reduced brood size, etc) contrast with traits of other avian species (e.g., passerines), making them great model species for examining mechanisms of various life-history elements, such as parental care. As such, a good understanding of seabird breeding behaviour enables a better prediction of future changes in the ecosystem, more adequately adjusting eco-evolutionary models and a better protection of target species.

To answer many questions related to the breeding ecology of seabirds, it is crucial to document nest presence/absence of parents. Obtaining nest presence/absence data, however, can be challenging. In many studies, direct observations and/or video recordings of birds' presence and behaviour at nest site can be applied (e.g. Wojczulanis-Jakubas *et al.*, 2018; Grissot *et al.*, 2019a). Although in many cases these methods can be quite efficient, they have their constraints (e.g., too few individuals being followed, non-continuous sampling over time, or low spatial and temporal accuracy). Thus, technological achievements and their integration into ecological research may be of great help. In recent years, the use of animal-borne devices that record several different types of data at the individual level that are otherwise unobtainable in large numbers or at large temporal or spatial scales, have helped fill many gaps in our knowledge of many species.

Geolocators (GLS) are archival miniaturised light-based loggers (see Phillips *et al.*, 2004), widely used to document migratory pathways and non-breeding grounds of seabirds at unprecedented temporal and spatial scales (Croxall *et al.*, 2005; Frederiksen *et al.*, 2012; Dias *et al.*, 2013; Fayet *et al.*, 2017; Davies *et al.*, 2021; Fauchald *et al.*, 2021; Strøm *et al.*, 2021). Most devices also have a saltwater immersion sensor (i.e. conductivity sensor) and a growing number of studies demonstrate the suitability of these GLS data for investigating bird behaviour, such as moulting phenology of seabirds (Gutowsky *et al.*, 2014; Cherel *et al.*, 2016; Grissot *et al.*, 2019b) or foraging patterns (Leal *et al.*, 2017; Clay *et al.*, 2019). Questions have recently been raised whether they could also be used to study key behaviour during the breeding period (e.g. nest attendance and foraging patterns), and thus also be used in studies of breeding ecology.

In this study, we developed a methodological workflow to examine key breeding behaviour based on GLS data (light levels and conductivity data) in a small Arctic, rock crevice-nesting seabird, the Little Auk, *Alle alle*. This species is considered a good ecological model for many ecological and evolutionary questions (Stempniewicz, 2001; Wojczulanis-Jakubas *et al.*, 2021), including birds' responses to ongoing climate changes and anthropogenic pressure (Renedo *et al.*, 2020; Wojczulanis-Jakubas *et al.*, 2021) as well as coordination of parental care (Wojczulanis-Jakubas *et al.*, 2018; Grissot *et al.*, 2019a). To understand the breeding biology of the Little Auk is therefore very important not only on its own but also for other species in analogical and/or ecological context. Nesting in dark rockcrevices in areas and periods of constant daylight (polar day), as well as regularly foraging at sea, the Little Auk is an ideal candidate for using light and conductivity data from GLS loggers to document their presence/absence in the nest.

Technological devices invariably perform differently than expected such that an accuracy assessment, using a well-established method as a comparison, is needed to determine how meaningful and precise the recorded information is (Hughes *et al.*, 2021). To evaluate the suitability of GLS in the issue of accuracy and biological sense, we here compared behavioural patterns established from GLS to those obtained with video recordings, a conventional method previously used for this species (Grissot *et al.*, 2019a).

Although impact of GLS deployment on birds has already received a lot of attention, most studies have so-far considered this impact regarding individual breeding success and survival only (Phillips *et al.*, 2003; Guilford *et al.*, 2012; Costantini & Møller, 2013; Bodey *et al.*, 2017; Geen *et al.*, 2019; Brlík *et al.*, 2020; Pakanen *et al.*, 2020). Few studies have focused on birds' behavioural changes induced by carrying a device (Gillies *et al.*, 2020), as such changes may not be detectable by solely looking at breeding success, due to the ability of birds to behaviourally compensate a handicap of their own or of their partner (e.g. Harding *et al.*, 2004). However, carrying a device could still have a deleterious effect on the birds through a modification of behaviour and thus distort the study results. We thus also examined the effect of device deployment on various parameters, including behaviour.

Methods

We carried out the fieldwork in the well-studied Little Auk breeding colony in Hornsund (77˚00′ N, 15˚33′ E), one of the densest breeding concentration of Little Auks on the west coast of Spitsbergen (approx. 590 000 breeding pairs; Keslinka *et al.*, 2019). During the 2020 field season, we monitored 32 breeding pairs, splitting them into two groups: one with a GLS logger being deployed on both pair members (N = 12 pairs; hereafter logged group) and the other being a control group (i.e. no loggers deployed; N = 20 pairs). In both groups we established phenology (hatching and fledging date) by checking nests every day for a week, around an expected hatching or fledging event. We also evaluated breeding success, based on whether or not the breeding attempt led to a successful fledging, and chick growth rate by weighing chicks every three days.

Colony attendance and behaviour of both logged and control pairs were video-recorded. We placed a separate camera (commercial HD model of JVC, Japan) in front of the entrance of each monitored nest. Such a setting enabled a recording of presence and behaviour of focal birds within a 3 m radius of their nest entrance, an area where breeding birds spend most of their time when in the colony (personal observations and unpublished data). All recordings were performed in a time-lapse mode (1 frame per second), thus capturing all bird presence and behaviour of interest, while economizing memory space on the camera. For each nest, we performed several continuous sessions of at least 48 hours, throughout the incubation and chick rearing periods. To compare the methods, we selected only the sessions from nests that successfully carried out their breeding attempt, to avoid noise around behaviour associated with breeding failure (i.e. un-hatched egg or un-fledged chick), resulting in a sample size of 26 nests (N = 10 for the logged and N = 16 for the control group). We aimed to record two sessions per nest during each of the breeding periods (i.e. incubation and chick rearing). During incubation, recordings were made on the same calendar days for all the nests, and the two sessions were separated by a 5 day gap. Based on back-calculations from hatching dates, the nests were monitored on average 17 days (min-max: 12-22) before hatching for the first incubation session and 10 (min-max: 5-19) for the second. During the chick rearing (when parental behaviour is more dependent on chick age, see Stempniewicz, 2001; Harding *et al.*, 2004), we adjusted the timing of recording in each focal nest to the date of hatching (i.e. recordings were performed on different calendar days but corresponding to a given chick age), aiming to early (mean chick age: 3 days, min-max: 1-4) and mid (chick age: 12) chick rearing period.

To identify individuals during the video recording, both partners in both groups were marked with unique combinations of coloured leg-rings, and colour marks on breast feathers (dyed with non-toxic, waterproof markers, Sharpie, USA). The birds of the logged group were additionally fitted with C65 Super GLS model (Migrate Technology Ltd., Cambridge, UK). The loggers were fixed to a colour darvic leg ring using vulcanising tape and cable ties, with total device weight of 2 g (ca. 1% of the lightest individual’s body mass). Total handling time, including logger deployment, never exceeded 10 minutes.

Data processing

All data manipulations and statistical analyses were performed in R version 4.1.2 (R Core Team 2021), using custom made functions or existing packages, then specified in the relevant context.

GLS data. Raw light and conductivity (i.e. immersion in salt water) data from the loggers were extracted using the IntigeoIF software v1.14 (Migrate Technology, Ltd., Cambridge, UK) in a form of two separate files. The logging mode for light data was set to sample the light level every minute, and from that only the maximum value within a 5 min bout was stored (continuous value between 1.136 and 1163.944). For conductivity data, the sampling interval was set at 30 sec, with the number of wet samples within a 10 min bout being stored (i.e. discrete value between 0 and 20). The two different sampling and storing rates resulted in one record per 5 min bout for light data and one record per 10 min bout for conductivity data.

Video data. The video material was processed using VLC software (VideoLAN, France) or QuickTime player (Apple Inc. USA). While watching the videos, we noted the time (with 1 sec accuracy) when focal individuals appeared/disappeared on the screen and when they entered/exited the nest. We also noted the presence/absence of food (established by evaluating the size of the gular pouch). We then established continuous time-intervals for each focal bird for each recording session, with three behavioural modalities: (1) “nest” – the time interval between a focal individual entering and exiting the nest; (2) “colony” – the time interval between a focal individual was visible in the nest vicinity but not in the nest (i.e. seen repeatedly on the screen, with less than a 1 h gap in between each screen presence); and (3) “foraging” – the time interval between a focal individual disappearing for more than an hour, or reappeared with food. We choose the threshold of 1 h for the foraging trip based on previous studies on foraging durations (Welcker *et al.*, 2009; Brown *et al.*, 2012; Jakubas *et al.*, 2012, 2016, 2020) and personal observations of marked individuals. Due to the presence in this population of a bi-modal foraging strategy (see Welcker *et al.*, 2009), the behavioural category “foraging” was split into “short trips” and “long trips” for the chick rearing period, following the method previously used by Welcker *et al.* (2009) and Grissot *et al.* (2019a). We also considered two other behavioural modalities in further analyses: “not-nest” – with “colony” and “foraging” modalities considered together, and “not-foraging” – with “nest” and “colony” considered together (Fig. 1).

Due to camera failure and/or bad quality of the framing around the nest entrance, some sessions had to be discarded, thus sample size varied slightly among the analyses (see Table 1).

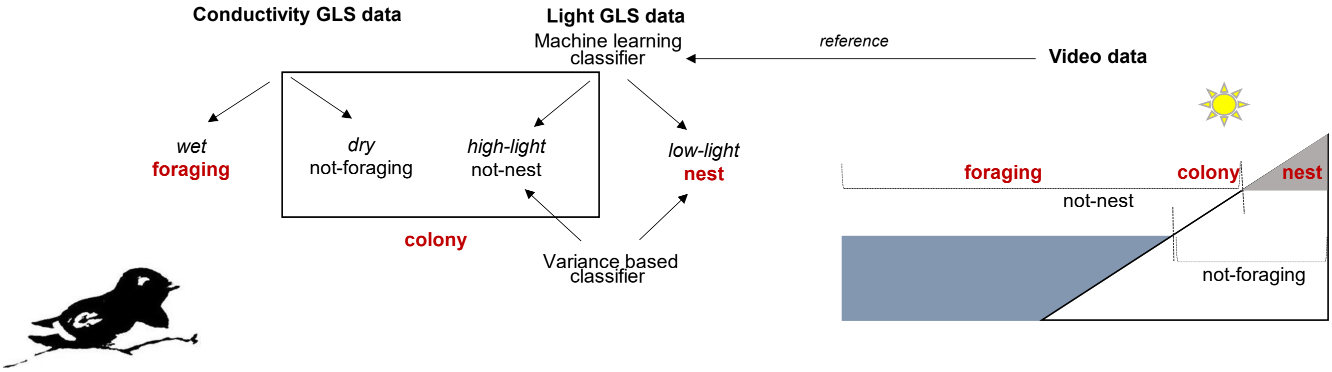

Figure 1. Scheme of how we established the different behavioural patterns. To the left, the figure represents how we used our methodological workflow from GLS data to establish behavioural patterns. To the right, it represents the monitored colony, and how video data was used to establish behavioural patterns.

Due to the different time resolutions of video data and GLS data (1 sec vs 5 or 10 min intervals, respectively), we discretised both data sets into 1 min bouts. For GLS data, we split each time-interval of 5 or 10 min into the corresponding number of 1 min bouts. For video data, we summed the durations of behaviour happening in each of the 1 min bout and attributed the predominant behavioural category (e.g. lasting for ≥ 31 sec if two behaviour happening within the same minute).

GLS behavioural patterns. To establish bird behaviour from GLS data, we first considered the light and conductivity data separately, classifying them in two categories each (*low-light*/*high-light*, and *dry*/*wet*, respectively). For splitting conductivity data, we used a simple rule: bouts containing a value strictly superior to 0 (i.e. 1 to 20) were classified as “wet”, and those equal to 0 were considered “dry”. To split light data, we applied two types of classifiers. In the first approach, we used an unsupervised classifier with a threshold value that split data into two groups while minimizing the sum of their variances, given log-transformed data distribution (hereafter variance-based approach). With this approach the threshold value was established at 13 (see supplementary material Fig. S1), thus all the bouts with values being equal or lower to 13 were classified as *low-light*, and all the rest as *high-light*. In the second approach, we used machine-learning technique, a supervised classifier that used a reference for the *low- light* and *high-light* values. As reference we used the “nest” and “not-nest” behavioural modalities from the discretised video data of the logged bird group (restricted sample size provided in Table 1). To this end, we transformed video data into a binary variable, with 1 for “nest”, 0 for “not-nest” and attributed them to timely corresponding light values from the GLS data. We then split this dataset randomly (using the function *createDataPartition()* from *caret* package (Kuhn, 2008) into training and testing (75% vs 25% of the original dataset). We ran logistic regression on the training data set, with the binary variable ("nest"/"not-nest") being the response variable and light as the explanatory variable (using *glm(y ~ x, family = binomial(link=logit))* from the *stats* package (R Core Team 2021). The prediction of this model was then applied to the testing dataset, to obtain a Receiver Operating Characteristic (ROC) curve; this step was done using the *roc()* function from the *pROC* package (Robin *et al.*, 2011). The Area Under the Curve (AUC) was used to measure probability of True Positive Rate (TPR) against False Positive Rate (FPR), at various threshold values. Since both "nest" and "not nest" behaviour, were equally valuable to establish behavioural patterns, the optimal threshold was chosen to respect a trade-off between the TPR and the FPR values, using the Youden's J statistics (Youden, 1950; Fluss *et al.*, 2005). The final threshold value we used to split the light data had an AUC of 0.981 (see Fig. S1), corresponding to an "outstanding discrimination" according to Hosmer & Lemeshow (2013), and an accuracy of 0.952 (i.e. the classifier rightly attributed 95% of the 1 min bouts in the training dataset). The prediction of the model was then applied to the whole light dataset (i.e. including times when birds were not recorded), and values equal or superior to the chosen threshold were classified as *low-light*, while those below the threshold were classified as *high-light*.

Once light and conductivity data were classified in two groups (*low-light*/*high-light* and *dry/wet* respectively), we combined this information to translate it into behavioural modalities. For this purpose, we considered two approaches with different number of behavioural modalities. Firstly, we considered two behavioural modalities: "nest" and "not-nest", which were the most straightforward given the nature of GLS data. We considered as "nest" all the bouts classified as *low-light* and *dry*, and "not-nest" the rest of the bouts (Fig. 1). In a second approach, we distinguished three behavioural categories: "nest", "colony" and "foraging". This approach better reflects the complexity of breeding behaviour exhibited by the study species, and thus is a desired data format for future studies on its breeding ecology using GLS data. Here, apart from "nest" (*low-light* and *dry*), we considered as "colony" all bouts that were *high-light* and *dry*, and as "foraging" all *wet* bouts regardless of their light value (Fig.1), since it could change in an unpredictable way when birds dive.

Data analysis

Methods comparison. We assessed the accuracy of all the behavioural characterisations of GLS data using video data as reference and calculating Cohen's kappa for all meaningful data sets combinations (see below, and Table 1 for a detailed summary). The Cohen's kappa is a measure of inter-rater reliability that uses a contingency table to measure the percentage of agreement while taking into consideration the degree to which the agreement could be attributed to chance (Cohen, 1960). We performed the analyses using the *Kappa()* function from the package *vcd* (Meyer *et al.*, 2021). We calculated the Cohen's kappa coefficients separately for incubation, early and mid-chick rearing datasets because bird behaviour differs between incubation and chick rearing, and further between early and mid-chick rearing phases), in terms of duration of time spent in the nest and at sea. These behavioural differences could potentially impair accuracy of GLS established behavioural modalities. Nevertheless, we also calculated the Cohen's kappa irrespective to the breeding stage, to assess overall accuracy of the method. To interpret the Cohen's Kappa used we followed criteria proposed by Altman (1999), that states that if the value of Kappa is 0 the reliability is poor, [0.01 – 0.20] it is slight, [0.21 – 0.40] it is fair, [0.41 – 0.60] it is moderate, [0.61 – 0.80] it is substantial, and [0.81 – 1.0] it is almost perfect.

GLS impact assessment. To establish whether GLS deployment has an impact on logged birds and/or pairs, we ran separate generalised linear mixed models, using the *glmer()* function from the package *lme4* (Bates *et al.*, 2015) on eight response variables. All models included the group (logged vs control) as an explanatory variable and, when pseudoreplication was present, we included the identity of the individual and the pair as random effects (identity of individual was nested in identity of the pair, as the behaviour of an individual could be affected by the behaviour of its partner). Family and link function differed for each model depending on the nature of the response variable, and additional explanatory variables, as well as their interactions were added when relevant (e.g. sex of the individual, chick rearing session, etc; Table 2).

We chose eight response variables for their ecological significance, aiming to consider individual (1-3) and pair (4) behaviour as well as breeding outcome (5-8). Based on the non-discretised video data we calculated: (1) the amount of time that a bird spent in the nest when incubating the egg (i.e. duration of each incubation bout); (2) the amount of time that a bird foraged to provision its chick (i.e. duration of the short foraging trips); (3) the amount of time that a bird spent foraging to maintain its own body reserves (i.e. duration of the long foraging trips) and (4) the index of parental coordination for each pairs during the mid-chick rearing period (following Wojczulanis-Jakubas *et al.*, 2018; Grissot *et al.*, 2019a). Using regular nest control data at hatching, we established pair hatching success (5), classifying them as "hatched" or "un-hatched". Based on regular chick weighting data we obtained the last three response variables that were related to the chick growth rate. To this end, we fitted a non-linear logistic model using the *nls()* and *SSlogis()* function from the *stats* package and extracted: (6) the asymptotic weight reached by the chick (hereafter asymptote), (7) the number of days needed to reach half of the asymptotic weight (hereafter X_{mid}) and (8) the slope of the linear part of the growth (hereafter scale).

We tested significance of explanatory variables with the *Anova()* function, using type III Wald Chi-square tests from the package *car* (Fox & Weisberg 2011), and removed from the model the variables that were not significant. Then, we confirmed the better fit of the model using the Akaike information criterion with the function *AIC()* from the *stats* package (R Core Team 2021) and the function *Weights()* from *MuMIn* package (Bartoń, 2020), with lowest AIC and highest weight indicating the best model (see Table 2). When qualitative explanatory variables or their interactions were found significant, post-hoc Tukey tests were performed to assess specific differences, using the *emmeans()* function from the *emmeans* package (Lenth, 2022). Assumptions of homoscedasticity and normal distribution of residuals in all the candidate models were verified.

Results

The accuracy of GLS established behavioural categorization, obtained with Cohen's Kappa ranged from 0.83 ± 0.002 to 0.99 ± 0.001 for most of the datasets, corresponding to almost perfect reliability, according to Altman (1999). A substantial reliability was obtained when considering the chick rearing period and the three modalities approach (Kappa = 0.78 ± 0.004; 0.79 ± 0.004 for the variance-based and machine learning classifiers, respectively). The only low, with moderate reliability, Cohen's Kappa of 0.56 ± 0.011 was found for the variance-based classifier (resp. 0.57 ± 0.011 for the machine learning classifier) for the mid-chick rearing subset and three modalities approach (Table 1). Thus, as expected, the differences in the birds' behaviour at different breeding stages affected the accuracy of the classification, with it being highest during incubation, a bit lower in the early chick rearing period and the lowest for the mid-chick rearing period (Table 1). Classifying light data with machine-learning approach provided a slightly better accuracy compared to variance-based classifier, but the difference was more-or-less negligible (by 0.1 in the value of Cohen's Kappa). The accuracy for the two behavioural modalities was in general higher than for the three modalities (Table 1).

Table 1. Cohen's Kappa measured for the comparison between behavioural patterns obtained with GLS data (processed using the Variance based or Machine learning classifiers) and video data. CI: 95% Confidence Interval, N: number of 1 min bouts included in the comparison, N_nest: number of nests present in the comparison dataset, N_ind: number of individuals present in the comparison dataset

Comparison between	Modalities	Dataset	Kappa	CI	N	N_nest	N_ind
Video and Variance based Classifier	nest / not nest	Full	**0.94**	0.002	199387	9	18
		Incubation	**0.94**	0.002	108864	8	16
		Chick rearing	**0.93**	0.002	90523	8	16
		Early Chick rearing	**0.93**	0.003	57050	7	14
		Middle Chick rearing	**0.86**	0.010	33473	4	8
Video and Machine learning Classifier	nest / not nest	Full	**0.95**	0.001	199387	9	18
		Incubation	**0.96**	0.002	108864	8	16
		Chick rearing	**0.94**	0.002	90523	8	16
		Early Chick rearing	**0.95**	0.003	57050	7	14
		Middle Chick rearing	**0.85**	0.011	33473	4	8
Video and Variance based Classifier	nest / colony / foraging	Full	**0.83**	0.002	199387	9	18
		Incubation	**0.85**	0.003	108864	8	16
		Chick rearing	**0.79**	0.004	90523	8	16
		Early Chick rearing	**0.83**	0.004	57050	7	14
		Middle Chick rearing	**0.56**	0.010	33473	4	8
Video and Machine learning Classifier	nest / colony / foraging	Full	**0.84**	0.002	199387	9	18
		Incubation	**0.86**	0.003	108864	8	16
		Chick rearing	**0.80**	0.004	90523	8	16
		Early Chick rearing	**0.84**	0.004	57050	7	14
		Middle Chick rearing	**0.56**	0.010	33473	4	8

Among the eight response variables considered, carrying a GLS was found to significantly affect the duration of incubation bouts (GLMM, Gamma family, $\chi^2 = 15.82$, $P < 0.001$), and the duration of long trip during the chick rearing (GLMM, Gamma family, $\chi^2 = 24.74$, $P < 0.001$). In the case of the incubation bouts duration, the sex of the individual, as well as its interaction with being equipped with a GLS were also significant (GLMM, Gamma family, $\chi^2 = 13.78$ resp. 8.09, $P < 0.001$ resp. $P = 0.004$). Both sexes of the logged group had a similar duration of incubation bouts (Tukey, $P > 0.05$, $z = -0.512$) and every other combination were significantly different (Tukey, $P < 0.01$ for every other pair-wise comparison; see Fig. 2) resulting in non-logged males having the shortest incubations bouts.

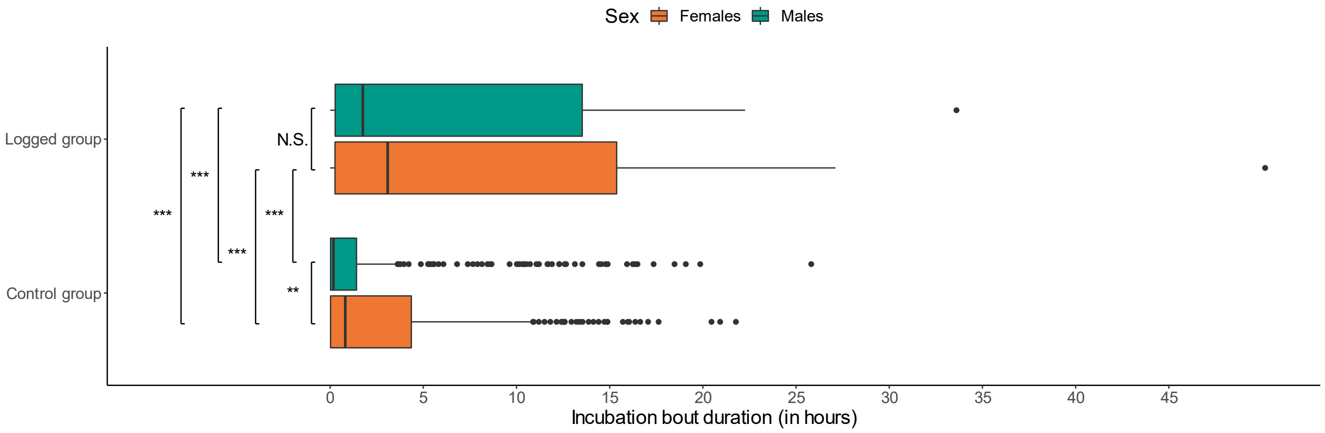

Figure 2. Differences in the duration of incubation bouts. The boxes depict interquartile ranges, with median as a bold line inside the box. Whiskers indicate variability outside the upper and lower quartiles. Dots represents the outlier points. Difference between every combination was tested with pair-wise post-hoc Tukey test, and significance is indicated on the left. (N.S. : P > 0.05; * : P < 0.05; ** : P < 0.01; *** : P < 0.001).

For the model considering long trips as a response variable, the chick rearing session as well as its interaction with carrying a GLS were also significant (GLMM, Gamma family, $\chi^2 = 100.97$ resp. 18.94, $P < 0.001$). Every possible combination tested with the post-hoc Tukey test had significantly different durations of long foraging trips (Tukey $P < 0.001$), except when considering the logged and control groups during mid-chick rearing (Tukey, $P > 0.05$, $z = 0.115$). Overall, during mid chick rearing, logged and control individuals had similar long trips durations, while during early chick rearing, logged individuals had the shortest long trips (see Fig. 3).

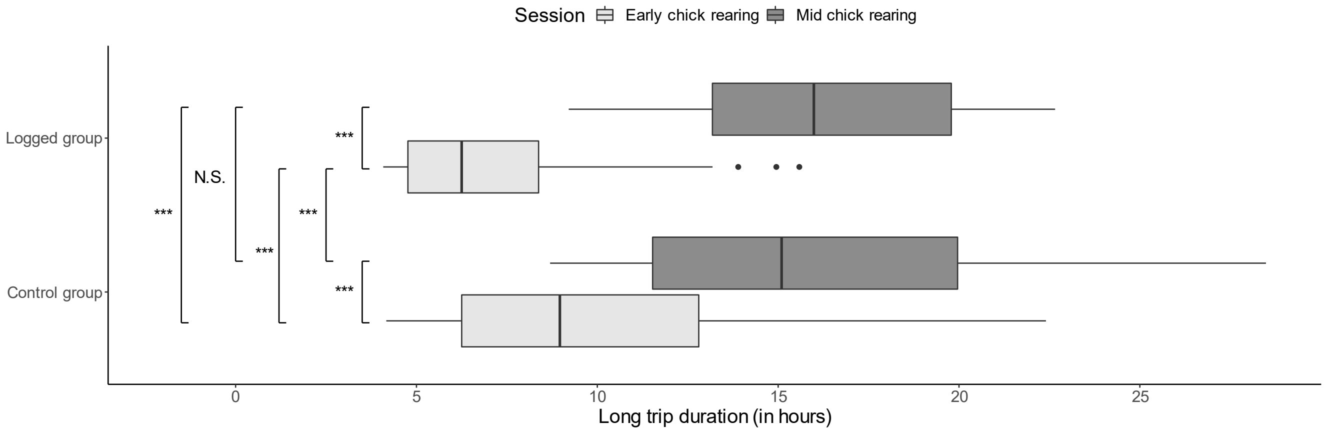

Figure 3. Differences in the duration of long foraging trips. The boxes depict interquartile ranges, with median as a bold line inside the box. Whiskers indicate variability outside the upper and lower quartiles. Dots represents the outlier points. Difference between every combination was tested with pair-wise Post-hoc Tukey test, and significance is indicated on the left. (N.S. : P > 0.05; * : P < 0.05; ** : P < 0.01; *** : P < 0.001).

The duration of short foraging trips was significantly affected by the sex of the individual (GLMM, Gamma family, $\chi^2 = 4.91$, $P = 0.03$) only, with males performing shorter short trips than females (GLMM, Gamma family, $t = 2.216$), as well as by the chick rearing session (GLMM, Gamma family, $\chi^2 = 6.83$, $P = 0.01$), with early chick rearing being characterised by shorter short trips (GLMM, Gamma family, $t = 2.216$).

The coordination index during mid-chick rearing was not significantly affected by carrying a GLS (LMM, $F = 1.88$, $P > 0.05$), even though both models with or without this explanatory variable had the exactly the same weight values and the latter model had a marginally lower AIC (see Table 2). Finally, the hatching success as well as all three chick growth parameters were not significantly affected by the carrying of a GLS, and no additional explanatory variables were considered for these models.

Discussion

We developed a method by which to document behavioural patterns of burrow-nesting birds using GLS data during the breeding season. Within our workflow, we tested different behavioural patterns (e.g., nest attendance alone or in combination with colony attendance and foraging) and different types of classifiers (i.e., unsupervised and supervised), to identify factors that could influence the accuracy of GLS- established patterns and to assess other limits of our method. The results of our comparison with more traditional, video-established patterns clearly indicated a great accuracy and biological sense of GLS-documented patterns. Our study also highlights the effects of GLS deployment, showing some fine-scale behavioural changes, even though there were no apparent consequences on breeding outcome.

Comparing GLS-documented behavioural patterns with those obtained from video data revealed an overall very close agreement, mostly falling within Altman's (1999) "almost perfect" agreement category. Nonetheless, full agreement was never reached and the reason of the observed differences between the two methods was more related to the device setting than data processing, as both types of classifiers we tested (i.e. unsupervised and supervised) showed very similar results. Indeed, by storing only the maximum light within a 5 min bout, many fine-scale changes in the amount of light received by the device is simply removed from the light data. As a result, very short visits to the nest might be overlooked in the GLS-documented nest attendance patterns. This is supported in our results by the fact that the kappa agreement between video and GLS data is lower for "nest"/"not nest" when looking at

Table 2. Model selection based on Akaike Information Criterion (ΔAIC: differences in AIC; wAIC: AIC weights) for the eight response variables. Significant explanatory variables are highlighted in grey. The best-fitting model is represented between the dotted lines.

Response variable	Explanatory variable 1	Explanatory variable 2	Explanatory variable 3	Interaction 1	Interaction 2	Random factor 1	Random factor 2	ΔAIC	wAIC
Duration of incubation bouts	gls	sex		gls:sex		Nest	Individual	**0**	0.96
	gls	sex				Nest	Individual	6.56	0.04
	gls					Nest	Individual	11.28	0
						Nest	Individual	22.92	0
Duration of short trips	gls	sex	session	gls:sex	gls:session	Nest	Individual	2.61	0.09
	gls	sex	session		gls:session	Nest	Individual	0.78	0.23
	gls	sex	session			Nest	Individual	1.91	0.13
		sex	session			Nest	Individual	**0**	0.34
			session			Nest	Individual	1.06	0.2
						Nest	Individual	6.43	0.01
Duration of long trips	gls	sex	session	gls:sex	gls:session	Nest	Individual	3.77	0.1
	gls	sex	session		gls:session	Nest	Individual	1.99	0.24
	gls		session		gls:session	Nest	Individual	**0**	0.66
	gls		session			Nest	Individual	18.02	0
			session			Nest	Individual	21.57	0
						Nest	Individual	105.57	0
Coordination index	gls							0.01	0.5
								0	0.5
Breeding success	gls							1.7	0.3
								0	0.7
Growth rate's Asymptote	gls							1.61	0.31
								0	0.69
Growth rate's Xmid	gls							1.86	0.28
								0	0.72
Growth rate's Scale	gls							1.98	0.27
								0	0.73

the subset of mid-chick rearing, the period when parents spend as little time in the nest as required for chick feeding (they rarely brood the chick at this stage; Stempniewicz, 2001), compared to incubation, when parents spend extensive periods of time in the nest incubating the egg. Similarly, by storing the number of wet counts within a 10 min bout some issues can emerge leading to non-perfect agreement. In this case, no data are removed as all the samples are stored within the final count of wet samples within a 10 min bout. However, the chronology of wet samples within this bout is lost and can also cause mismatch between video and GLS data, especially during transitions between phases of wetness and dryness or vice versa. Besides, the data extracted from the video was still precise to the second, whereas light data from GLS was summarised into 5 min intervals, and conductivity data into 10 min intervals. The data discretisation made both types of data – video and GLS – comparable by downsampling video and GLS data into 1 min intervals. Consequently, video resolution was diminished (from 1 sec to 1 min), while maintaining reasonable level, therefore reducing the resolution difference between video and GLS data. Nevertheless, some events could have been overlooked using the GLS data, consequently reducing the total agreement of the two methods. As a solution, future studies could consider trying other sample rate settings when deploying GLS.

Despite the very good ability of the GLS-based method to establish all behaviours of interest, there is some confusion in the definition of the “colony” and “foraging” behaviours based on video data and GLS data. We expected that, given the very nature of GLS data and the characteristics of our study species (crevice nesting during the polar day), identifying periods of darkness would be the most reliable. Our results show that indeed, establishing a pattern of two modalities “nest” / “not nest” performed better than the more elaborate three modalities “nest” / “colony” / “foraging”. Lower differentiation of the three modalities could come from the different way the two behavioural categories “colony” and “foraging” are determined when using GLS data and video data. With GLS data, *“high light”* and *“dry”* conditions denote “colony” behaviour, whereas “wet” conditions (regardless of light values) denote “foraging”. With video data on the other hand, a bird present on the screen (with absences of less than 1 h) is denoted as “colony” and a bird absent from the screen for more than an hour, or coming back with food in its gular pouch is denoted as “foraging”. Consequently, the transition phase between being in the colony and foraging, namely the flying time in between the two is treated differently in GLS and video data processing, the former including it in “foraging” category while the latter includes it in “colony” behaviour. Additionally, to define “foraging” from the video data we assumed that a bird not present on the screen for more than an hour was away from the colony and foraging. This assumption could lead to some artificial reduction of the ability of the GLS method to discriminate properly between “foraging” and “colony”. Given the aforementioned concerns, one could question the choice of these two categories. They were chosen to be as close as possible to the ones used in Grissot *et al.* (2019a), so as to be able to use GLS data to study various Little Auk parental behaviours (e.g., coordinated chick provisioning as identified in Wojczulanis-Jakubas *et al.*, 2018; Grissot *et al.*, 2019a) whenever the limits of traditional approaches such as video data or direct observations are reached. Our results show that although three modalities are distinguishable using our workflow based on GLS data, these categories should be treated with caution, especially during the mid-chick rearing period when the accuracy to establish the three behaviours of interests of the method was the lowest (although it could also be accentuated by the small sample size available for this period). Future studies should consider for instance having more or better defined categories and using the data provided by conductivity sensor of the GLS more extensively.

Both classifiers (supervised and unsupervised) could be used indistinctively within our methodological workflow, without any impact on the overall performance of the method, as shown by the results of our comparison between the two different types of classifiers. Therefore, given conditions similar to the ones present in our study, the unsupervised classifier (i.e. variance based approach) can be reliably used to establish behavioural patterns, and future studies investigating breeding behaviour using GLS do not need extensive deployment of video cameras. This potentially provides great opportunities for many breeding ecology studies of species similar to the Little Auk (crevice/burrows nesting in polar day conditions), as it would reduce various constraints associated with video recording (number of followed individuals, time required for processing video recordings, etc), without jeopardizing the accuracy of the established breeding patterns. However, we would still recommend some extent of method validation (using a well-established method like video recordings), whenever dealing with different nesting modes (e.g. burrow or ledge breeders) or breeding environment (e.g. lower latitude not exposed to polar day during the breeding season).

Our results highlight that the deployment of GLS loggers on Little Auks does not affect directly their hatching success and breeding outcome (e.g., chick growth rate), which is concordant with results of another study measuring the effect of GLS on body condition in this species (Dufour *et al.*, 2021). Thus, we could tentatively conclude that there are no apparent arguments against deploying GLS in the species. However, while looking at behaviour such as duration of incubation bouts and foraging trips, we found some differences between logged and control individuals. Deploying any device on an animal may affect its fitness and behaviour, thus the documentation of device effect is of prime importance both in terms of methodology and animal welfare (Costantini & Møller, 2013; Bodey *et al.*, 2017; Geen *et al.*, 2019; Brlík *et al.*, 2020). Most studies exploring the effect of a device considered various proxies of individuals fitness (survival and probability of future reproduction, body condition), and it has often been concluded that there is no direct effect of a device on individual fitness. However, even if device deployment does not apparently influence individual fitness, it may modify behaviour (e.g. duration of foraging trips, various parameters associated with parental care; Bodey *et al.*, 2017; Gillies *et al.*, 2020). It is therefore, crucial to include a variety of fine scale behaviour while assessing deployment impact of any device. When potentially modified behaviour is also a variable of interest in a study, as in this one, it becomes even more important to assess, acknowledge and account for the device effect.

Results indicating that logged individuals carry out longer incubation bouts than control individuals are hard to interpret with the current data set, but we suggest that carrying a logger may somehow hinder movement when on land, leading to individuals preferring to stay in the nest continuously, rather than breaking the incubation bouts into shorter bouts (with short time intervals off the nest). It may be also somehow associated with an accrued risk of egg damage while moving around and entering/exiting the nest. Another possible explanation of increased duration of incubation bouts of logged individuals resides in the carrying a GLS somehow hindering the flight or foraging performance of logged individuals. We did not directly investigate duration of foraging trips during incubation, but incubating Little Auks are highly dependent on the foraging duration of their partner, as the egg cannot be left unattended for long periods of time (Stempniewicz, 2001; Grissot *et al.*, 2019a). Therefore, the longer incubation of one bird may simply be a reflection of its partner's longer foraging. Indeed, theoretical approaches suggest that a reduction in care by one parent might lead to at least partial compensation by its partner (Johnstone & Hinde, 2006; Griffith, 2019; Wojczulanis-Jakubas, 2021), and many studies experimentally tested this hypothesis by handicapping one partner, reducing its share of parental duties, and showing compensation by the other partner (Paredes *et al.*, 2005; Bijleveld & Muller, 2009; Wiebe, 2010; Gillies *et al.*, 2021). For instance, handicapped Manx Shearwaters, *Puffinus puffinus*, during the incubation period performed significantly longer trips than normal that were compensated by their partner lengthening their incubation shift (Gillies *et al.*, 2021). Furthermore, Paredes *et al.*

(2005) showed that deploying animal-borne devices could handicap individuals carrying them in terms of foraging efficiency, leading to compensation by their unlogged partner. In our study both partners were logged, and we could speculate that the foraging efficiencies of both were reduced during the incubation period, and that each bird compensated for the partner's longer foraging by incubating longer. Although the direct driver of the observed pattern is still unknown, relevance of the device deployment effect is very important to consider in future studies.

Results concerning the chick rearing period are harder to interpret, as we found no effect of GLS on the short trips, and a reduction of the duration of long trips during the early chick rearing. The latter is inconsistent with many studies considering the device effect on foraging trip duration (e.g. Paredes *et al.*, 2005; reviewed in Bodey *et al.*, 2017). Nonetheless, the majority of these studies investigated the duration of foraging trips during the chick rearing with a deployment just prior to its onset, which was not the case in our study. This could potentially blur the picture, if one considers possible habituation to the device and reduction of handicap with time. Long term effects of logger deployment are regrettably often overlooked, or only consider survival and fitness (Pakanen *et al.*, 2020; Gillies *et al.*, 2020). As such, habituation effects have been understudied. Our results showed some extent of behavioural change during the chick rearing period, but in a direction contra to the commonly reported one, and therefore highlight the importance of considering the long-term behavioural effects of deployment. We did not find a significant difference in the mid chick rearing coordination level between logged and control pairs, but we suggest that future studies, especially ones aiming to use GLS data to investigate coordination, should further investigate how it is affected by device deployment.

To sum up, our study provides a useful framework by which to use GLS data (light and conductivity) to document behavioural modalities (colony and nest attendance) of Little Auks during the breeding season, especially during incubation and early chick rearing period. Device deployment did not seem to affect breeding parameters of the logged individuals, although some behavioural changes could be noticed (e.g. prolonged incubation bouts and reduced foraging trips, but no apparent effect on parental coordination). These changes should be taken into account while using GLS data. Overall, the framework is likely to work well in other crevice/burrow nesting seabirds, but in open-nesting species a similar method validation is recommended.

Acknowledgments

We thank Dorota Kidawa for technical support, the Polish Polar Station for hosting us in pandemic times, and Łukasz Pracki for his precious IT help in the field. We also thank Rob Barrett for proof-reading the manuscript and, as a native English speaker and specialist in ecology, making substantial improvements.

Ethical note

All the fieldwork was carried out under supervision of KWJ (having the relevant qualifications and experience). We handled all the birds for no more than ca 10 minutes and released them unharmed. We recorded and handled the birds under permission of the Norwegian Food Safety Authority (ID 23259) and the Governor of Svalbard (20/00373-2).

Disclosure statement

The authors have no potential conflict of interests with respect to the research, authorship, and/or publication of this article.

Data availability

All data will be made available on a Dryad Digital Repository during submission process.

Funding

The study was supported by Norway through the SEATRACK project (https://seapop.no/en/seatrack/, Norwegian Research Council grant no. 192141), and by Poland through National Science Centre (no: 2017/25/B/NZ8/01417 to KWJ).

Author Contributions

Antoine Grissot (AG), Katarzyna Wojczulanis-Jakubas (KWJ) and Clara Borrel (CB) conceived the ideas and designed methodology; Malin K. Johansen (MKJ) and Hallvard Strøm (HS) provided GLS loggers with necessary equipment; AG, KWJ, CB, Lauraleen Altmeyer (LA) and Marion Devogel (MD) collected the data; AG and CB analysed the data; KWJ, MKJ and HS acquired the financial support, AG and CB led the writing of the original draft. All authors contributed critically to the following drafts and gave final approval for publication.

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II. Supplementary Materials

Use of geolocators for investigating breeding ecology of a rock crevice-nesting seabird: method validation and impact assessment

Antoine Grissot[1*], Clara Borrel[1,2,3], Marion Devogel[1], Lauraleen Altmeyer[1,2,3], Malin Kjellstadli Johansen[4], Hallvard Strøm[4], Katarzyna Wojczulanis-Jakubas[1]

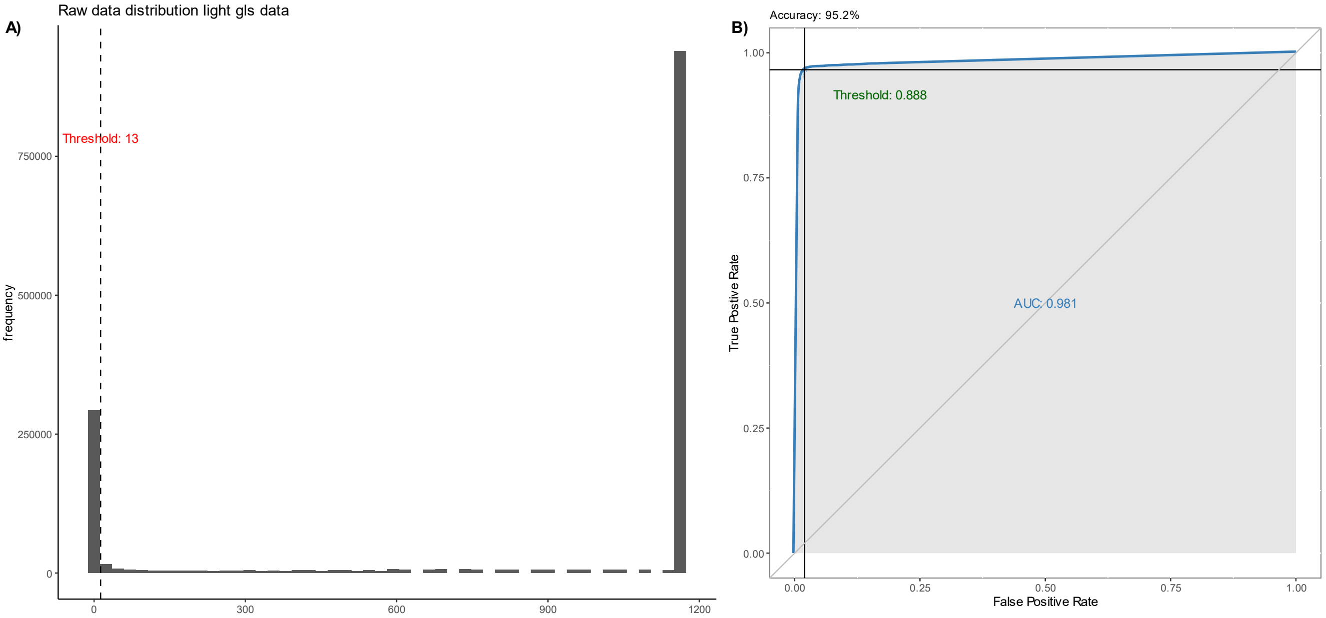

Figure S1. Comparison of how the threshold between “high light” and “low light” was obtained using the two types of classifiers. A) Variance based approach (unsupervised classifier) : Histogram of light value distribution for every 1 min bout. Threshold obtained is the value that minimises the sum of variances of the two obtained groups. B) Machine learning approach (supervised classifier) : Receiver Operating Characteristic (ROC) curve in blue with Area Under the Curve (AUC) shadowed in grey. Threshold obtained by making a trade-off between the True Positive Rate (TPR) and the False Positive Rate (FPR) values, using the Youden’s J statistic (Youden, 1950)

General Discussion and Perspectives

Parental care being a crucial element of animal reproduction for so many species, it is naturally a hot topic in behavioural ecology and, as such it is not surprising that the ways it is considered by the scientific community are constantly challenged and furthered. The work I performed during my PhD training is in this spirit - the three chapters of the present thesis represent a step further in the investigation of how parental care can be apprehended through the perspective of cooperation, instead of focusing on the sexual conflict created by the distribution of care between partners. Cooperation between Little Auk parents in the form of coordination of chick provisioning had already been reported (Wojczulanis-Jakubas *et al.*, 2018). However, my work extended the investigation of cooperation in parental care in this species, from studying a single phase of the chick rearing breeding stage, to an integrative approach considering every part of the breeding period. Furthermore, the new method that was developed may soon allow investigating it on an even broader temporal scale. Besides, cooperation between parents for the providing of care was not only investigated *per se*, but factors that influence it and its fitness consequences were also tackled. Such an approach allows a better understanding of evolutionary factors influencing the presence of care as well as the cooperation between breeding partners for its providing. Obviously, a lot more can be investigated on parental cooperation and coordination of parental performance, in this species as well as in many others, closely related or not.

I. Integrative approach to coordination of parental performance

The pair cooperation framework applied to parental care is a relatively recent concept of behavioural and evolutionary ecology and, as such, is expanding quite rapidly (Griffith, 2019). The number of species investigated within this framework is increasing, and more and more patterns and contexts of coordination of parental performance are highlighted. The temporal scale at which it is investigated is of great importance, given the very nature of the behavioural activities considered, and the investment in time and resources these activities represent for parents (Trivers, 1972; Ghalambor & Martin, 2001). However, temporal scale is often overlooked (see Chapter 2), and many studies consider a single time-window within a breeding stage to assess how parents coordinate their activities (e.g., Tyson *et al.*, 2017; Kavelaars *et al.*, 2021). In the present thesis, I built a more integrative approach to the study of parental performance by considering coordination of parental activities in all the breeding stages, analysing fine scale changes within each stage, and temporal dependence to one another. Reported results of changes in coordination levels within the incubation and chick rearing periods in the Little Auk support the importance of temporal scale, highlighting that the phase of the breeding season does matter and should be taken into account while considering parental coordination overall (Chapter 2). Therefore, considering a single time-window could lead to underestimating the pair cooperation, or the balance between costs and benefits of coordinating parental care. Indeed, given life-history traits or changes in environmental conditions, it is to be expected that each steps of the breeding season can be characterised by different challenges for parents, and thus further studies on coordination of parental activities should consider using an integrative approach as well.

The method proposed and developed (presented in Chapter 3), based on the deployment of miniaturised loggers, can be a great tool for further extending the temporal scale used to study coordinated parental performance. The results of the method comparison show that the developed methodological framework is reliable, and allows to establish meaningful behavioural patterns of breeding activities. Besides, impact assessment showed no effect of device deployment on breeding (although some behavioural changes in logged individuals could be observed). Even though a method can always be improved, the obtained results suggest that data obtained from GLS deployed on Little Auk pairs can be used for the investigation of the coordination of parental activities. Given continuous mode of recording of GLS, it will allow to investigate the parental coordination of the Little Auk on a temporal scale never achieved before. It can be expected that future studies using such a temporal scale will confirm and further enrich the results obtained in Chapter 2 on within-season changes in coordination of parental performance. Importantly, the developed methodological framework is likely to be applicable to a variety of crevice/burrow nesting seabirds, like the Little Auk, and potentially other avian groups. However, because each species may have its own specificity, it would be recommended to perform a pilot study including method validation and impact assessment, before implementing the method to a new study system.

II. Evolutionary factors influencing cooperation in parental care

To evolve and be evolutionary stable, parental care has to be beneficial for parents exhibiting this strategy (Hamilton, 1964), and the same can be said about cooperation in parental care (through coordination of activities between parents; see Griffith *et al.*, 2019; Wojczulanis-Jakubas, 2021). Life-history traits and environmental conditions are the best candidates for factors that could influence parental care and coordination. During my PhD training, I investigated how environmental conditions in the foraging ground affect the coordination level during the mid phase of the chick rearing period (see Chapter 1). No difference in coordination level between five examined seasons, that were environmentally significantly different from each other, could be observed. This was despite the fact that the level of coordination exhibited by the studied population was higher for the situation when highly energetic food was being delivered. These intriguing results suggested that the range of environmental variation handled in the study could be still below a critical threshold of extreme conditions. However, in the light of the findings of Chapter 2, it could also be suggested that the period investigated (mid phase of the chick rearing period), being characterised by a lower coordination compared to earlier phases, might blur the environmental effects. Therefore it would be interesting to tackle again the effects of environmental conditions in the foraging grounds using coordination in other phases of the breeding season, perhaps more relevant for the fitness of the parents and/or offspring.

One of the aim of Chapter 1 was to establish whether coordination of parental performance is a fixed parental strategy or represent flexible response to current foraging conditions in this species. We hypothesised that if coordination is a flexible trait varying in relation to foraging conditions, levels should vary along with differences in environmental conditions. The absence of difference in coordination level in environmentally different seasons could suggest that it is not a flexible trait. However, because the effects could be blurred by the breeding phase investigated (as mentioned above), it would be interesting to directly test if some pairs are consistent in the way they coordinate their performance, and if it is linked for instance to intrinsic characteristic (individual qualities, pair similarity/dissimilarity, duration of the pair bond, etc). Most studies, including Ghalambor and Martin (2001), focused on how life-history traits could influence the presence and amount of care provided at the species level, comparing for instance closely-related. However, life-history traits are equally susceptible to have an influence at the level of the individual or the pair, therefore it would be interesting to compare individuals and pairs of different characteristics, and see how that shapes their coordination levels. From the data collected during the span of my PhD. training, and that will additionally be collected in the coming field season, I will have enough material to start tackling this interesting question as a next step into my journey of studying cooperation in parental care.

III. Perspectives and future directions

Along with how intrinsic factors can influence the parental cooperation and coordination of performance, I would now be interested into investigating the mechanisms that allow the set up and maintenance of cooperation. This area is understudied (but see Gillies *et al.*, 2022), despite being crucial for an overall understanding of cooperation, both on a behavioural point of view and considering evolutionary stability. Among the proposed mechanisms of parental cooperation used for the coordination of parental activities is physical reunion, offspring cues (Gillies *et al.*, 2022) and vocal interactions between partners (Mariette, 2019). The Little Auk is a very vociferous seabird and partners display frequently, both before and after pair formation. Consequently, physical reunions and vocal interactions seem to have a great potential as mechanisms of parental cooperation. Our team is currently working on disentangling how Little Auk parents communicate and if this is linked with the way they coordinate their parental performance.

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Appendix

I. Statements of co-authorship

A. Candidate statement

Uniwersytet Gdański
Wydział Biologii
Katedra Ekologii i Zoologii Kręgowców
ul. Wita Stwosza 59, 80-308 Gdańsk
tel. (58) 523 61 41 (sekretariat),

Katedra Ekologii i Zoologii Kręgowców

Gdańsk, 14.06.2022

MSc Antoine Grissot

I hereby confirm that I am the first author of the following paper:

Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K., & Wojczulanis-Jakubas, K. (2019). Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. *Frontiers in Ecology and Evolution*, 7, 349
http://doi.org/10.3389/fevo.2019.00349

My role as first author consisted in: Conceptualisation. Formal analysis, and Writing original draft, reviewing & editing.

I confirm as well I will be first author of the manuscripts gathered in the Chapters 2 and 3 when published, having led Conceptualisation, Data curation, Formal analysis, Investigation and Writing.

Signature

Antoine Grissot

B. Co-authors statements

UNIVERSIDAD DE
COSTA RICA

San Jose, Costa Rica, may-10 2022

Marcelo Araya-Salas PhD, Research Associate

I hereby confirm that I am a co-author of the following paper:

Grissot, A., **Araya-Salas, M.**, Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K., & Wojczulanis-Jakubas, K. (2019). Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. *Frontiers in Ecology and Evolution*, 7, 349
http://doi.org/10.3389/fevo.2019.00349

My role as co-author consisted in: conceptualization, writing, reviewing and editing.

I confirm that Antoine Grissot was the leading author of this paper. He processed the raw video material, analysed formally the data, conceived and wrote the manuscript and played the role of corresponding author.

Marcelo Araya S

Uniwersytet Gdański
Wydział Biologii
Katedra Ekologii i Zoologii Kręgowców
ul. Wita Stwosza 59, 80-308 Gdańsk
tel. (58) 523 61 41 (sekretariat),

Katedra Ekologii i Zoologii Kręgowców

Gdańsk, 23.05.2022

prof. dr hab. Dariusz Jakubas

I hereby confirm that I am a co-author of the following paper:

Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K., & Wojczulanis-Jakubas, K. (2019). Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. *Frontiers in Ecology and Evolution*, 7, 349
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Uniwersytet Gdański
Wydział Biologii
Katedra Ekologii i Zoologii Kręgowców
ul. Wita Stwosza 59, 80-308 Gdańsk
tel. (58) 523 61 41 (sekretariat),

Katedra Ekologii i Zoologii Kręgowców

Gdańsk, 17.05.2022

Dr Dorota Kidawa

I hereby confirm that I am a co-author of the following paper:

Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K., & Wojczulanis-Jakubas, K. (2019). Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. *Frontiers in Ecology and Evolution*, 7, 349
http://doi.org/10.3389/fevo.2019.00349

My role as co-author consisted in: funding acquisition, investigation in the field, review & editing the manuscript.

I confirm that Antoine Grissot was the leading author of this paper. He processed the raw video material, analysed formally the data, conceived and wrote the manuscript and played the role of corresponding author.

Dorota Kidawa

D. Kidawa

INSTITUTE OF OCEANOLOGY
POLISH ACADEMY OF SCIENCES

Sopot 11.05.2022

dr Rafał Boehnke

I hereby confirm that I am a co-author of the following paper:

Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K., & Wojczulanis-Jakubas, K. (2019). Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. *Frontiers in Ecology and Evolution*, 7, 349
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My role as co-author consisted in: Investigation and Writing - review & editing.

I confirm that Antoine Grissot was the leading author of this paper. He processed the raw video material, analysed formally the data, conceived and wrote the manuscript and played the role of corresponding author.

Signature

Boehnke

INSTITUTE OF OCEANOLOGY
POLISH ACADEMY OF SCIENCES

Sopot, 11.05.2022

Prof. dr hab. Katarzyna Błachowiak-Samołyk

I hereby confirm that I am a co-author of the following paper:

Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K., & Wojczulanis-Jakubas, K. (2019). Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. *Frontiers in Ecology and Evolution*, 7, 349
http://doi.org/10.3389/fevo.2019.00349

My role as co-author consisted in: data curation, funding acquisition, writing – review & editing.

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Signature

Uniwersytet Gdański
Wydział Biologii
Katedra Ekologii i Zoologii Kręgowców
ul. Wita Stwosza 59, 80-308 Gdańsk
tel. (58) 523 61 41 (sekretariat),

Katedra Ekologii i Zoologii Kręgowców

Gdańsk, 23.05.2022

dr hab. Katarzyna Wojczulanis-Jakubas, prof. UG

I hereby confirm that I am a co-author of the following paper:

Grissot, A., Araya-Salas, M., Jakubas, D., Kidawa, D., Boehnke, R., Błachowiak-Samołyk, K., & Wojczulanis-Jakubas, K. (2019). Parental coordination of chick provisioning in a planktivorous Arctic seabird under divergent conditions on foraging grounds. *Frontiers in Ecology and Evolution*, 7, 349
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