

Behavioural rhythms and parental cooperation in biparentally incubating shorebirds



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Cover illustration: incubating western sandpiper, *Calidris mauri*
made by M. Bulla from a photograph by M. Šálek

For Barbora and Majlen

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Summary

All organisms exhibit alternating phases of different behaviours. These behavioural rhythms are thought to be under strong selection, influenced by the rhythmicity of the environment. Whereas behavioural rhythms are well studied in isolated individuals under laboratory conditions, in free-living populations, individuals have to temporally synchronize their activities with those of others. The behavioural rhythms that emerge from such social synchronization and the underlying evolutionary and ecological factors that shape them remain poorly understood.

Here, we address this issue for biparental care – a complex social behaviour and a particularly sensitive phase of social synchronization – in which pair members potentially compromise their individual rhythms. We use non-model organisms – biparentally-incubating shorebirds – where parents synchronize to achieve continuous coverage of developing eggs, and we use an array of monitoring techniques to record incubation in the wild. We combine a within-species approach (i.e. detailed description of incubation rhythms and field experiments to reveal the drivers of the rhythms using a single species; **Chapter 1-3 & 5**), with a between-species approach (i.e. comparing incubation rhythms of biparental and uniparental species; **Chapter 4**), and a phylogenetically informed comparative analyses (i.e. descriptive and hypotheses driven analyses across shorebirds; **Chapter 6**).

Specifically, we tested: (1) how parents share their incubation duties over the day, incubation period and season (**Chapter 1**), and whether incubation behaviour correlates with off-nest behaviour (**Chapter 2**); (2) whether incubating parents compensate for the absence of their partner's care (**Chapter 3**); (3) whether a complete switch to uniparental incubation is possible (**Chapter 4**); (4) whether energetic demands of incubation constrain incubation rhythms (**Chapter 5 & 6**); and finally (5), whether the diversity in incubation rhythms relates to phylogeny, predation risk, energetics and environmental fluctuations (**Chapter 6**).

We first found – in a high Arctic breeding shorebird, the semipalmated sandpiper, *Calidris pusilla* (**Chapter 1**) – that overall the daily timing of incubation shifted over the incubation period (i.e. in females from evening–night to night–morning incubation) and over the season. However, the timing varied considerably among pairs: some displayed day-night incubation rhythm, others free-running like incubation rhythm (i.e. pairs shifted the start of incubation bouts between days so that each parent experienced similar conditions across the incubation period). Off-nest behaviour of the semipalmated sandpiper parents varied between sexes, across time and weather conditions, but it did not explain the diverse incubation rhythms (**Chapter 2**). We later confirmed this lack of evidence for energetic constraint of incubation in a field experiment (**Chapter 5**) and via comparative analyses (**Chapter 6**). Off duty parents roamed on average 224 m from their nest, implying that direct

communication with the incubating partner is unlikely (**Chapter 2**). These results suggest that parents communicate only during their brief exchange on the nest.

Second, despite this lack of communication between parents, overall, the parents partially compensated for an experimentally-induced temporary absence of their partner's care (**Chapter 3**). However, the individual responses span the entire range of what is possible (no, partial and full compensation). Whether some parents may lack the energy for full compensation, or are less responsive to their partner's absence, is unclear; however, we provide tentative evidence for both. Essentially, since incubating parents do not feed, even the fully compensating parents later left their nest unattended. Nevertheless, where removed parent never returned, nests were incubated uniparentally for median of 4 days (range 0-10 days, $N = 7$ nests).

Third, we found natural cases of such uniparental incubating in 8 out of 15 biparentally incubating shorebird-species (**Chapter 4**). Such uniparental incubation resembled the incubation of uniparental species. Strikingly, in 5 species we document cases where uniparentally incubating parents brought their clutch to hatching, which in these species reveals a potential for a flexible switch from biparental to uniparental care.

Fourth, contrary to prior believe, reducing the energetic demands of incubation by heating or insulating the nest cup had no effect on the length of incubation bouts (**Chapter 5**). These results convincingly demonstrate that incubation rhythms in semipalmated sandpipers are not primarily driven by the energetic state of the incubating bird.

Last, in a large scale comparative study that made use of 729 nests from 91 populations of 32 species we found a remarkable within- and between-species diversity in the socially synchronized incubation rhythms (**Chapter 6**). The length of incubation bouts was unrelated to variables reflecting energetic demands, but species relying on crypsis had longer incubation bouts than those that are readily visible or actively protect their nest against predators. Rhythms that could be potentially entrained to the 24-h light-dark cycle were less likely at high latitudes and absent in 18 species. Although half of our species are tidal away from their breeding grounds, and some forage in tidal areas also during breeding, in only 5% of nests did pairs display a rhythm that can be entrained by the tide. Hence, unlike the 24-h light-dark cycle, tidal life-history seems to play, at best, a negligible role in determining incubation rhythms.

In sum, we reveal unexpected within- and between-species diversity in socially synchronized incubation rhythms of biparental shorebirds (**Chapter 1, 3, 4, & 6**). Our results demonstrate that under natural conditions social synchronization can generate much more diverse rhythms than previously expected, and that these rhythms often defy the 24-h day, even in day-night environments (**Chapter 6**). Whereas our descriptive, experimental and comparative evidence consistently rules out risk of starvation as a key factor underlying the diversity and timing of these rhythms (**Chapter 2, 5 & 6**), we provide novel evidence for the link between the diversity of the rhythms and anti-predation strategy (**Chapter 6**).

General introduction

“You share your ability to internally keep track of the time of day
with practically every other creature on earth”

— Till Roenneberg, *Internal Time*, 2012

Behavioural rhythms

For all organisms, the exact timing of behaviour to both daily and seasonal environmental cycles is crucial for survival and successful reproduction (Emerson et al. 2008; Yerushalmi & Green 2009). Consequently, the study of biological rhythms is a vibrant and interdisciplinary research area in biology (Dunlap et al. 2004).

It all started with the plants

The earliest record of daily behavioural rhythm dates back to the fourth century BC and describes the opening of the tamarind tree's (*Tamarindus indica*) leaves during the day and their closing during the night (Bretzl 1903). More than 2,000 years later, the French astronomer de Mairan noted that a heliotrope plant sustains the very same rhythm in leaf movement even in continuous darkness (de Mairan 1729). This is the first recorded observation of a daily rhythm that persist even in the absence of changes in day and night (Gardner et al. 2006; Roenneberg 2012) and thus the first record of an internal clock. Nevertheless, it took another 200 years before biologists started to investigate this internal clock (Dunlap et al. 2004; Roenneberg 2012).

Going wild

It is now accepted that the activity rhythms of organisms, from bacteria to humans, are typically the output of internal ‘biological clocks’ that are synchronized to the daily environmental cycle (Dunlap et al. 2004) and are largely genetically determined and conserved across species (Young & Kay 2001; Koskenvuo et al. 2007; Helm & Visser 2010). However, the field of biological rhythms has been dominated by studies of single individuals of a few model organisms under standardized laboratory conditions (Kronfeld-Schor et al. 2013). As highlighted in a special feature on the animal clocks in the wild:

“to begin to understand the adaptive significance of the clock, we must expand our scope to study diverse animal species from different taxonomic groups, showing diverse activity patterns, in their natural environments” (Kronfeld-Schor et al. 2013).

Studies on behavioural rhythms have been taken into the wild only recently and with surprising outcomes (van Oort et al. 2005; Lesku et al. 2012; Vanin et al. 2012; Steiger et al. 2013; Rattenborg et al. 2016).

Social synchronization

Behavioural rhythms of individuals are not only synchronized by the environmental cycles, but are also shaped by the social environment - including potential mates, allies, competitors, prey, or predators (Mrosovsky 1996; Davidson & Menaker 2003; Mistlberger & Skene 2004; Castillo-Ruiz et al. 2012; Bloch et al. 2013). As a result of such social interactions, individuals can temporally segregate their daily activities (e.g. prey avoiding predators, subordinates avoiding dominants), or synchronize their activities (e.g. foraging in group, communal defence against predators, pairs reproducing or caring for offspring; Schoener 1974; Regal & Connolly 1980; Davidson & Menaker 2003; Castillo-Ruiz et al. 2012; Bloch et al. 2013).

Although social synchronization of conspecifics has been documented across taxonomic groups (Davidson & Menaker 2003; Castillo-Ruiz et al. 2012; Bloch et al. 2013; Kronfeld-Schor et al. 2013), and although the behavioural rhythms that emerge from social synchronization have occasionally been studied in captive individuals (Davidson & Menaker 2003; Castillo-Ruiz et al. 2012; Bloch et al. 2013; Kronfeld-Schor et al. 2013; Paul et al. 2015), we know little about socially emerged rhythms in the wild (Mrosovsky 1996; Davidson & Menaker 2003; Mistlberger & Skene 2004; Castillo-Ruiz et al. 2012; Bloch et al. 2013). Subsequently, we know even less about the factors that influence socially synchronized rhythms such as evolutionary history, energetic demands, predation risk and periodicity in the environment.

Here, we address this in the context of biparental care – a form of care that is rare across the animal kingdom, but common among cichlid fishes, crocodylians and primates, and dominant among birds (Kendeigh 1952; Silver et al. 1985; Reynolds et al. 2002; Cockburn 2006; Balshine 2012; Trumbo 2012).

Biparental care

Biparental care – provisioning of offspring by both, female and male parents – represents a complex social behaviour and a particularly sensitive phase of social synchronization (Emlen & Oring 1977), because pair members potentially compromise their individual rhythms.

Biparental care rhythms

However, the rhythm of biparental care is virtually unexplored. For example, although chick feeding of parents in passerine birds serves as a model system for theoretical and experimental understanding of parental investment and parental cooperation (Houston & Davies 1985; McNamara et al. 1999; McNamara et al. 2003; Harrison et al. 2009; Lessells 2012; Schlicht et al. 2016), we still lack a detailed description of the chick-feeding rhythm within and across days, over the entire chick feeding period, and across many pairs.

Similarly, although incubation by both parents prevails in 50% of avian families and in almost 80% of non-passerine ones (Deeming 2002b), the rhythm of biparental incubation, is rarely

explored continuously over the incubation period. The little we know comes from species with incubation bouts lasting >24h, where timing of incubation within a day does not play a role: albatrosses (e.g. Weimerskirch et al. 1986; Weimerskirch 1995), penguins (e.g. Davis 1982; Weimerskirch et al. 1992; Gauthier-Clerc et al. 2001), and petrels (e.g. Chaurand & Weimerskirch 1994).

Moreover, despite the prevalence of biparental incubation, with exception of seabirds (e.g. Jouventin & Weimerskirch 1990; Weimerskirch 1995; González-Solís et al. 2000; Weimerskirch et al. 2007; Pinet et al. 2012), the behaviour of the off-duty parents has rarely been described in detail. This is puzzling because biparental incubation is a mutually exclusive behaviour (i.e. only a single parent incubates at a time) and usually nest attendance is continuous (i.e. incubating parent is starving). Hence, the off-duty behaviour of parents is an integral part of the biparental incubation rhythm (e.g. Chaurand & Weimerskirch 1994; Dearborn 2001) and can help elucidate how parents achieve cooperation (e.g. who drives the incubation rhythm).

Here, we address these discrepancies for biparental incubation rhythms of shorebirds. We first focus on within- and between-pair differences in incubation rhythm of semipalmated sandpiper, *Calidris pusilla*, breeding in harsh conditions of high Arctic (**Chapter 1 & 2**), and then on within- and between species differences in incubation rhythms across biparental shorebirds (**Chapter 4 & 6**).

Response to reduced care of a partner

Biparental care is often a source of conflict because both parents gain from parental care provided by either of the parents, but each parent only pays the costs of its own care (Trivers 1972; Lessells 2012). How then parents achieve synchronization and cooperation is not always clear.

Theoretical models predict that chick-feeding parents in passerine birds should achieve cooperation by partially compensating for the reduced care of their partner (Houston & Davies 1985; McNamara et al. 1999; McNamara et al. 2003). However, partial compensation is unlikely when breeding attempts fail due to a small decrease in parental care (Jones et al. 2002). Such a situation is typical of extreme environments where unattended offspring are subject to severe predation pressure, as in gull or frigatebird colonies (Dearborn 2001; Jones et al. 2002); overheating, as in deserts (AlRashidi et al. 2011); or cooling, as in the Arctic or Antarctica (Gauthier-Clerc et al. 2001; Hicklin and Gratto-Trevor 2010). In such cases, the synchronization of care among parents is expected to increase; parents are then expected to compensate fully or not at all for reduced care of their partner (Jones et al. 2002).

Experiments that targeted cooperation during biparental incubation are dominated by permanent removal of a parent (Burley 1980; Erckmann 1981; Bowman & Bird 1987; Brunton 1988; Duckworth 1992; Pinxten et al. 1995), and by handicapping a parent by testosterone implants (De Ridder et al. 2000; Alonso-Alvarez 2001; McDonald et al. 2001;

Schwagmeyer et al. 2005), or by attachment of extra weights (Wiebe 2010). These manipulations have long-lasting effects that are irreversible within one breeding attempt. However, the study of cooperation over the short-term is inevitable when testing whether incubating parents compensate fully or not at all for the absence of their partner's care, because parents that incubate in extreme environments cover their eggs continuously (i.e. do not feed) and hence cannot withstand full compensation for ever (Chaurand & Weimerskirch 1994; Weimerskirch 1995; Dearborn 2001). Also, short-term manipulations mimic the response of parents to natural short-term deficiencies in their partner's care, and thus allow testing whether such a response also affects subsequent bouts of care (i.e. whether the response has carry over effects). Yet, short-term reversible manipulations of female and male incubation effort are scarce and the evaluation of individual differences in response to such short-term change in parental care even more so (Gibbon et al. 1984; Kosztolányi et al. 2003; Kosztolányi et al. 2009).

Here, we investigated the response of parents to the temporary absence of a partner's care during the biparental incubation of a small (23-32 g) high Arctic breeding semipalmated sandpiper (**Chapter 3**).

Switching from biparental to uniparental care

Often it is unclear whether cooperation among parents is necessary, that is whether biparental care is obligatory or whether uniparental care is possible. Recent theory and empirical findings suggest that the adult sex-ratio of a population should drive its specific form of care (e.g. all else being equal, if the sex ratio is male skewed, males should be the more caring sex; Forsgren et al. 2004; Kokko & Jennions 2008; Kokko & Jennions 2012; Liker et al. 2013; Parra et al. 2014; Remes et al. 2015). Whether such outcomes are evolutionary fixed to the typical sex-ratio of the species, or arise through flexible response of individuals to the current sex-ratio of the population, remains unclear. Nevertheless, the flexible response might be limited by evolutionary history (e.g. males of avian species that have lost the brood patch are unlikely to incubate, or uniparental incubation in biparental birds might be unlikely if parents are unable to maintain their energetic balance).

We thus investigated in 15 biparentally incubating shorebird-species whether switch from biparental to uniparental incubation is possible and if so whether such nests are successful (**Chapter 4**).

Role of energetics

Avian incubation is energetically demanding (e.g. Vleck 1981; reviewed by Williams 1996; and by Tinbergen & Williams 2002; Piersma et al. 2003). However, it is debated whether these demands constrain incubation rhythms (i.e. the length, constancy, and timing of incubation bouts) in cases where both parents incubate (Williams 1996; Tinbergen & Williams 2002) because parents may always have enough off-nest time to replenish their energy reserves, depleted during their previous incubation session. The two experimental

studies addressing this issue in biparentally incubating birds yielded contradictory results (Cresswell et al. 2003; Kosztolanyi et al. 2009).

Here, to resolve this issue we use experimental approach (applied to same species and study site as in the previous experiment; Cresswell et al. 2003), re-analyses of the previous experiment (Cresswell et al. 2003), as well as comparative phylogenetic method (**Chapter 5 & 6**).

Drivers of between species diversity

Whereas the rhythm of biparental incubation is rarely explored in detail (i.e. across incubation period and in many individuals), the sketchy, often anecdotal, records suggest that between-species diversity might be immense (Kendeigh 1952; Skutch 1957; Deeming 2002b). Although phylogenetic comparative analyses of incubation rhythms are non-existent, we may expect the role of key behavioural drivers such as evolutionary history, energetics, predation risk and environmental cycles. We test for all with a comparative phylogenetic method (**Chapter 6**).

Specifically, we test five hypotheses. First, an observation that related organisms tend to resemble each other for most aspects of the phenotype (Blomberg et al. 2003) suggests that the evolutionary history often plays a key role in the between species diversity of a specific trait (Pärtel et al. 2007; Dale et al. 2015; Remes et al. 2015). Consequently, it is not unlikely that evolutionary history influences also the similarities and differences in between species incubation rhythms.

Second, if energetic demands of incubation constrain also incubation rhythms of biparental species (Williams 1996; Tinbergen & Williams 2002), individual incubation sittings (incubation bouts) of large species should be longer than those of small species as large species deplete their energy stores slower (i.e. radiate less body heat per unit of mass) than small species. Also, as harshness of environment increases with latitude, species breeding in high latitudes should have shorter incubation bouts because – everything else being equal – energy stores will deplete faster in cold environments.

Third, since predation is a major cause of breeding failure in birds (Ricklefs 1969) and, in general, parental activity on the nest increases nest predation (Martin et al. 2000; Smith et al. 2012), we may expect incubation rhythms to mirror the anti-predation strategies. Thus, in species that rely primarily on parental crypsis selection will favour fewer change-overs at the nest, and hence longer incubation bouts, since activity near the nest can reveal the nest's location to potential predators (Martin et al. 2000; Smith et al. 2012). In contrast, species that are clearly visible when sitting on the nest or that rely on active anti-predation behaviour, obtain no advantage from minimizing activity. For these species, bout length can shorten, which may be advantageous for other reasons (e.g. reduced need to store fat).

Fourth, behaviour of nearly all organisms displays 24-h rhythmicity (Dunlap et al. 2004). However, during summer, the 24-h variation in light decreases with latitude and above

Arctic Circle leads to continuous polar daylight (Hut et al. 2013). Such reduced variation in 24-h light intensity likely cause a loss of 24-h rhythmicity (van Oort et al. 2005; Lesku et al. 2012; Steiger et al. 2013). As a consequence, incubation rhythms should exhibit a latitudinal cline (Hut et al. 2013) with rhythm of species and individuals from low latitudes following the 24-h day-night cycle more than rhythm of those from higher latitudes.

Fifth, apart from 24-h behavioural rhythms, organism living in intertidal zones also display tidal behavioural rhythms (Naylor 2010). Thus, we expect shorebirds that live in intertidal zones throughout most of their life to exhibit circa-tidal incubation rhythms.

Biparental care in shorebirds

Shorebirds breed globally, across ecological contexts (Figure 1), and have diverse parental care strategies ranging from equal share of care by the female and male to uniparental care in which only one of the two parents provides all care (del Hoyo et al. 1996; Thomas et al. 2007). Thus, shorebirds have been used to study the evolution of parental care, as well as the link between parental care and sexual selection (Reynolds & Szekely 1997; Thomas & Szekely 2005; Thomas et al. 2007; Olson et al. 2009; Liker et al. 2013). Nevertheless, incubation by both parents is the most common form of care for eggs in shorebirds (Szekely & Reynolds 1995).

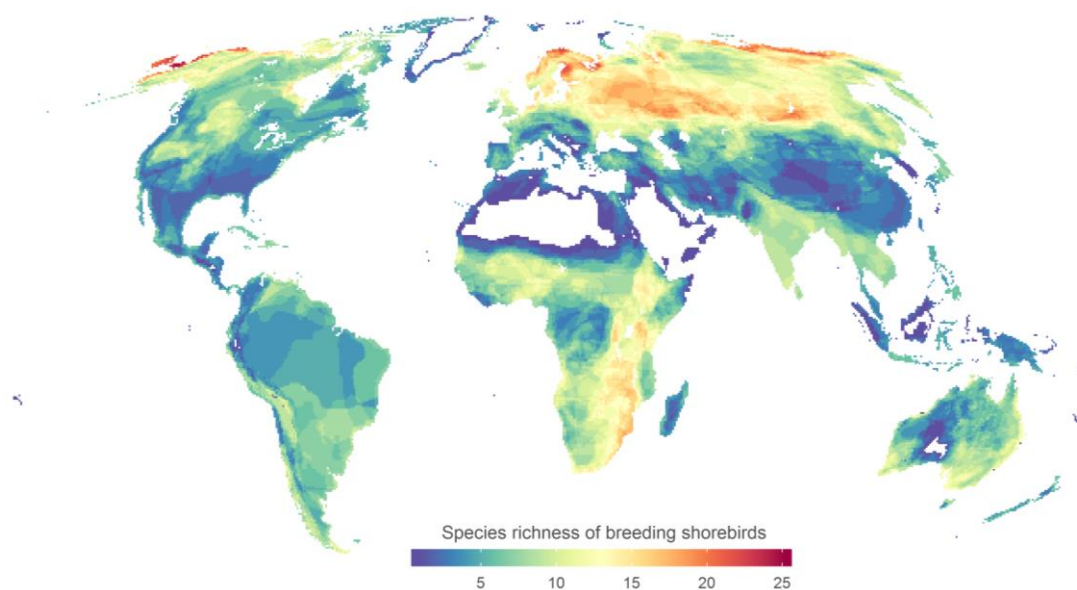


Figure 1 | Global distribution of breeding shorebirds. The species richness of breeding shorebirds at a given location is represented by colour from low (blue) to high (red) and was reconstructed using ‘rangeMapper’ (version 0.3) and ‘ggplot2’ (2.1) R packages (Wickham 2009; Valcu et al. 2012; R-Core-Team 2016), and unpublished data (Department of Behavioural Ecology & Evolutionary Genetics, Max Planck Institute for Ornithology; contact person: Mihai Valcu, valcu@orn.mpg.de).

Biparental shorebirds are typically monogamous (del Hoyo et al. 1996), mostly lay three or four eggs in an open nest on the ground (del Hoyo et al. 1996), and attend their eggs almost continuously (Deeming 2002a). Pairs achieve this through synchronization of their activities

such that one of them is responsible for the nest at a given time (i.e. an incubation bout). Alternating female and male bouts generate an incubation rhythm with a specific period length (cycle of high and low probability for a parent to incubate).

Given the range of ecological context, variable biparental care and minimum of confounding factors, shorebirds are well suited to investigate the link between biparental care and environment, parental cooperation and evolutionary history (Chapter 1-6; Székely & Reynolds 1995; Kosztolanyi et al. 2009; AlRashidi et al. 2010; AlRashidi et al. 2011; Vincze et al. 2013; Székely et al. 2014).

Aims

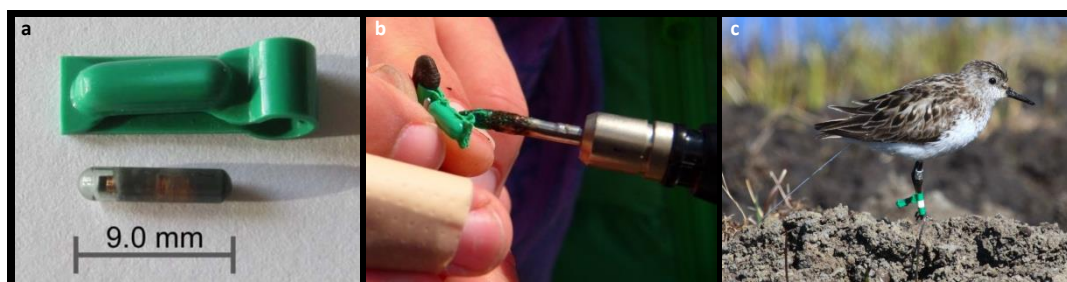
The general aim of this thesis is to describe the socially emerged rhythms of parental care, as well as to test the drivers of such rhythms, in biparentally incubating shorebirds. We use data from entire incubation period to reveal the differences within- and between-individuals (**Chapter 1-3 & 5**), within- and between-species (**Chapter 4 & 6**), as well as within- and across-days (**Chapter 1-6**). We experimentally test whether parents compensate for the temporary absence of their partner's care (**Chapter 3**) and whether this changes their incubation rhythms (**Chapter 3 & 4**). We further use a mix of descriptive, experimental and comparative approaches to test whether the incubation rhythms are constrained by energetic demands of incubation (**Chapter 2, 5 & 6**), and a comparative approaches to test whether the rhythms are shaped by evolutionary history, risk of predation and environmental cycles (**Chapter 6**).

Incubation rhythm of semipalmated sandpiper

Specifically, in **Chapter 1** and **2** (Bulla et al. 2013a; Bulla et al. 2015a), we first describe biparental incubation rhythms and the respective off-nest behaviour in the semipalmated sandpiper. In **Chapter 1**, we ask how parents divide their incubation duties over the incubation period, considering both variation and central tendency. In 48 nests we measured quality of incubation as incubation temperature and incubation constancy (nest attendance), and amount of incubation as length of incubation bouts. We further quantified how sexes divided the incubation within a day, over the incubation period and over the season. Simultaneously, we investigated the respective off-nest behaviour of 32 off-duty parents from 17 nests (**Chapter 2**). We ask how far from the nest the off-duty parents roamed, whether off-duty parents visited their incubating partner, and if not, whether the off-nest distance prohibited continuous communication between off-duty and incubating parent. We further describe the behaviour of the off-duty parents, i.e. how they spent their off-nest time. We then test whether off-nest distance and behaviour differed between sexes, varied with time and weather, and predicted the length of following incubation bouts.

To record incubation continuously and throughout the incubation period, we have developed a custom monitoring system based on radio-frequency identification (RFID) that

we used in combination with temperature probe placed between the eggs (**Chapter 1**). A thin antenna loop, placed around the nest cup and connected to the reader, registered the presence of tagged parents at the nest; the passive tag was embedded in a plastic flag (Picture 1). The system, which was powered by four AA-batteries, recorded incubation for well over a month. Temperature recordings made it possible to identify whether a bird was incubating even in the absence of RFID readings: an abrupt change in temperature demarcated the start or end of incubation. We tracked the off-duty behaviour with automated telemetry and by observing the off-nest behaviour of radio-tagged parents during cold and warm parts of the day (**Chapter 2**).



Picture 1 | Attachment of passive tags. **a**, Glass passive-integrated tag was embedded in a flag. **b**, The flag was placed on the bird's tarsus and the part that sticks out was closed using an AA-battery powered soldering device (Weller BP645). **c**, The semipalmated sandpiper banded with unique colour-ring combination including the green plastic-flag with the passive transponder, and equipped with radio-tag glued to its rump (note the antenna protruding behind the tail). Credits: **a**, M. Bulla; **b**, M. Šálek; **c**, E. Stich.

Response to reduced care of a partner

Then, in **Chapter 3** we experimentally test at 25 nests how parents of semipalmated sandpipers compensate for temporary absence of their partner's care. We removed a parent at the end of its regular incubation bout and released it 24-hours later. In this way, we made a temporarily widowed bird responsible not only for its own incubation bout, but also for the following incubation bout of its partner. We then investigated the change in the nest attendance between control and treated period, whether this change differed between females and males, how variable the change was between individuals, and whether the time of day, pre-experimental share of incubation or responsiveness of the parents explained such variability.

Based on theoretical models (Houston & Davies 1985; McNamara et al. 1999; Jones et al. 2002; McNamara et al. 2003), we have anticipated four possible scenarios. **a**) No compensation – the bird leaves the nest for the supposed incubation bout of its partner. This may either reflect no immediate response to the partner's absence, or a lack of knowledge about the partner's absence. **b**) Full compensation - the bird continues incubating for the entire supposed incubation bout of its partner. In addition, the bird may attempt full compensation, but when its energy reserve is depleted **c**) may leave the nest, or **d**) may continue incubating, but with decreasing nest attendance, that is, leave the nest for short feeding bouts like uniparental species do. Both cases **c** & **d**) represent partial compensation.

Switching from biparental to uniparental incubation

As a follow up of the removal experiment (**Chapter 3**), in **Chapter 4** we investigate whether uniparental incubation exists naturally within 15 species of biparental shorebirds, and if so how the uniparental incubation rhythm differs from biparental rhythm and from uniparental rhythm of uniparental species. Crucially, to reveal whether biparental shorebirds have a potential for a flexible switch from biparental to uniparental care, we have recorded whether the uniparentally incubating nests were successful.

Role of energetics

In **Chapter 5** (Bulla et al. 2015b) we use two methods to experimentally test the ‘energetic demands hypothesis’, which postulates that the length of an incubation bout should depend on a bird’s energetic state (Williams 1996; Deeming 2002a; Cresswell et al. 2003). Therefore, using the semipalmated sandpiper that breeds in the harsh conditions of the high Arctic, we tested whether saving incubating bird’s energy by heating or insulating its nest cup had an effect on the length of its incubation bouts.

Within- and between-species diversity and drivers of incubation rhythms

Last, in **Chapter 6** (Bulla et al. 2016a) we use comprehensive comparative dataset on biparental incubation rhythms across shorebirds to (a) describe the within- and between-species diversity in socially synchronized rhythms, and (b) to demonstrate how these diverse rhythms relate to phylogeny, predation risk, energetics and environmental cycles, that is, to the key drivers of nearly any behaviour. We used diverse monitoring systems to collect primary data from 91 populations of 32 shorebird species belonging to 10 genera. We then extracted the length of 34,225 incubation bouts from 729 nests, and determined the period length - the cycle of female and male probability to incubate - for pairs in 584 nests.

Supporting information

The data and R-scripts to reproduce the presented analyses and figures are freely available online (Bulla et al. 2013b; Bulla 2014; Bulla et al. 2014c; Bulla et al. 2014a; Bulla et al. 2014b; Bulla 2015, 2016a, b, c; Bulla & Kempenaers 2016; Bulla et al. 2016b; c; see also the web-links or citations in the respective chapters). At the end of each chapter we present also supporting information. Where appropriate (**Chapter 1, 3-6**), we also visualised raw incubation data and/or extracted incubation data for each nest; such figures are freely available via the publisher’s web page (**Chapter 1, 5 & 6**; see the web-links in the respective papers), or via Open Science Framework (**Chapter 3**: <https://osf.io/mx82q/>; **Chapter 4**: <https://osf.io/3rsny/>; **Chapter 6**: <https://osf.io/wxufm/>). All supporting information (except for data and R-scripts) is also available on the CD that accompanies this thesis.

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Chapter 1

Biparental incubation patterns in a High Arctic breeding shorebird: how do pairs divide their duties?

Martin Bulla, Mihai Valcu, Anne L. Rutten, Bart Kempenaers

In biparental species, parents may be in conflict over how much they invest into their offspring. To understand this conflict, parental care needs to be accurately measured, something rarely done. Here, we quantitatively describe the outcome of parental conflict in terms of quality, amount, and timing of incubation throughout the 21-day incubation period in a population of semipalmated sandpipers (*Calidris pusilla*) breeding under continuous daylight in the high Arctic. Incubation quality, measured by egg temperature and incubation constancy, showed no marked difference between the sexes. The amount of incubation, measured as length of incubation bouts, was on average 51 min longer per bout for females (11.5 h) than for males (10.7 h), at first glance suggesting that females invested more than males. However, this difference may have been offset by sex differences in the timing of incubation; females were more often off nest during the warmer period of the day, when foraging conditions were presumably better. Overall, the daily timing of incubation shifted over the incubation period (e.g., for female incubation from evening–night to night–morning) and over the season, but varied considerably among pairs. At one extreme, pairs shared the amount of incubation equally, but one parent always incubated during the colder part of the day; at the other extreme, pairs shifted the start of incubation bouts between days so that each parent experienced similar conditions across the incubation period. Our results highlight how the simultaneous consideration of different aspects of care across time allows sex-specific investment to be more accurately quantified.

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Original Article

Biparental incubation patterns in a high-Arctic breeding shorebird: how do pairs divide their duties?

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In biparental species, parents may be in conflict over how much they invest into their offspring. To understand this conflict, parental care needs to be accurately measured, something rarely done. Here, we quantitatively describe the outcome of parental conflict in terms of quality, amount, and timing of incubation throughout the 21-day incubation period in a population of semipalmated sandpipers (*Calidris pusilla*) breeding under continuous daylight in the high Arctic. Incubation quality, measured by egg temperature and incubation constancy, showed no marked difference between the sexes. The amount of incubation, measured as length of incubation bouts, was on average 51 min longer per bout for females (11.5 h) than for males (10.7 h), at first glance suggesting that females invested more than males. However, this difference may have been offset by sex differences in the timing of incubation; females were more often off nest during the warmer period of the day, when foraging conditions were presumably better. Overall, the daily timing of incubation shifted over the incubation period (e.g., for female incubation from evening–night to night–morning) and over the season, but varied considerably among pairs. At one extreme, pairs shared the amount of incubation equally, but one parent always incubated during the colder part of the day; at the other extreme, pairs shifted the start of incubation bouts between days so that each parent experienced similar conditions across the incubation period. Our results highlight how the simultaneous consideration of different aspects of care across time allows sex-specific investment to be more accurately quantified.

Key words: Arctic, *Calidris pusilla*, continuous daylight, incubation pattern, incubation timing, negotiation, nest attendance, parental care division, semipalmated sandpiper, sexual conflict.

INTRODUCTION

Parental care is beneficial to offspring, but it is also costly, both energetically and in terms of lost opportunities for other activities such as self-maintenance or mating. Whereas these costs are paid by each parent individually, the benefits are shared by both. This, Trivers (1972) argued, creates potential for conflict between the parents because it is advantageous to minimize one's own investment while capitalizing on the benefits that arise from the investment of the partner.

Theoretical models predict the outcomes of this conflict by considering 2 strategies (reviewed by Lessells 2012). In the first, the amount of parental investment is fixed at a specific level or follows a behavioral rule that determines the level of care irrespective of previous care of the partner. In the second strategy, the level of care is a result of behavioral negotiation.

Most of these models are not tailored to a specific empirical system (van Dijk et al. 2012), so their assumptions and subsequent empirical tests often miss some of the complexity of parental care (e.g., by modeling or measuring the individual costs inaccurately). For example, most studies measure the total amount of care (reviewed by Harrison et al. 2009), but this is not the same as measuring costs of care because providing better quality of care or providing care during tougher conditions may lead to higher costs. Also, even if both pair members invest overall equally, there may be large differences between pairs in how they achieve this, resulting in variation in patterns of care (i.e., different outcomes of parental conflict).

Quantifying such between-individual variability in investment is essential to approximate the variation that selection can act on (Bolnick et al. 2011) or to identify different parental care strategies. Therefore, an important step in understanding parental conflict and its outcome is to describe the complexity of parental care (e.g., in terms of quality, amount, and timing), including its temporal and between-individual variation. However, such detailed

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descriptions are rare, although they would provide the basis for specific models and subsequent empirical tests of the processes behind the described patterns of parental care.

Parental care takes a variety of forms; in birds, incubation of eggs is crucial for successful reproduction (Deeming 2002a). Although previous studies have investigated sex differences in particular aspects of incubation (Kleindorfer et al. 1995; reviewed by Deeming 2002b; Auer et al. 2007), we are not aware of any study that examined incubation patterns in terms of incubation quality, amount, and timing simultaneously, quantitatively, and throughout the incubation period.

Here, we used a continuous recording system to quantitatively describe the incubation patterns in a population of semipalmated sandpipers (*Calidris pusilla*), a common, Arctic-breeding, socially monogamous shorebird. We quantified how parents divided their duties over the incubation period, considering both variation and central tendency. Specifically, we measured 4 aspects of incubation: incubation temperature and incubation constancy (both measures of quality), length of incubation bouts (amount), and distribution of incubation within a day, over the incubation period, and over the season (timing).

The biparental incubation system of semipalmated sandpipers is well suited for these investigations for 3 reasons. First, several factors that may confound the outcomes of parental conflict in other systems can be excluded here. 1) Variation in clutch size is limited: semipalmated sandpipers lay 4 (rarely 3) eggs (Hicklin and Gratto-Trevor 2010). 2) Spatial variation in environmental conditions in the high-Arctic breeding grounds is small compared with temperate habitats; our study site consists of a homogeneous tundra environment. 3) In our high-Arctic study site, the nonincubating parent seems to provide no other form of care because it leaves for feeding grounds up to 2–3 km away from the nest (Ashkenazie and Safriel 1979a; Jehl 2006; our own observations). Second, the extreme rates of energy expenditure in the high Arctic (Piersma et al. 2003) should elevate the conflict over parental care. Third, biparental incubation is a type of parental care that involves mutually exclusive behavior (Kosztolanyi et al. 2009) and therefore, unlike other forms of care such as offspring provisioning, parents cannot change their contribution independently of each other.

METHODS

Study area and species

We studied a population of semipalmated sandpipers near Barrow, Alaska (71°32'N, 156°65'W), between 1 June and 16 July 2011; Ashkenazie and Safriel (1979a) have described the area in detail. In brief, the site consists of polygonal soils with a high-Arctic tundra vegetation (sedges, mosses, and lichens). Ambient temperatures are generally low, below 5 °C (Supplementary Figure S1a). However, surface tundra temperatures can reach up to 28 °C (Supplementary Figure S1b). Barrow has continuous daylight: the sun never sets between mid-May and the end of July. Nevertheless, environmental conditions show consistent and substantial diel fluctuations: tundra temperatures are ~85% and light intensity ~90% lower at night than during the day (Supplementary Figure S1b and c). In contrast, diel fluctuations in wind speed are less pronounced (Supplementary Figure S1d). Diel fluctuations may also exist in predatory pressure because the Arctic fox (*Alopex lagopus*), the main mammalian predator of shorebird eggs (e.g., Liebezeit and Zack 2008), is active mainly during night hours (Eberhardt et al. 1982). However, this

effect is absent or strongly reduced in our study site because of an intense fox removal program in the Barrow area (foxes are shot and trapped). As a result, there was a tendency for increased nest predation (probably by avian predators such as skuas, *Stercorarius* sp.) during the day (Supplementary Figure S2).

Semipalmated sandpipers are small shorebirds and are monomorphic in plumage, but with females on average slightly larger than males (Supplementary Figure S3). The birds arrive at the Barrow breeding ground between the end of May and early June; males immediately establish territories; pairs form within 3–6 days, and egg laying starts shortly after (Ashkenazie and Safriel 1979a). A complete clutch has 4, rarely 3, eggs and a 4-egg clutch is typically laid in 5 days (Sandercock 1998). The species is socially monogamous, and extrapair paternity is rare (our unpublished data). Both sexes develop 2 lateral brood patches, and both parents incubate. Incubation lasts 19–22 days. Chicks are precocial, and females tend to desert the family 2–8 days after hatching (Ashkenazie and Safriel 1979a; Hicklin and Gratto-Trevor 2010).

Sampling of individuals

Nonincubating birds were captured with mist nets ($N = 22$) and incubating birds with spring traps ($N = 125$). Spring traps were triggered from a distance by fishing line, and the captured bird was released from the trap within approximately 20 s. No eggs were damaged by this catching method. Adults were marked with an aluminum US Geological Survey band, a unique combination of 4 color bands, and a green flag with embedded glass passive-integrated tag (Biomark: 9.0 mm × 2.1 mm, 0.087 g, 134.2 kHz, ISO FDXB, <http://www.biomark.com/>; Supplementary Picture S1). For the purpose of another project and following Warnock and Warnock (1993), 40 individuals were equipped with a radio transmitter (PicoPip Ag392, Biotrack, <http://www.biotrack.co.uk/>; 1.18 g, which was 4.4% of the mean and 5.1% of the smallest bird's body mass). Briefly, the feathers above the uropygial gland of the bird were trimmed (short feather shafts left), and the transmitter was glued to the skin and shafts with Loctite® super glue. This technique is fast and has fewer behavioral effects compared with harness or implant techniques, and the transmitters drop off within a few weeks as the feathers regrow (reviewed by Warnock and Takekawa 2003). We took a small (ca. 50 µl) blood sample from a brachial vein for sexing, weighed each bird (to the nearest 0.1 g) using a digital balance, and measured tarsus, culmen, and total head (to the nearest 0.1 mm) with calipers and measured wing (to the nearest 0.5 mm) with a ruler.

Monitoring of incubation

Nests were found by systematically searching the tundra and by observing the behavior of birds flushed during laying or incubation (Sandercock and Gratto-Trevor 1997). The start of incubation and hatching was estimated by laying date for clutches found during laying and by measuring the height and inclination of the eggs floated in water for clutches found complete. This floating technique is based on the fact that eggs lose weight as the embryo develops: freshly laid eggs sink to the bottom of a water column and lay horizontal; as eggs develop, they rise with their blunt end and eventually float on the water surface (Liebezeit et al. 2007; median estimation of all floated eggs within the nest was used). Each nest was visited at the estimated hatching date to capture both parents to estimate their condition; to measure, bleed, and ring the chicks; and to determine the fate of the nest.

Incubation was monitored using a custom-made radio frequency identification device (RFID; designed by Calima Engineering, <http://www.calima.de>, in cooperation with the Max Planck Institute for Ornithology) in combination with a temperature probe (similar method used by [Reneerkens et al. 2011](#)). A thin antennae loop (\varnothing 9 cm) was fitted into the nest cup and connected to a datalogger approximately 0.5 m outside of the nest ([Supplementary Picture S2a–c](#)). This system registered the identity of a tagged bird on the nest every 5 s throughout the incubation period (for technical details, see legend in [Supplementary Picture S2](#)). To determine whether a bird was incubating, independent of the RFID reader, a minute external temperature probe (\varnothing 2.5 mm, 0.2 °C accuracy; Talk Thermistor, PB-5005-0M6) was placed in the middle of the nest between the 4 eggs and connected to a temperature logger (Tinytag Talk 2, TK-4023, Gemini Data Loggers, www.tinytag.info) placed 0.5 m outside of the nest. The probe was in level with the tops of the eggs ([Supplementary Picture S2d](#)) and secured with a toothpick. The logger recorded the temperature every 2 min for the entire incubation period.

For 8 nests, the incubation behavior was also monitored by a video-recording system (custom designed by Jan Petrů, Czech Republic). An external lens (\varnothing 2 cm, length 4 cm) and a microphone (\varnothing 0.75 cm, length 2.2 cm) were positioned 1–3 m from the nest and were connected to the recorder hidden in the vegetation 5 m away from the nest. The recorder was supplied by a 12-V, 31-Ah, or 44-Ah battery hidden another 5 m away, allowing continuous recording for 2–4 days.

Monitoring of egg incubation temperatures

To determine whether females and males differed in egg incubation temperatures, in 14 nests, instead of adding an external temperature probe, one egg was replaced with a solid egg (from PVC-U, painted to resemble a sandpiper egg; [Supplementary Picture S3](#)) with a high-resolution MSR® temperature probe (0.2 °C accuracy) positioned just under the egg surface. The fake egg was secured in the nest with a pin, and the probe was connected to an MSR® 145 datalogger (MSR® Electronics GmbH, Switzerland, <http://www.msr.ch/en/>) positioned outside the nest. Temperature was logged every 5 s throughout the incubation period. The fixed position of the probe in the fake egg and the fixed position of the fake egg in the nest allowed us to compare the within-nest sex differences in incubation temperatures.

Disturbance

Data collection would be impossible without us walking through the study area. As a consequence, the birds were disturbed. To control for this disturbance, each field-worker carried a GPS (Garmin, Oregon 450) that recorded the person's position whenever he/she moved 10 m within the study site. This allowed us to calculate the distance between each person and each nest at a given time. The probability of an incubating bird leaving the nest was under 10% whenever the closest person to the nest was further than 210 m away (our unpublished data). Therefore, we defined the absence or presence of disturbance at a given nest and at any one time based on whether a field-worker was present within 210 m of that nest.

Tundra temperatures

The surface tundra temperature was recorded next to each nest in vegetation similar to that surrounding the specific nest cup. Two types of loggers were used: the MSR® 145 at the nests with a fake egg (recording interval 5 s; [Supplementary Picture S2c](#) and [d](#)) and the HOBO Pendant® Temperature Data Logger (0.47 °C accuracy,

UA-002-64, Onset Computer Corporation, <http://www.onsetcomp.com/>) at all other nests (recording interval 1 min). The housing of the MSR and HOBO logger differs in color. This could in principle affect the temperature recordings. However, both loggers recorded similar temperatures when placed next to each other (details are not presented), and the potential differences did not affect the extraction of incubation data (discussed in the next section).

Extraction of incubation behavior

Egg temperatures were used to discriminate between incubation and nonincubation periods as described in detail in [Supplementary Figure S4](#). Briefly, constant incubation temperatures higher than tundra temperatures were interpreted as continuous incubation; the start of incubation was determined from a steep increase, the interruption of incubation from a steep decrease in nest temperature ([Supplementary Figure S4](#); see also Fig. 2 in [Reneerkens et al. 2011](#)). We automated the procedure using an R-script and validated the method by comparing the assigned incubation with plots of the raw data ([Supplementary Figure S4](#)) and with the video recordings.

The temperature-based determination of incubation/nonincubation was overlaid with the RFID data, which allowed assigning each incubation bout to a parent ([Supplementary Figure S4](#)). Subsequently, the length of each incubation bout was extracted as the total time allocated to a single parent. The constancy of incubation was calculated as the percentage of time a bird actually incubated within a given incubation bout (i.e., sat tightly on the eggs as opposed to egg rolling, nest maintenance, or being off the nest). The exchange gap duration was defined as the time between the departure of one parent and the return of the other parent.

Timing of incubation-related events

The visualization of the raw RFID and temperature recordings allowed us to pinpoint the precise timing of desertion, depredation, or hatching; therefore, we adjusted the field data accordingly.

Statistical analyses

R, version 2.15.2 (R Development Core Team 2012), was used for statistical analyses and the lme4 package ([Bates and Maechler 2010](#)) for the mixed-effects modeling.

Quality and amount

Sex differences in quality of incubation (incubation temperature and constancy) and amount of incubation (length of incubation bouts and exchange gaps) over the incubation period were tested by generalized linear mixed effect models (GLMMs) with the incubation feature as the dependent variable and with sex in interaction with day of incubation as fixed effects. Potentially confounding variables were added as fixed effects: disturbance (0, 1), start of incubation within the season (in interaction with day of incubation), body mass and size (both sex centered), and whether the bird carried a radio transmitter (0, 1). Culmen length was used as a proxy for body size ([Ashkenazie and Safriel 1979b](#)); culmen correlates with other body size measures (in our study, Pearson correlation coefficients [95% confidence interval {CI}]; tarsus: $r = 0.51$ [0.35–0.64], $t_{97} = 5.9$, $P < 0.0001$; total head: $r = 0.87$ [0.82–0.91], $t_{98} = 17.9$, $P < 0.0001$; wing: $r = 0.5$ [0.34–0.64], $t_{98} = 5.7$, $P < 0.0001$). All predictors (except sex) were mean centered ([Schielzeth 2010](#)). Incubation temperatures were z -transformed (mean centered and standard deviation scaled) within the nest and thus were made comparable between nests. The distribution of

incubation constancy was normalized by arcsine transformation. The incubation constancy model was also controlled for the type of temperature probe (inside fake egg [0] or between the eggs [1]). The bout length model investigated also the sex-specific effect of the length of the previous (partner's) incubation bout (off-nest bout of the focal bird) on the length of the current bout. The random structure of the models contained nest as a random intercept and z -transformed day of incubation as random slope. To follow current recommendations (Simmons et al. 2011), the Supplementary Tables report simple GLMMs without covariates. The results of all GLMMs include adjusted approximations of P values based on multiple comparisons (simultaneous inference) of predictors using the `glht` function from the `multcomp` package (Hothorn et al. 2008).

Timing

To investigate whether females and males incubate during different (cold—unfavorable for foraging—or warm—favorable for foraging) parts of the day, incubation period, or season (i.e., defined as start of incubation within the season), the following procedure was applied. We sampled the entire data set of approximately 8.4 million per 5-s recordings of incubation; an autocorrelation of the data points was avoided by stratifying the sample to 0.025% incubation data points per nest, with points at least 2.5 h apart from each other. The sample was limited to the usable data (e.g., bouts with hatching or nests with only 4 incubation bouts were excluded; details are in the Sample sizes section). Binary coding was created (female incubation = 1 and male incubation = 0). The 5000 iterations of this process generated data sets with median (range) sample size of 1722 (1680–1768) incubation data points. These data were used as the binomial dependent variable in subsequent GLMM. We overcame the circular properties of time by converting it to radians and decomposing it into 2 linear variables: $\sin(\text{rad})$ and $\cos(\text{rad})$. Both $\sin(\text{rad})$ and $\cos(\text{rad})$ were entered in the model as explanatory variables in a 3-way interaction with the day of the incubation period and start of incubation within the season. Nest was included as a random intercept, and $\sin(\text{rad})$ and $\cos(\text{rad})$ were included as random slopes. The reported results of this exercise are summaries of the 5000 iterations (CIs are nonparametric).

Sample sizes

The aim was to follow the entire breeding population on the study site for the entire incubation period. In total, we found 83 nests. We acquired the mass of both parents from 51 nests and morphometric measurements for both parents from 50 of those nests. Twenty-one nests were depredated and 3 nests deserted before or shortly after initiation of data collection; one nest was excluded because it was used to test the monitoring system (increased disturbance); an additional 7 nests were excluded because they were found only close to hatching. Thus, the basic data set, used for further analyses, consisted of over 8.9 million per 5-s readings from 51 nests, with median (range) = 20.4 (6.7–31.3) incubation days/nest. For these nests, we excluded the first 2 incubation bouts after first parent catching, the bout where the nest was deserted or depredated, and all bouts that ended within 6 h before the start of hatching. We further excluded all nests with less than 4 incubation bouts ($N = 3$). Thus, the final data set consisted of 887 incubation bouts from 48 nests (median [range] = 18 [4–42] bouts/nest; median [range] start of incubation = 7 [1–26] June). Bouts for which the temperature recordings were missing were excluded from the analysis of incubation constancy and exchange gaps, leaving a total of 809 incubation bouts from 47 nests (median [range] = 16 [4–42] bouts/nest). Data sets were further reduced in the mixed models because only birds for

which morphometric measurements were available were included. The data set for the models on the constancy of incubation consisted of 762 incubation bouts from 47 nests (median [range] = 15.5 [3–42] bouts/nest). This data set was further reduced in the model on the length of incubation bouts because to investigate the effect of the previous (partner's) bout, a continuous data set is required. Hence, we excluded the first incubation bout in each nest (the previous bout is absent) and nests where only one bird was measured. This left 729 incubation bouts from 39 nests (median [range] = 18 [3–41] bouts/nest). The data set for the model on the incubation temperatures (only nests with a fake egg) consisted of 307 incubation bouts from 14 nests (median [range] = 21.5 [9–42] bouts/nest). The data sets are available from the Dryad Digital Repository (<http://doi.org/10.5061/dryad.nh8f0>).

RESULTS

Quality of incubation

Incubation temperatures did not change systematically over the incubation period or over the season (start of incubation within season) and on average did not differ between females and males (Figure 1a and Table 1). Within-nest variance accounted for 78% of overall phenotypic variance (Table 1). Body mass and size of the bird had no effect on incubation temperature nor did the attachment of a radio transmitter (Table 1).

Overall, the median constancy of incubation within an incubation bout was 94.9% (range: 43–100%; $N = 809$ incubation bouts from 47 nests). Constancy of incubation within incubation bouts did not change systematically over the incubation period or over the season, but on average females had 0.9% higher incubation constancy per incubation bout than males (Figure 1b and Table 2). This corresponds to approximately 6 min of longer incubation bouts by females (given a median bout length of 11.45 h). Within-nest variance accounted for 77% of overall phenotypic variance (Table 2). Size and body mass of the bird had no effect on its incubation constancy nor did the attachment of a radio transmitter (Table 2).

In short, these results indicate that overall the quality of incubation varied little over the course of incubation and played a minor role in sex-specific investment.

Amount of incubation

The median length of all incubation bouts was 11 h 27 min (range: 3.4 min–18.2 h; $N = 887$ bouts from 48 nests). Bout length increased systematically over the incubation period (by ca. 9 min/day; Figure 2). The increase was consistent across nests (between-nest variation in the change of bout length over the incubation period accounted for less than 1.1% of the variance) but independent of the start of incubation within the season and independent of sex (Figure 2 and Table 3). On average, females incubated 51 min (95% CI: 26–76 min) longer per incubation bout than males (Figures 2 and 3 and Table 3); thus, the median proportion of female incubation over the entire incubation period was 51.4% (range: 45.5–57%; $N = 48$ nests). After controlling for sex differences, incubation bout length did not depend on body mass or size and was unaffected by an individual wearing a radio tag or not (Table 3). Despite the general trend, in 16 of 48 nests (33%), the median bout length of the female was shorter than that of the male (Figure 3). Incubation bout length was positively correlated among pairs (Figure 3), indicating that if one parent had a longer median incubation bout than that of the rest of the population,

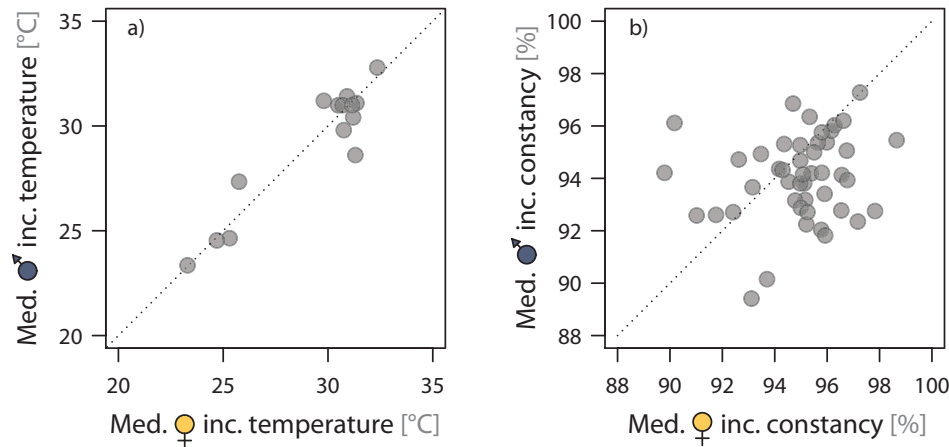


Figure 1

Within-pair differences in (a) the median fake-egg incubation temperature and (b) the median constancy of incubation. Each dot represents 1 nest. Incubation temperatures are not comparable between nests because the position of the temperature probe within the fake egg and of the fake egg within a nest is not exactly the same in each nest. Incubation constancy is comparable between nests.

Table 1

Model (GLMM) estimates of median z -transformed incubation temperature per incubation bout in relation to sex and incubation period with disturbance, presence of radio tag, body mass, culmen length, and start of incubation within the season as confounding variables

Fixed effects	Estimate	95% CI	<i>P</i>
(Intercept)	0.155	(−0.031, 0.342)	0.18
Disturbance	0.02	(−0.161, 0.201)	1
Radio tag	0.219	(−0.036, 0.474)	0.15
Culmen	−0.045	(−0.154, 0.065)	0.93
Body mass	−0.014	(−0.077, 0.048)	1
Start of incubation	0.004	(−0.039, 0.047)	1
Day of incubation	0.016	(−0.018, 0.049)	0.86
Sex (male) ^a	0.046	(−0.096, 0.188)	0.98
Sex × Day of incubation	0.002	(−0.027, 0.031)	1
Start of incubation × Day of incubation	−0.001	(−0.008, 0.006)	1
Random effects	Variance		
Nest (intercept)	0.0337		
z -Transformed (day of incubation)	0.0177		
Residual	0.1864		

$N = 307$ median z -transformed incubation temperatures per incubation bout from 14 nests. Fixed effects, except sex, were mean centered (culmen and body mass were centered within each sex). Median incubation temperatures were calculated from raw incubation temperature-values z -transformed within each nest. Results of the model without confounding variables are presented in Supplementary Table S1.

^aRelative to female.

so had its partner. This partner matching is also present within the pairs' incubation period: the length of the previous (partner's) incubation bout (which is the off-nest bout of the focal bird) strongly predicted the length of the current incubation bout of both sexes (Figure 4 and Table 3).

There was no detectable exchange gap (<5 s) during 51% of the exchanges ($N = 809$ exchanges at 47 nests); the median length of all detectable exchange gaps was 35 s (range: 5 s–6.7 h; $N = 399$ detectable gaps from 44 nests). Both the probability of a detectable exchange gap and the length of detectable exchange gaps decreased over the incubation period, irrespective of the sex of the exchanging bird (Figure 5 and Tables 4 and 5). Within-nest

Table 2

Model (GLMM) estimates of incubation constancy per incubation bout (arcsine transformed) in relation to sex and incubation period with disturbance, type of temperature probe, presence of radio tag, body mass, culmen length, and start of incubation within the season as confounding variables

Fixed effects	Estimate	95% CI	<i>P</i>
(Intercept)	1.342	(1.328, 1.355)	<0.0001
Disturbance	−0.023	(−0.042, −0.005)	0.0039
Temperature probe type	0.003	(−0.024, 0.031)	1
Radio tag	−0.003	(−0.029, 0.022)	1
Culmen	−0.003	(−0.014, 0.008)	0.99
Weight	−0.001	(−0.007, 0.004)	1
Start of incubation	−0.001	(−0.003, 0.001)	0.93
Day of incubation	−0.001	(−0.005, 0.004)	1
Sex (male) ^a	−0.02	(−0.036, −0.004)	0.0042
Sex × Day of incubation	0.003	(0, 0.006)	0.16
Start of incubation × Day of incubation	0	(−0.001, 0)	1
Random effects	Variance		
Nest (intercept)	0.0001		
z -Transformed (day of incubation)	0.0017		
Residual	0.0057		

$N = 762$ incubation constancies per incubation bout from 47 nests. Fixed effects, except sex, were mean centered (culmen and body mass were centered within each sex). Results of the model without confounding variables are presented in Supplementary Table S2.

^aRelative to female.

variance in the length of detectable exchange gaps accounted for 80% of the overall phenotypic variance (Table 5).

Taken together, these results indicate that the amount of incubation changed over the incubation period and was female biased.

Timing of incubation: general incubation pattern

The median proportion of female incubation within the cold period was 72.6% (range: 0–100%; $N = 356$ days from 48 nests). Thus, overall, females incubated more during the cold period of the Arctic day (i.e., when the tundra temperatures were on average below overall median tundra temperature, roughly between 21:30 and 09:30), whereas males incubated more during the warmer period when foraging conditions were more favorable.

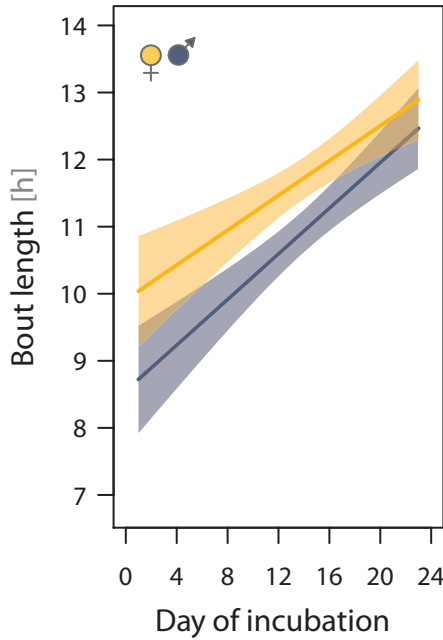


Figure 2 Increase in incubation bout length over the incubation period. The solid lines represent the model fit, and the shading represents the 95% CIs. Model results are presented in Table 3, and the distribution of the raw data is depicted in Supplementary Figure S5.

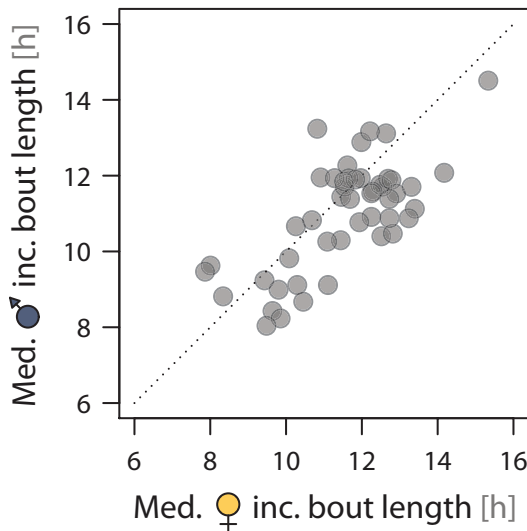


Figure 3 Between- and within-pair differences in the median length of incubation bouts. Each dot represents 1 nest. The correlation of the median bouts between sexes: Pearson correlation coefficient (95% CI): $r = 0.71$ (0.53–0.83), $t_{46} = 6.8$, $P < 0.0001$.

Table 3 Model (GLMM) estimates of incubation bout length (in minutes) in relation to sex, incubation period, and length of the previous bout with disturbance, presence of radio tag, body mass, culmen length, and start of incubation within the season as confounding variables

Fixed effects	Estimate	95% CI	P
(Intercept)	692.2	(663.9, 720.5)	<0.0001
Disturbance	38.9	(9.4, 68.4)	0.002
Radio tag	8	(−39.8, 55.9)	1
Culmen	−2.6	(−20.6, 15.4)	1
Body mass	−0.9	(−10.5, 8.7)	1
Previous bout length	0.4	(0.3, 0.6)	<0.0001
Start of incubation	2.2	(−1.8, 6.1)	0.76
Day of incubation	7.8	(2.8, 12.8)	0.0001
Sex (male) ^a	−50.9	(−76.3, −25.5)	<0.0001
Sex × Previous bout	−0.1	(−0.3, 0)	0.29
Sex × Day of incubation	2.4	(−3.5, 8.4)	0.95
Start of incubation × Day of incubation	0	(−0.6, 0.6)	1
Random effects	Variance		
Nest (intercept)	2032		
z-Transformed (day of incubation)	165		
Residual	13 779		

$N = 729$ incubation bouts from 39 nests. Fixed effects, except sex, were mean centered (culmen and body mass were centered within each sex). Results of the model without confounding variables are presented in Supplementary Table S3.

^aRelative to female.

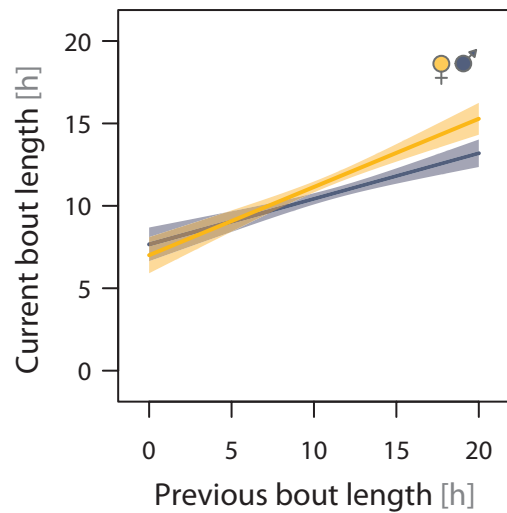


Figure 4 Positive relationship between incubation bout length and previous bout length (partner's bout; off-nest bout of the focal bird). The solid lines represent the model fit, and the shading represents the 95% CI. Model results are presented in Table 3.

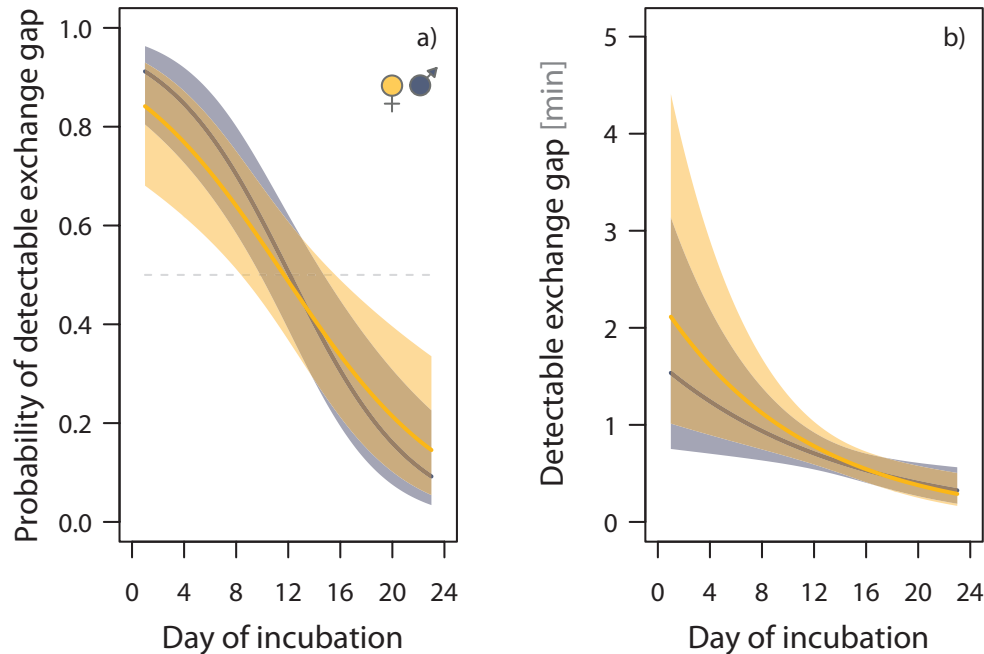


Figure 5

Decrease in (a) the probability of a detectable exchange gap (≥ 5 s) and (b) the length of detectable exchange gaps over the incubation period. The solid lines represent the model fit, the shading represents the 95% CI, and the horizontal dashed line in (a) represents the equal probability. Model results are presented in Tables 4 and 5, and the distribution of the raw data is depicted in Supplementary Figure S6.

Table 4

Model (binomial GLMM) estimates of the probability of a detectable exchange gap (≥ 5 s) in relation to sex and incubation period with disturbance, type of temperature probe, presence of radio tag, body mass, culmen length, and start of incubation within the season as confounding variables

Fixed effects	Estimate	95% CI	P
(Intercept)	-0.124	(-0.848, 0.6)	1
Disturbance	-0.046	(-0.674, 0.583)	1
Temperature probe type	-1.644	(-3.518, 0.23)	0.13
Radio tag	0.049	(-1.721, 1.819)	1
Culmen	0.033	(-0.356, 0.422)	1
Body mass	0.1	(-0.112, 0.313)	0.87
Start of incubation	-0.065	(-0.177, 0.046)	0.64
Day of incubation	-0.155	(-0.269, -0.041)	0.0014
Sex (male) ^a	0.064	(-0.455, 0.585)	1
Sex \times Day of incubation	-0.054	(-0.166, 0.058)	0.85
Start of incubation \times Day of incubation	-0.004	(-0.019, 0.012)	1
Random effects	Variance		
Nest (intercept)	1.72		
z-Transformed (day of incubation)	0.38		

$N = 762$ exchanges from 47 nests. Fixed effects, except sex, were mean centered (culmen and body mass were centered within each sex). Results of the model without confounding variables are presented in Supplementary Table S4.

^aRelative to female.

Table 5

Model (GLMM) estimates of detectable exchange gap duration (in seconds, log transformed) in relation to sex and incubation period with disturbance, type of temperature probe, presence of radio tag, body mass, culmen length, and start of incubation within the season as confounding variables

Fixed effects	Estimate	95% CI	P
(Intercept)	3.894	(3.481, 4.306)	<0.0001
Disturbance	-0.113	(-0.592, 0.366)	1
Temperature probe type	0.579	(-0.295, 1.453)	0.47
Radio tag	0.007	(-0.738, 0.753)	1
Culmen	-0.035	(-0.333, 0.264)	1
Body mass	-0.054	(-0.201, 0.093)	0.97
Start of incubation	0.037	(-0.026, 0.1)	0.64
Day of incubation	-0.09	(-0.167, -0.013)	0.01
Sex (male) ^a	-0.114	(-0.512, 0.284)	0.99
Sex \times Day of incubation	0.02	(-0.063, 0.103)	1
Start of incubation \times Day of incubation	-0.003	(-0.07, 0.064)	1
Random effects	Variance		
Nest (intercept)	0.305		
z-Transformed (day of incubation)	0.139		
Residual	1.815		

$N = 385$ exchange gaps from 44 nests. Fixed effects, except sex, were mean centered (culmen and body mass were centered within each sex). Results of the model without confounding variables are presented in Supplementary Table S5.

^aRelative to female.

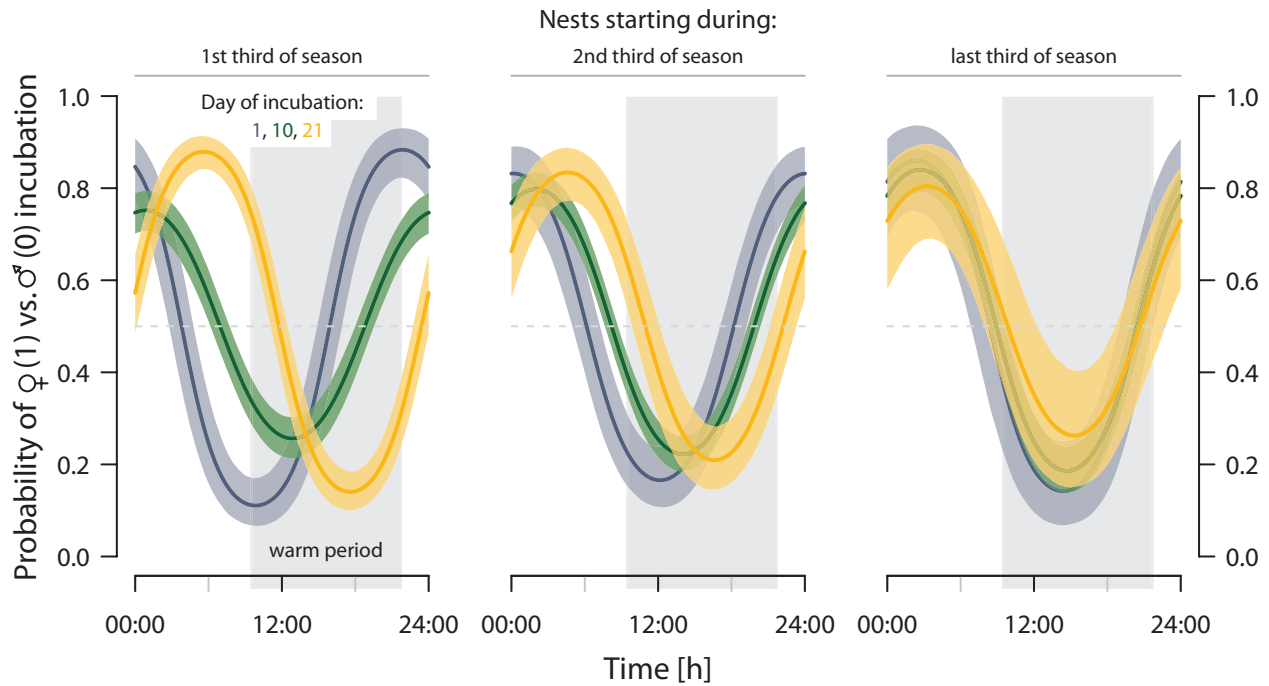


Figure 6 Shift in the probability of female (vs. male) incubation during specific time of a day over the 21-day incubation period and with respect to the start of incubation within the season. Color lines represent the mean predicted probability of 5000 GLMMs for the 1st (dark blue), the 10th (green), and the 21st (yellow) day of incubation; color shadings represent the nonparametric CIs that contain 95% of the 5000 fits. Left panel: predictions from 6 June (first nest started on 1 June); middle panel: 13 June; right panel: 19 June. The distribution of the nests across the season is in [Supplementary Figure S7](#). The horizontal dashed line indicates an equal share of incubation, and the gray shaded rectangle represents the time when the tundra temperatures were on average above overall median tundra temperature, that is, the warmer period of the Arctic day. Nest-specific incubation patterns for all 48 nests are in [Supplementary Actograms](#).

Table 6 Summary of 5000 model (binomial GLMM) estimates of the probability that the female (vs. male) incubates in relation to time of a day, incubation period, and start of incubation within the season

Fixed effects	Estimate	95% CI	Number of iterations ($P < 0.05$)	P
(Intercept)	0.059	(−0.021, 0.14)	318	0.94
cos(time)	0.915	(0.757, 1.079)	4998	0.0004
sin(time)	0.755	(0.61, 0.906)	5000	0
Day of incubation	0.007	(−0.01, 0.024)	101	0.98
Start of incubation	0.006	(−0.006, 0.018)	133	0.97
Start of incubation × Day of incubation	0	(−0.002, 0.003)	22	1
cos(time) × Day of incubation	−0.066	(−0.098, −0.034)	4494	0.10
cos(time) × Start of incubation	0.02	(−0.003, 0.044)	0	1
cos(time) × Day of incubation × Start of incubation	0.003	(−0.002, 0.008)	284	0.94
sin(time) × Day of incubation	0.109	(0.079, 0.139)	5000	0
sin(time) × Start of incubation	0.026	(0.006, 0.046)	0	1
sin(time) × Day of incubation × Start of incubation	−0.012	(−0.017, −0.007)	4928	0.0144
Random effects	Variance	95% CI		
Nest (intercept)	0	(0, 0)		
cos(time)	4.67	(3.6, 6.0)		
sin(time)	2.37	(1.84, 3.04)		

Median (range) $N = 1722$ (1680–1768) incubation data points from 48 nests. Time of a day (in radians) was decomposed into sin and cos; the remaining fixed effects were mean centered. Estimates are means, and their 95% CIs (nonparametric) are 0.025 and 0.975 quintiles, of the fixed effect estimates of 5000 GLMMs. Variances are mean values, and 95% CIs are 0.025 and 0.975 quintiles, of the random effects from 5000 GLMMs. The median (range) partial autocorrelation coefficient of GLMMs was 0.038 (0.001–0.074) in lag 1 and −0.264 (−0.311 to −0.214) in lag 2.

The timing of incubation, however, shifted over the breeding season and as incubation progressed (Figure 6 and Table 6). In early nests, female incubation shifted from evening–night to night–morning over the incubation period (Figure 6, left panel: 1st third of season). This shift (of ca. 7.5 h) weakened

over the season (Figure 6, middle panel: 2nd third of season) and became absent in late nests (Figure 6, right panel: last third of season). Note that we had fewer nests starting in the second half of the season and running for more than 10 days (Supplementary Figure S7).

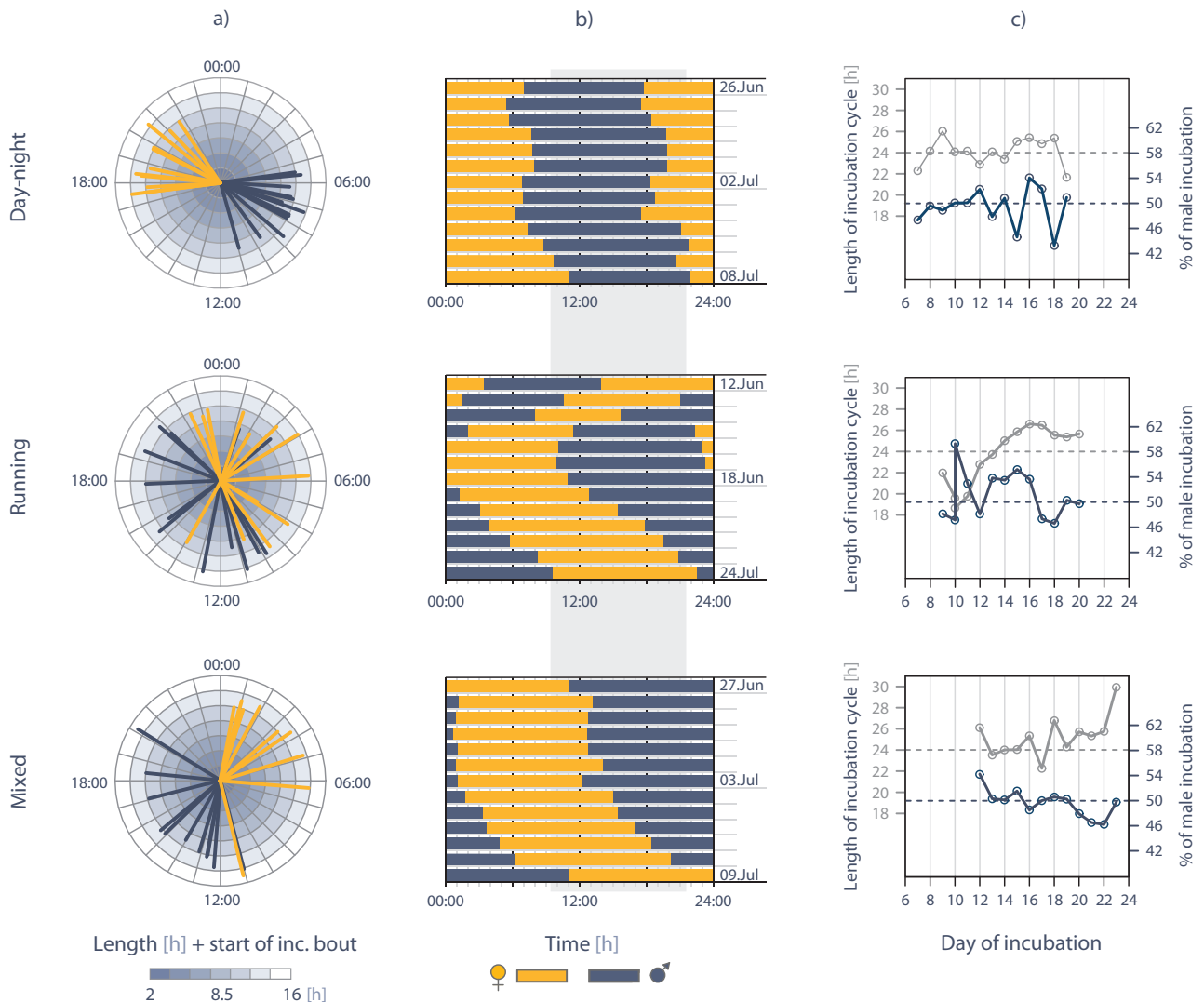


Figure 7

Examples illustrating the variation in the division of amount and timing of incubation in semipalmated sandpiper pairs. Each row represents 1 specific nest, illustrating a day–night pattern, a running pattern, and a mixed pattern (see text for details). (a) Division of incubation within a day (yellow lines = female, dark blue lines = male; the position of each line marks the start of an incubation bout, the length of the line reflects incubation bout length). (b) Visualization of incubation bouts of females and males across the incubation period (gray shading = approximate warmer period of the day, i.e., the time when the tundra temperatures were on average above median tundra temperature). (c) Changes in the length of the incubation cycle (i.e., the sum of the female and subsequent male bout length; solid gray line, left y axis) and male share of incubation (i.e., the percentage of male incubation within each cycle; solid dark blue line, right y axis) across the incubation period. The dashed lines indicate a 24-h cycle (gray, left y axis) and equal share of incubation (dark blue, right y axis). For illustration, the early or late incubation period is excluded, such that all 3 nests show the same part of the incubation period.

In short, these results show incubation patterns that are potentially specific to different parts of the breeding season.

Timing of incubation: different incubation patterns

The observed variation in incubation patterns, within season or between nests (random slopes of $\sin[\text{time}]$ and $\cos[\text{time}]$ accounted for all variance; Table 6), has different consequences for female–male division of incubation.

At one extreme were nests where the length of the incubation cycle (female + male incubation bout) roughly followed a 24-h period (Figure 7, day–night). These nests showed a distinct division of female and male incubation within a day throughout

most of the incubation period; even if parents divided the amount of incubation roughly equally (in the example in Figure 7, the male incubated 49.5% of the time), one parent incubated during the night (i.e., the colder part of the 24-h day) and the other during the day (i.e., the warmer part of the Arctic day; in the example in Figure 7, 81% of the male incubation occurred during this time).

At the other extreme were nests where the length of the incubation cycle substantially deviated from a 24-h period (Figure 7, “running”). As a result, the time of day when parents exchanged became progressively earlier (usually during the 1st half of incubation) or later (usually during the 2nd half of incubation) as incubation advanced (Figure 7b). This allowed both parents to experience similar incubation/off-nest conditions but during different days

within the incubation period. Unlike the day–night extreme, both pair members incubated during the warmer part of the day; in the example depicted in [Figure 7](#), the total male share of incubation was 51%, and 49% of his incubation fell in the warmer period of the Arctic day.

In between these extremes were nests that ran moderately over the incubation period, so that the general day–night (cold–warm) division between partners remained, or nests where the periodicity was close to 24h during part of the incubation, but larger or smaller than 24h during another part (e.g., [Figure 7](#), “mixed”; nest-specific incubation patterns for all 48 nests are depicted in [Supplementary Actograms](#)).

DISCUSSION

Using a continuous monitoring system, we quantitatively described incubation patterns in a population of semipalmated sandpipers breeding in the high Arctic. The incubation patterns and hence sex-specific costs varied considerably between pairs. Our results show that the amount of incubation (bout length) generally increased over the incubation period, causing a shift in the daily timing of incubation; the degree of this shift seemed dependent on the time within the season. We also found that incubation bout lengths were positively correlated between pair members. The exchange gaps became shorter or disappeared over the incubation period, suggesting that pair members became better synchronized. The quality of incubation varied little over the course of incubation and was similar for females and males. Females incubated on average longer than males; thus, in the absence of other data, one would conclude that in this species, females invested more in incubation than males. However, our results further show that females incubated more often during the colder part of the day (night) when foraging efficiency is expected to be lower and predation pressure may be different than during the warmer part of the day (day). This suggests that the female-biased amount of incubation might be offset by a more favorable timing of incubation. We discuss our findings in relation to sex-specific costs of care and resolution of the conflict between the parents.

Possible explanations for sex differences in incubation

Why did female semipalmated sandpipers incubate longer and more constantly than males? Early in incubation, females might incubate longer than males because males might spend more time defending their territories. However, this interpretation is unlikely because male incubation bouts were consistently shorter across the entire incubation period ([Figure 2](#)). Alternatively, females might be able to sit longer and more constantly because they are larger and can carry more resources than males and therefore could afford the costs of incubating longer (i.e., females might experience the same relative costs of incubation as males). However, females seem to have higher energy expenditure during incubation than males ([Ashkenazie and Safriel 1979b](#)). Also, size dimorphism appears an unlikely explanation because body size and mass did not explain much of the variation in the length of incubation bouts or in incubation constancy among females or males ([Tables 2 and 3](#)). The longer incubation bouts and higher incubation constancy of females might be directly related to the sex difference in timing of incubation for the following reasons.

First, the bird incubating during the colder part of the Arctic day (most often the female) may be forced to sit tighter on the eggs

to prevent their cooling or to minimize the detectability of the nest if predators are more abundant or more active, both leading to higher incubation constancy. Indeed, including time of day in the constancy model reduced the sex effect ([Supplementary Table S6](#)). However, predatory pressure is an unlikely explanation for this effect, at least in our study site, because predation events occurred predominantly during the day ([Supplementary Figure S2](#)).

Second, females may incubate longer because during incubation, they are less energy constrained. The availability of arthropods, the main shorebird prey, strongly correlates with ambient temperatures ([Corbet 1966](#); [Danks and Oliver 1972](#); [Schekkerman et al. 2003](#); [Tulp and Schekkerman 2008](#)), making foraging easier during the warmer part of the Arctic day. Furthermore, because diel fluctuations in wind speed are minimal ([Supplementary Figure S1](#)), being off nest during the warmer “day” will be energetically less demanding than being off nest during the colder “night.” These demands might be extreme because energy expenditure in high-Arctic breeding shorebirds often reaches ceilings of sustainable energy turnover rates ([Piersma et al. 2003](#)). Thus, foraging during the colder period will reduce the net energy intake rate of the feeding bird as prey availability is lower and the need for thermoregulation is higher. Hence, incubating during the cold part of the day and foraging during warm periods seem advantageous. Yet, it is unclear why females are more likely to capitalize on this advantage.

An unanswered question is whether the sex difference in the amount of incubation is related to the level of brood care. Females of this species are more likely to desert the brood earlier than the males ([Ashkenazie and Safriel 1979a](#); [Hicklin and Gratto-Trevor 2010](#)). Thus, the variation in the timing of desertion may be linked to the investment during incubation, that is, females that dedicate more to incubation may tend to desert the brood earlier (e.g., because they have depleted their resources) or later (e.g., because they may be high-quality females that generally can invest more in the brood).

Variation in incubation patterns: current and previous findings

There was relatively little between-nest variation in the amount and quality of incubation ([Tables 1–3](#)), but pairs varied considerably in their timing of incubation. This resulted in unexpected variation in incubation patterns ([Figure 7](#)). Perhaps the most important difference between these patterns, in terms of costs of incubation, is that only in the “running” pattern, both parents could forage during the warmer parts of the day or be exposed to similar risk of predation, at least on some days.

The running pattern, however, is not the only possible scenario that would lead to a relatively equal division of incubation during the colder part of the day. Theoretically, parents could have shorter incubation bouts (e.g., of a few hours) allowing both of them to forage when it is more efficient. However, this would lead to more frequent exchanges and might be counter selected if it increases predation risk ([Smith et al. 2012](#)). Alternatively, parents could keep regular 24-h incubation cycles but with changeovers that would allow each partner to experience part of the colder and part of the warmer period of each day.

It is difficult to assess whether the observed variation in incubation patterns is also present in other species because continuous data throughout the incubation period are scarce. Moreover, the literature is dominated by studies on species with incubation bouts lasting >24h (albatrosses, e.g., [Weimerskirch et al. 1986](#);

Weimerskirch 1995; penguins, e.g., Davis 1982; Weimerskirch et al. 1992; Gauthier-Clerc et al. 2001; and petrels, e.g., Chaurand and Weimerskirch 1994), where timing of incubation within a day does not play a role. In the remaining species, the available (noncontinuous) data suggest that a day–night incubation pattern is typical for day–night environments (reviewed by Skutch 1957). Continuous laboratory observations confirmed female-biased night incubation in masked doves, *Oena capensis* (Hoffmann 1969), and in ring doves, *Streptopelia risoria* (Wallman et al. 1979; Ball and Silver 1983); the same may occur in other Columbiformes (Hoffmann 1969). In contrast, continuous incubation records of (radioactively tagged) black-legged kittiwakes, *Rissa tridactyla*, revealed varying incubation patterns, including “day–night,” and “running” (Coulson and Wooller 1984). In shorebirds (based on the recordings of few nests or days), both female-biased (e.g., Jehl 1973; Ward 1990) and male-biased (e.g., Byrkjedal 1985; Sullivan Blanken and Nol 1998; Currie et al. 2001) night incubation have been reported.

Possible causes of variation in incubation patterns

The causes, consequences, and adaptive significance of the observed incubation patterns (Figure 7) await exploration.

Our results suggest that these patterns are to some extent season specific (Figure 6), that is, nests that started in the first half of the season tended to show a running pattern, whereas late nests more often showed a day–night pattern. To confirm this trend, a larger sample size is required, particularly for late-starting nests (Supplementary Figure S7). One possible explanation for the within-seasonal variation is that a different subset of birds is incubating later in the season (e.g., individuals that are of lower quality or that are reneesting after a predation event). Alternatively, the within-seasonal variation may be influenced by the change in weather conditions from early to late breeding season.

Whether additional or different mechanisms drive the described patterns remains unclear. Here, we discuss how the patterns can arise through variation in response to external environmental cues, variation in individuals' internal clock, or variation in the settlement of parental conflict among pair members over the amount and timing of incubation, or through a combination of these.

External environmental cues

The typical day–night pattern (24-h cycle) may arise even under continuous light, when individuals use other external cues (e.g., light intensity or quality, temperature) as zeitgeber (Steiger et al. 2013). A running pattern may then arise if individuals are less sensitive to such subtle cues. Early experimental evidence suggests that incubation patterns may indeed be influenced by photoperiod: in carrier pigeons, domesticated *Columba livia*, pairs showed running or variable incubation patterns when exposed to continuous light (no fluctuations in light intensity), whereas pairs kept a day–night incubation pattern (with male incubation during the day, as under natural conditions) when exposed to a 12:12 h light:dark cycle (Schmidt-Koenig 1958). The day–night pattern remained when parents experienced different darkness levels at night. However, the time of the exchanges varied more than during the strict day–night light regime (Schmidt-Koenig 1958). Thus, the observed variation in incubation patterns could reflect individuals that differ in their responsiveness to more subtle zeitgebers in the Arctic.

Internal clock

The observed variation in incubation rhythms (Figure 7) might also be linked to individual variation in the internal clock. Disruption or shifts in daily rhythms (e.g., due to changing light regimes) may lead to severe costs (Aschoff et al. 1971; Foster and Wulff 2005; LeGates et al. 2012). Therefore, if a specific zeitgeber (e.g., day–night, tide) drives the daily behavioral rhythm of individuals during most of their life, it might be advantageous for individuals to keep their rhythm also in an environment where the specific zeitgeber is absent. Because semipalmated sandpipers are predominantly tidal (Hicklin and Gratto-Trevor 2010), a running pattern might reflect the tide-bound internal clock of individuals (including the time when birds become hungry and get the urge to forage). Short female–male cycles (due to short incubation bouts) during early incubation might reflect the approximately 12.5-h cycle of low and high tide, whereas the long incubation cycle during late incubation might reflect 2 low–high tide cycles (25 h). Keeping the shifting tidal pattern while incubating in the high Arctic, where food availability fluctuates with time of day, may be beneficial if it allows both parents to forage during the times of the day when food is most abundant. Hence, the observed variation in timing patterns could reflect individuals that differ in life history (i.e., outside the breeding season live in environments driven by different zeitgebers).

Settlement of parental conflict

The observed variation in incubation patterns can also reflect between-pair differences in behavioral rules that determine the length of incubation bouts or in negotiations among pair members. During continuous biparental incubation, only one parent at a time can be off nest (e.g., to feed), so one or both parents will need to adjust their individual schedules (e.g., feeding, resting) and possibly compromise their internal clock (discussed above). In migratory birds such as semipalmated sandpipers, pair members can be running on different rhythms (e.g., depending on migratory routes and timing of migration). We do not know whether parents use behavioral rules, such that one parent forces its internal rhythm on the other, or whether parents negotiate and synchronize toward a new rhythm, which then leads to a particular incubation pattern. However, our observations support some scenarios more than others, and we discuss 3 possible behavioral rules and a negotiation scenario.

First, the incubation patterns may arise from the rule “when the foraging partner comes back to the nest, the incubating bird goes” (come-and-go rule); the observed variation in the patterns may then reflect differences in the decision of the returning birds about when to return to the nest. In support of this rule, we found striking synchronization between partners; exchanges between incubating birds were usually instantaneous (81% of exchange gaps were shorter than 1 min), despite large within-nest variation in incubation bout length (nearly 2 h). However, the come-and-go rule fails to explain why synchronization increased over time (the occurrence and length of exchange gaps decreased over the incubation period; Figure 5). Also, our observations suggest that both birds may determine the bout length because 1) the off-nest bird is often foraging or resting up to several kilometers away (Ashkenazie and Safriel 1979a; our unpublished data) and has to return to the nest before the changeover (which is mostly immediate, see above), 2) the sitting bird does not always leave when the partner returns (and may even chase away the incoming bird; Ashkenazie and Safriel 1979a), and 3) the sitting bird sometimes leaves the nest before the partner

returns (although rare, exchange gaps up to 6.7 h occur). Thus, the simple come-and-go rule seems unlikely.

Second, the patterns may arise from the rule “when the foraging partner comes back to the nest, the incubating bird decides when to leave”; then the variation in the patterns may reflect individual differences in the decision to leave the nest when the partner returns. Although plausible, it remains unclear what factors influence this decision and how the off-nest bird knows when to return.

Third, the incubation patterns may arise due to energy constraints; variation in the patterns may then reflect variation in the birds’ condition. Under this “energy rule,” the off-nest bird may return whenever it has replenished its energy reserves, and the incubating bird may leave whenever its energy reserves have dropped to a certain threshold. This scenario has been supported by experimental data suggesting that a parent prolongs its incubation bout when the energetic demands during incubation are lower (Cresswell et al. 2003). But a similar experiment and reanalyses of Cresswell et al.’s (2003) data revealed or depicted no such relationship (Bulla M, Cresswell W, Valcu M, Rutten AL, Kempenaers B, unpublished data). Hence, although there is no doubt that energetic constraints play some role in determining incubation patterns in biparental incubators (Chaurand and Weimerskirch 1994), these constraints do not seem to fully explain the patterns.

Finally, the patterns could arise due to a form of negotiation between the pair members; variation in the observed patterns would then reflect different outcomes of the negotiations. Our results support the predictions of 2 game-theory models of biparental negotiations. In the first model, parents match their amount of care when they have partial information about the brood need; investment of one parent serves as a signal of the brood need to the other parent (Johnstone and Hinde 2006). As predicted, we found that bout lengths of partners were positively correlated. However, these models seem to apply more to offspring feeding; whether incubating parents have only partial information about the need of their eggs seems unlikely. Also, the model does not explicitly consider repeated bouts of investment.

The second model explicitly considers repeated bouts of investment and predicts an increase in the amount of care for both parents with consecutive bouts of investment (Lessells and McNamara 2011). We observed exactly that, as incubation progressed, bouts increased in length. The model further suggests that the amount of parental care will depend on the parent’s quality; the higher quality parent will deliver more care. The observed variation in incubation patterns between pairs may, thus, reflect pairs with parents of different quality or in different condition. This is possible, but at least individual body mass (measured once) and size (proxy for individual condition and quality; e.g., Peig and Green 2009) explained little of the variation in the length of incubation bouts. In addition, although the Lessells–McNamara model incorporates quality of care, it does not consider timing of care. It assumes that the cost function for a parent is the same in all bouts of investment. But our results indicate that the costs of individual investment might vary over time, for example, by changes in the timing of incubation relative to optimal foraging opportunities.

In sum, variation in the incubation patterns is unlikely a result of birds differing solely in their decision to return to the nest or in their condition. Although differences in the decision of incubating birds to leave the nest or negotiations seem more likely to explain the various incubation patterns, experimental evidence is missing. Our findings suggest that current game-theory models of biparental

care are not yet directly applicable to biparental incubation because they do not explicitly consider amount, quality, and timing of care. Incorporating variation in the temporal cost of investment in these models might help understand the within-population variation in incubation patterns we described.

CONCLUSIONS

The significance of our findings is 3-fold. First, our study provides a quantitative framework for future work on biparental care patterns. The framework allows quantification of both general trends and within-population variation (suggesting possibly different incubation strategies). Second, our results reveal variation in biparental incubation patterns, with possibly different consequences for sex-specific costs of care. This highlights the need to investigate not only the central tendency but also the variation in costs of parental care over time. Whether similar variation is also present in other species or systems (e.g., breeding under less extreme environmental conditions) remains unknown. Finally, although our study is limited to observations of incubation, that is, misses other forms of parental care (e.g., brood care), it demonstrates that focusing only on one aspect of care or on a short snapshot of care in time may bias our perception of costs of parental care and therefore may be insufficient for understanding parental conflict and its outcomes.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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ELECTRONIC SUPPLEMENT - Pictures



Picture S1. Glass passive-integrated RFID tag embedded in a flag. The flag was put on the tarsus and the part that sticks out was closed using an AA battery powered soldering device (Weller BP645).



Picture S2. Incubation monitoring system. (a) The red RFID-coil detected the bird's identity. The coil was connected to the RFID reader (plastic box), placed either next to the nest in the open (b) or hidden in the vegetation (c). Data were processed by a custom board (Calima Engineering, <http://www.calima.de>) equipped with an EFM32-Gecko microcontroller (Energy-Micro, <http://www.energymicro.com/>) and stored on a 2 GB SanDisk Standard SD card. Electricity to run the system came from 6 or 12 standard AA batteries. (d) Tiny-Tag temperature probe, positioned between the eggs. This probe registered temperature in the nest (in 2 min intervals), and therefore allowed to differentiate between incubation and non-incubation. Alternatively, we used an MSR fake-egg temperature probe, connected to a data-logger (blue device in b, c). This device registered both incubation temperature and tundra temperature (every 5 s).



Picture S3. Fake-egg with inserted MSR temperature-probe and with attachment pin to secure it in the nest. For higher conductance the hole in the egg, which contains the probe, is filled with heat-sink grease. The probe is secured with silicon.

ELECTRONIC SUPPLEMENT - Figures

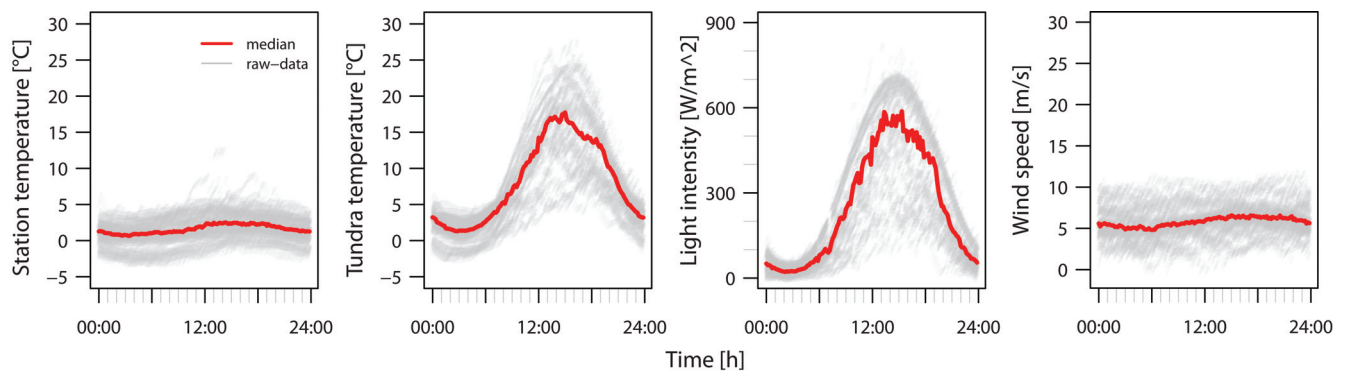


Figure S1: Daily fluctuations in (a) meteorological-station temperature (measured 2 m above the ground, NOAA Earth System Research Laboratory (<http://www.esrl.noaa.gov/>)), (b) average tundra temperature (our measurements; details are in Methods, section *Tundra temperatures*), (c) light intensity (NOAA), and (d) wind speed (10 m above the ground; NOAA; wind > 32 m/s is hurricane) between 1 June and 16 July 2011 in Barrow, Alaska.

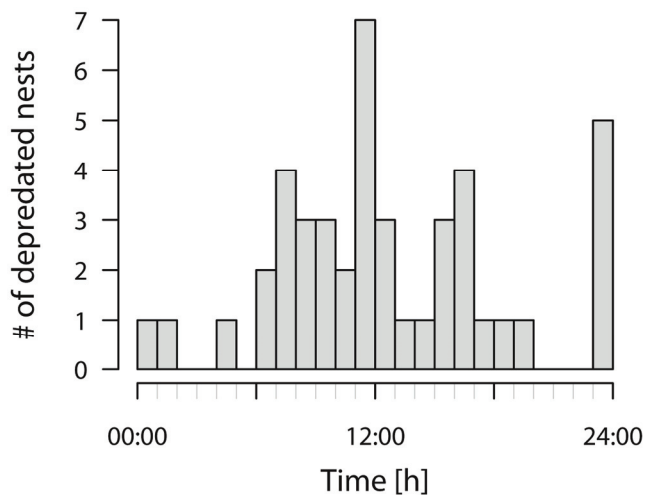


Figure S2. Daily fluctuations in predation events on semipalmated sandpiper nests. The date and time of predation corresponds to an unexpected and sudden end in incubation based on the visualised raw data from the ‘incubation monitoring system’.

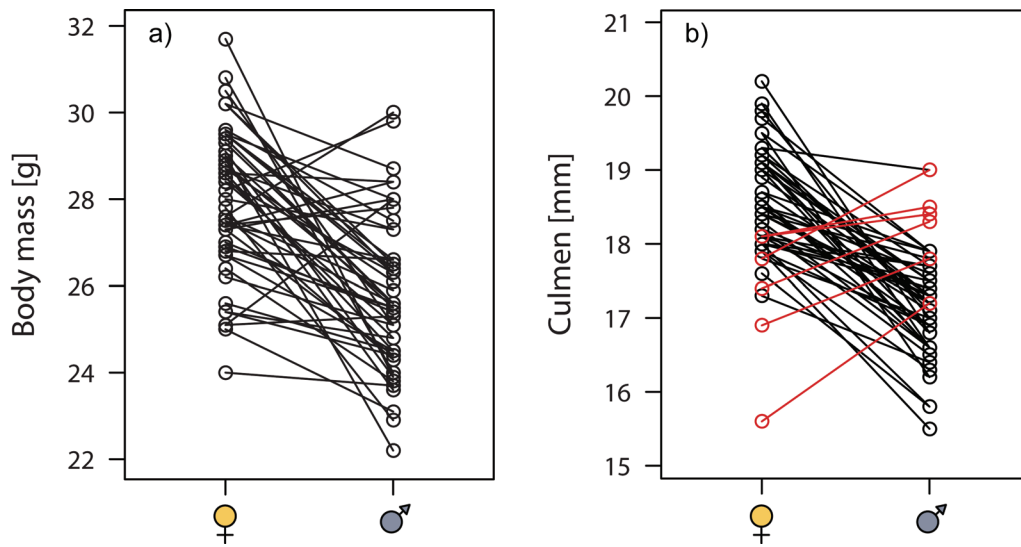


Figure S3. Variation in (a) body-mass and (b) culmen length of female and male semipalmated sandpipers. Lines connect individuals from the same nest. Red lines represent pairs with reversed dimorphism in culmen. Females were 2.2 (95% CI: 1.6 - 2.8) g heavier than males (Paired t test: $t_{50} = 7$, $P < 0.0001$), and had 1.3 (95% CI: 0.9 - 1.6) mm longer culmen (Paired t test: $t_{49} = 8$, $P < 0.0001$).

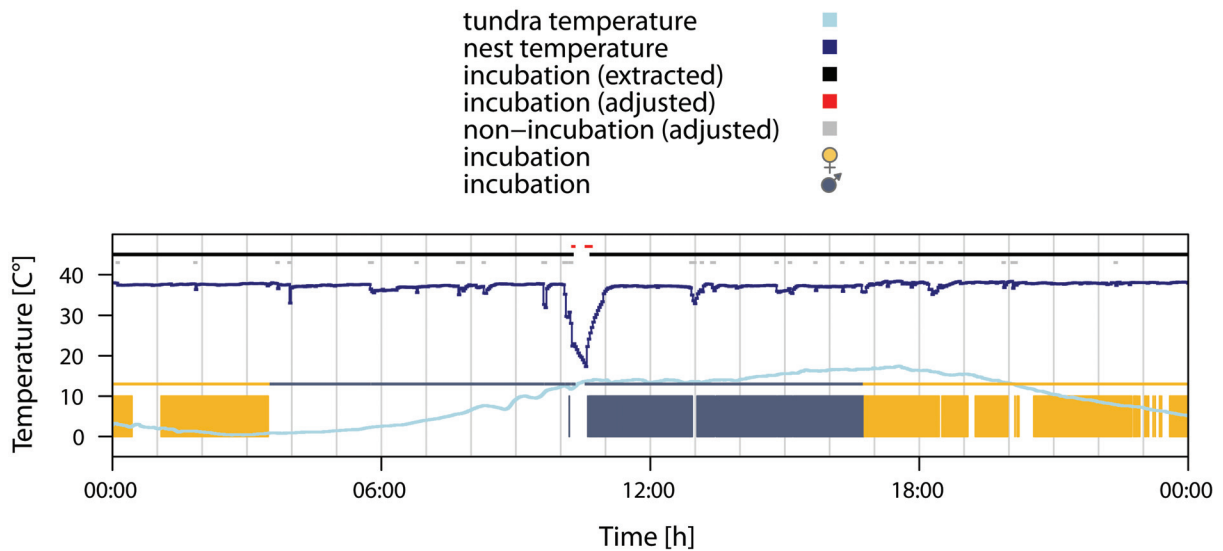


Figure S4. Example illustrating the extraction of incubation/non-incubation data.

To define periods of incubation/non-incubation from the nest temperatures, we used the following automated procedure. We assigned a time as ‘incubation’ (thick black line) whenever the nest temperature was above a threshold temperature, set as the running median nest temperature (with running time-window of 24h) minus 3°C (whenever the running median nest temperature was equal or above 17°C) or plus 3°C (whenever the running median nest temperature was below 17°C). Even if these conditions were not fulfilled, we assigned ‘incubation’ whenever the nest temperature was 12.5°C above the tundra temperature. This method missed the start of incubation after an incubation break (usually below the threshold) and the end of incubation (usually above the threshold). To correct for this, we calculated a difference in nest temperature between two consecutive readings and created a running mean of these differences with a time window of 2 minutes. If the ‘running mean of the difference’ was larger than a threshold (0.02°C) we considered a rise in nest temperature as incubation (red dots) and a drop in nest temperature as non-incubation (grey dots). This adjusting procedure was not applied if the nest temperature fulfilled all the following conditions: being (a) below 17°C, (b) below the running median nest temperature plus 3°C, and (c) 3°C or less above the tundra temperature. Threshold values are based on trial and error, visual assessment of the plotted data, and behaviour of birds as observed in the video recordings.

The temperature-based incubation data were overlaid with the RFID data (grey-blue and yellow vertical lines), which allowed us to assign each incubation bout to a parent. This method allowed also assignment of incubation/non-incubation to both partners even if only one bird was tagged (grey-blue line in the graph between ca. 03:30 and capture of the male at 10:30) or when the tag was not detected despite a bird's presence. The grey-blue and yellow lines represent the final assignment of incubation/non-incubation to each sex (note that some short non-incubation periods may not be visible in the graph, but are present in the data). At some nests the temperature logger malfunctioned, partially ($N = 4$) or completely ($N = 1$). If the RFID readings were continuous, incubation bouts were assigned based on the RFID data only. All automatic incubation/non-incubation assignments at all nests were checked visually and cases of obvious mis-assignment were corrected manually.

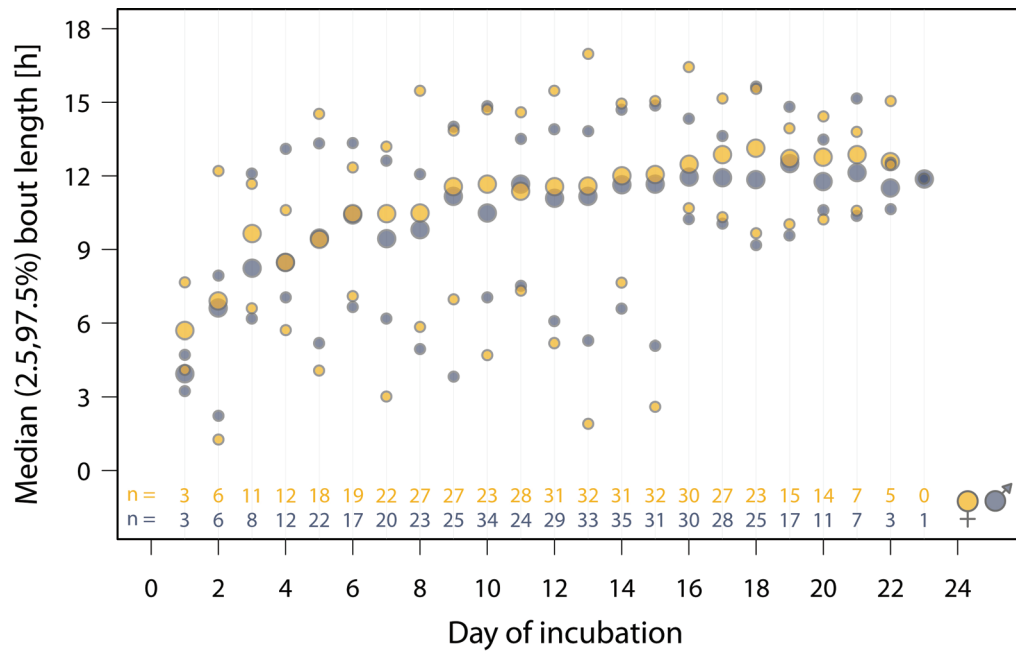


Figure S5. Increase in the length of incubation bouts across the incubation period. Large dots represent median, small dots the 2.5 and 97.5 percentile ($N = 887$ incubation bouts from 48 nests).

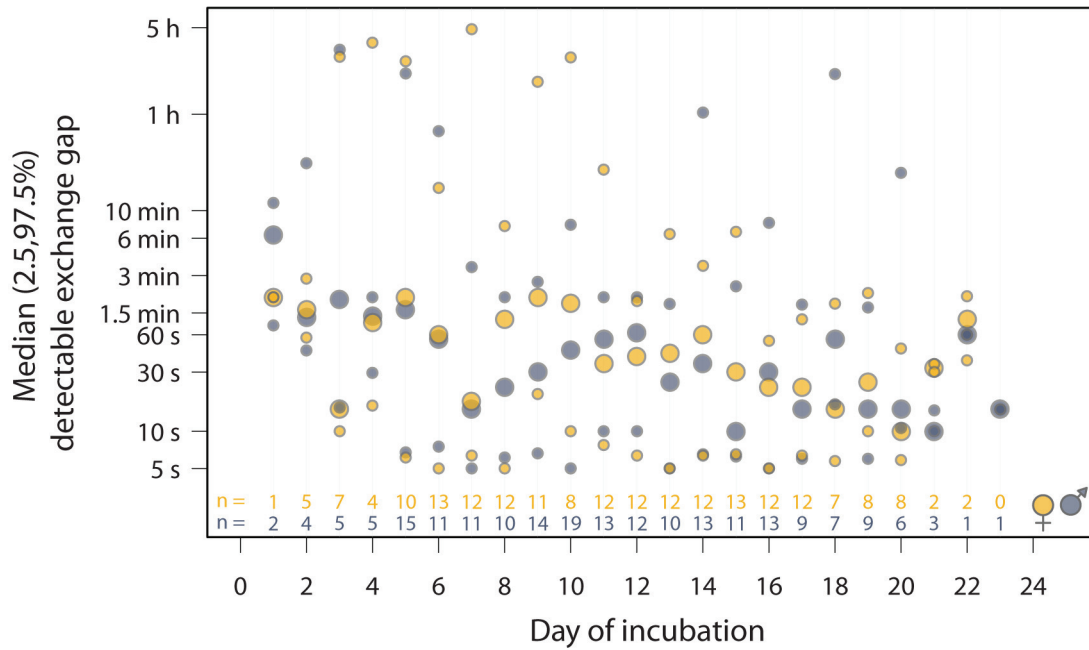


Figure S6. Decrease in the length of detectable exchange gaps across the incubation period (yellow = female is exchanging parent; grey-blue = male is exchanging parent). Large dots represent median, small dots the 2.5 and 97.5 percentile ($N = 399$ detectable exchange gaps from 44 nests). Y-axis is log-scaled.

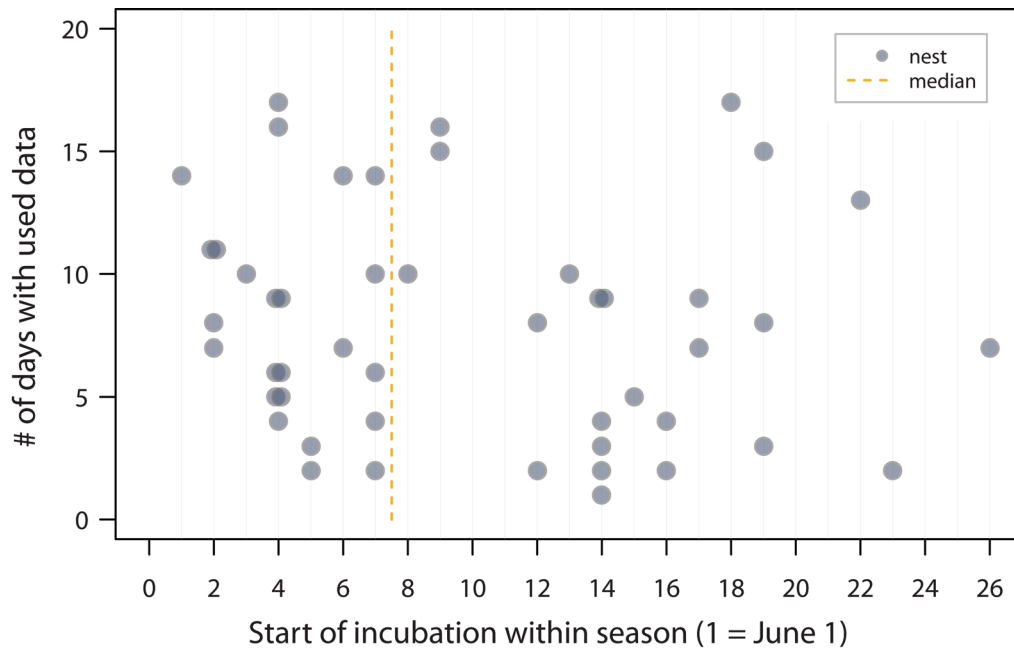


Figure S7. Distribution of the nests used in the models according to start date of incubation and the number of days for which data were included.

ELECTRONIC SUPPLEMENT - Tables

Table S1

Model (GLMM) estimates of median incubation temperature per incubation bout (z-transformed) in relation to sex and incubation period.

Fixed effects	<i>Estimate</i>	<i>95% CI</i>	<i>P</i>
(Intercept)	0.191	(0.103, 0.279)	< 0.0001
Day of incubation	0.008	(-0.011, 0.026)	0.70
Sex (male) [°]	0.039	(-0.085, 0.162)	0.86
Sex*Day of incubation	-0.001	(-0.026, 0.024)	1
Random effects	<i>Variance</i>		
Nest (intercept)	0		
z-trans (Day of incubation)	0.0004		
Residual	0.1966		

N = 307 median incubation temperatures per incubation bout from 14 nests. Fixed effects, except sex, were mean-centred. Raw incubation-temperature values were z-transformed within each nest.

[°]relative to female

Table S2

Model (GLMM) estimates of incubation constancy per incubation bout (arcsine-transformed) in relation to sex and incubation period.

Fixed effects	<i>Estimate</i>	<i>95% CI</i>	<i>P</i>
(Intercept)	1.343	(1.332, 1.355)	< 0.0001
Day of incubation	0	(-0.004, 0.003)	1
Sex (male) [°]	-0.023	(-0.037, -0.009)	0.0002
Sex*Day of incubation	0.003	(0, 0.005)	0.098

Random effects	<i>Variance</i>
Nest (intercept)	0
z-trans (Day of incubation)	0.0015
Residual	0.0058

N = 762 incubation constancies per incubation bout from 47 nests. Day of incubation (fixed effect) was mean-centred.

[°]relative to female

Table S3

Model (GLMM) estimates of incubation bout length (in minutes) in relation to sex, incubation period and length of previous.

Fixed effects	<i>Estimate</i>	<i>95% CI</i>	<i>P</i>
(Intercept)	688.9	(662.9, 714.9)	<0.0001
Previous-bout length	0.4	(0.3, 0.5)	<0.0001
Day of incubation	8	(3.6, 12.5)	<0.0001
Sex (male) [°]	-47.5	(-70.4, -24.5)	<0.0001
Sex*Previous-bout	-0.1	(-0.3, 0)	0.20
Sex*Day of incubation	2.1	(-3.2, 7.5)	0.83
Random effects			
	<i>Variance</i>		
Nest (intercept)	2 142		
z-trans (Day of incubation)	140		
Residual	14 000		

N = 729 incubation bouts from 39 nests. Fixed effects, except sex, were mean-centered.

[°]relative to female

Table S4

Model (binomial GLMM) estimates of the probability of a detectable exchange gap in relation to sex and incubation period.

Fixed effects	<i>Estimate</i>	<i>95% CI</i>	<i>P</i>
(Intercept)	-0.357	(-1.132, 0.417)	0.65
Day of incubation	-0.167	(-0.277, -0.058)	0.0006
Sex (male) [°]	0.03	(-0.422, 0.481)	1
Sex*Day of incubation	-0.04	(-0.134, 0.054)	0.71

Random effects	<i>Variance</i>
Nest (intercept)	3.21
z-trans (Day of incubation)	0.67

N = 762 exchange gaps from 47 nests. Day of incubation (fixed effect) was mean-centred.

[°]relative to female

Table S5

Model (GLMM) estimates of detectable exchange gap duration (in seconds, log-transformed) in relation to sex and incubation period.

Fixed effects	<i>Estimate</i>	<i>95% CI</i>	<i>P</i>
(Intercept)	3.953	(3.56, 4.345)	<0.0001
Day of incubation	-0.12	(-0.185, -0.055)	<0.0001
Sex (male) [°]	-0.11	(-0.456, 0.237)	0.87
Sex*Day of incubation	0.017	(-0.051, 0.085)	0.94

Random effects	<i>Variance</i>
Nest (intercept)	0.46
z-trans (Day of incubation)	0.135
Residual	1.806

N = 385 exchange gaps from 44 nests. Day of incubation (fixed effect) was mean-centred.

[°]relative to female

Table S6

Model (GLMM) estimates of incubation constancy per incubation bout (arcsine-transformed) in relation to sex and incubation period with disturbance, type of temperature probe, presence of radio-tag, length of incubation bout (h), time of a day – sin(rad), cos(rad) –, body mass and culmen length as confounding variables.

Fixed effects	<i>Estimate</i>	<i>95% CI</i>	<i>P</i>
(Intercept)	1.339	(1.325, 1.353)	<0.0001
Disturbance	-0.026	(-0.046, -0.006)	0.0029
Temperature probe type	0.006	(-0.024, 0.035)	1
Radio-tag	-0.006	(-0.033, 0.021)	1
Culmen	-0.004	(-0.015, 0.007)	0.98
Body mass	-0.001	(-0.006, 0.005)	1
Bout length	0.005	(0.001, 0.008)	0.0035
Start of incubation	-0.001	(-0.003, 0.001)	0.52
Day of incubation	-0.002	(-0.006, 0.003)	0.99
Sin (rad)	-0.011	(-0.023, 0.001)	0.12
Cos (rad)	-0.006	(-0.018, 0.006)	0.85
Sex (male) [°]	-0.016	(-0.033, 0.001)	0.087
Sex*Day of incubation	0.002	(-0.001, 0.006)	0.49
Random effects	<i>Variance</i>		
Nest (intercept)	0		
z-trans (Day of incubation)	0.0016		
Residual	0.0055		

N = 762 incubation constancies per incubation bout from 47 nests. Fixed effects, except sex, sin and cos, were mean-centered (culmen and body mass were centered within each sex).

[°]relative to female

Chapter 2

Off-nest behaviour in a biparentally incubating shorebird varies with sex, time of day and weather

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Biparental incubation is a form of cooperation between parents, but it is not conflict-free because parents trade off incubation against other activities (e.g. self-maintenance, mating opportunities). How parents resolve such conflict and achieve cooperation remains unknown. To understand better the potential for conflict, cooperation and the constraints on incubation behaviour, investigation of the parents' behaviour, both during incubation and when they are off incubation-duty, is necessary. Using a combination of automated incubation-monitoring and radiotelemetry we simultaneously investigated the behaviours of both parents in the biparentally incubating Semipalmated Sandpiper *Calidris pusilla*, a shorebird breeding under continuous daylight in the high Arctic. Here, we describe the off-nest behaviour of 32 off-duty parents from 17 nests. Off-duty parents roamed on average 224 m from their nest, implying that direct communication with the incubating partner is unlikely. On average, off-duty parents spent only 59% of their time feeding. Off-nest distance and behaviour (like previously reported incubation behaviour) differed between the sexes, and varied with time and weather. Males roamed less far from the nest and spent less time feeding than did females. At night, parents stayed closer to the nest and tended to spend less time feeding than during the day. Further exploratory analyses revealed that the time spent feeding increased over the incubation period, and that at night, but not during the day, off-duty parents spent more time feeding under relatively windy conditions. Hence, under energetically stressful conditions, parents may be forced to feed more. Our results suggest that parents are likely to conflict over the favourable feeding times, i.e. over when to incubate (within a day or incubation period). Our study also indicates that Semipalmated Sandpiper parents do not continuously keep track of each other to optimize incubation scheduling and, hence, that the off-duty parent's decision to remain closer to the nest drives the length of incubation bouts.

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Off-nest behaviour in a biparentally incubating shorebird varies with sex, time of day and weather

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Biparental incubation is a form of cooperation between parents, but it is not conflict-free because parents trade off incubation against other activities (e.g. self-maintenance, mating opportunities). How parents resolve such conflict and achieve cooperation remains unknown. To understand better the potential for conflict, cooperation and the constraints on incubation behaviour, investigation of the parents' behaviour, both during incubation and when they are off incubation-duty, is necessary. Using a combination of automated incubation-monitoring and radiotelemetry we simultaneously investigated the behaviours of both parents in the biparentally incubating Semipalmated Sandpiper *Calidris pusilla*, a shorebird breeding under continuous daylight in the high Arctic. Here, we describe the off-nest behaviour of 32 off-duty parents from 17 nests. Off-duty parents roamed on average 224 m from their nest, implying that direct communication with the incubating partner is unlikely. On average, off-duty parents spent only 59% of their time feeding. Off-nest distance and behaviour (like previously reported incubation behaviour) differed between the sexes, and varied with time and weather. Males roamed less far from the nest and spent less time feeding than did females. At night, parents stayed closer to the nest and tended to spend less time feeding than during the day. Further exploratory analyses revealed that the time spent feeding increased over the incubation period, and that at night, but not during the day, off-duty parents spent more time feeding under relatively windy conditions. Hence, under energetically stressful conditions, parents may be forced to feed more. Our results suggest that parents are likely to conflict over the favourable feeding times, i.e. over when to incubate (within a day or incubation period). Our study also indicates that Semipalmated Sandpiper parents do not continuously keep track of each other to optimize incubation scheduling and, hence, that the off-duty parent's decision to remain closer to the nest drives the length of incubation bouts.

Keywords: biparental care, *Calidris pusilla*, fluctuating environment, foraging, high Arctic, off-nest distance, sex-specific behaviour.

Parental care is costly because parents face a trade-off between caring for their offspring and caring for themselves (Martin 1987, 1995, 2002, Clutton-Brock 1991). Although biparental care, the most common form of care in birds (Cockburn 2006), involves cooperation between parents, it is also a source of conflict, because each parent benefits from shifting care for the current brood onto its partner (Trivers 1972). How parents resolve such

conflict and achieve cooperation remains unknown. However, the need for cooperation, as well as the extent of parental conflict, is accentuated in harsh environmental conditions and is likely to vary in fluctuating environmental conditions.

In climatically harsh conditions, individuals are often outside their thermo-neutral zone (e.g. Pierσμα & van Gils 2010), increasing both the cost of parental care and the cost of self-maintenance. For example, due to low temperatures and strong winds, Arctic-breeding shorebirds spend about twice as much energy compared with birds breed-

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ing in temperate areas (Piersma *et al.* 2003). Consequently, to facilitate optimal embryonic development, birds that breed in harsh environments attend their eggs nearly continuously (e.g. Norton 1972, Grant 1982, Margalida & Bertran 2000, Al-Rashidi *et al.* 2010, Bulla *et al.* 2014). However, environmental conditions such as light, temperature, prey availability and predator activity fluctuate within a day and across the season. Thus, the costs of parental care and of self-maintenance are also likely to fluctuate (e.g. for fluctuating costs of thermoregulation see Scholander *et al.* 1950, Chappell 1980, 1981, Piersma & van Gils 2010). Hence, some periods of the day or season are likely to be more favourable for parental care or for self-maintenance than others, which potentially intensifies parental conflict.

Here, we focus on biparental incubation, the most common pattern of care for eggs in birds (Deeming 2002), and a form of care to which only one parent can contribute at any given time. To further our understanding of cooperation and conflict resolution during biparental incubation, detailed descriptions of the parents' care and off-duty behaviour, including their timing, are necessary. Such descriptions reveal how parents share their incubation duties and what their predominant off-duty behaviours are, and may suggest where the constraints lie and which behavioural mechanisms parents use to decide about their share of parental care. With the exception of seabirds (e.g. Jouventin & Weimerskirch 1990, Weimerskirch 1995, González-Solís *et al.* 2000, Weimerskirch *et al.* 2007, Pinet *et al.* 2012), detailed descriptions of incubation and off-duty behaviour are rare and limited to a few individuals (e.g. Byrkjedal 1985a,b, Cresswell & Summers 1988, Whittingham *et al.* 2000).

In this study, we used a combination of an automated incubation monitoring system and radiotelemetry to study simultaneously incubation and off-nest behaviour of both parents in the Semipalmated Sandpiper *Calidris pusilla*, a 22–32 g biparental shorebird breeding under continuous daylight in the high Arctic.

Here, we aim to describe the off-duty behaviour of Semipalmated Sandpiper parents, i.e. their behaviour when their partner is incubating. The description addresses three issues. First, we assessed how far off-duty parents roam from the nest (off-nest distance) and what behaviours they perform (off-nest behaviour). Secondly, we identified factors

influencing off-nest distance and behaviour. We previously found that incubation patterns are sex and time-of-day specific; females tend to incubate at night and have longer incubation bouts on average than do males (Bulla *et al.* 2014). Thus, we first assessed the effects of these two factors on off-nest distance and behaviour (proportion of time spent feeding). We expected that the off-nest distance and the time spent feeding differ between the cold and warm part of the day, because low temperatures increase the energetic costs of thermoregulation and decrease the availability of arthropods, the main shorebird prey in the Arctic (Corbet 1966, Danks & Oliver 1972, Schekkerman *et al.* 2003, Tulp & Schekkerman 2008). We further tested whether the results hold when controlling for potentially confounding variables. These included the day within the incubation period (as temperatures increase over the breeding season), the time since an individual left its nest (because an individual is expected to feed more immediately after departing the nest), and weather conditions (strong winds intensify the need for thermoregulation (Bakken 1990, 1991) and, hence, might influence the off-nest distance and foraging behaviour). Finally, we assessed whether off-nest distance and behaviour correlate with the length of the off-duty bout or the length of the next incubation bout. For example, more intensely feeding parents may be able to incubate for longer in their next incubation bout.

METHODS

Study area and species

We studied a population of Semipalmated Sandpipers near Barrow, Alaska (71.32°N, 156.65°W), between 1 June and 16 July 2011. The study area and species have already been described in detail elsewhere (Ashkenazie & Safriel 1979a, Bulla *et al.* 2014).

In early June, the tundra was still frozen and largely snow-covered, but minimum temperature (unlike wind speed) increased over the breeding season (Fig. 1), and large parts of the tundra became snow-free in a matter of days (our pers. obs.). This warming affects the Sandpipers' diet, which shifts from mainly aquatic insect larvae in June to adult insects in July (Holmes & Pitelka 1968). Although daylight is continuous during the entire breeding period, tundra temperatures consistently fluctuate over the 24-h period (fig. 1 in

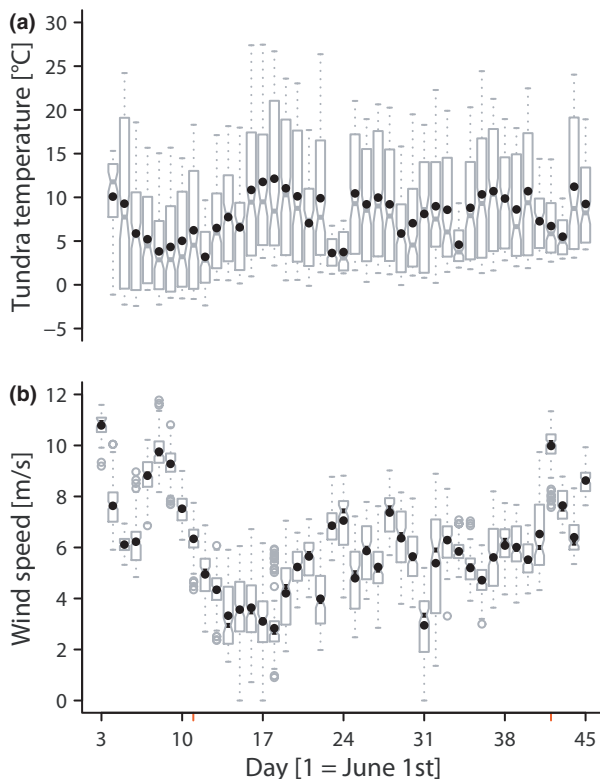


Figure 1. Changes in daily tundra temperature (a) (our measurements; detailed in Bulla *et al.* 2014) and wind speed (b) (NOAA Earth System Research Laboratory [http://www.esrl-noaa.gov/](http://www.esrl.noaa.gov/)) during the 2011 breeding season. For each day, 144 10-min average values were obtained, except for day 3 in (a) ($n = 36$), day 4 in (b) ($n = 72$) and day 45 in both ($n = 112$). Box plots give the mean (black dot), median (horizontal line inside the box), 25th and 75th percentiles (box), interquartile range or maximum/minimum value, whichever is the smaller (dashed bars), and outliers (open circles). Daily minimum temperature increased by $0.06\text{ }^{\circ}\text{C}/\text{day}$ (95% CI: $0.03\text{--}0.10\text{ }^{\circ}\text{C}/\text{day}$) (linear model controlled for temporal autocorrelation by including minimum temperature from previous day; $n = 41$). Although daily average wind speed in 2011 did not increase over the season, it increased over the actual observation period (indicated by red tick marks) by 0.06 m/s per day ($0.01\text{--}0.11\text{ m/s}$ per day; $n = 32$).

Steiger *et al.* 2013, fig. S1 in Bulla *et al.* 2014). Especially early in the season, tundra and water bodies often freeze over at 'night' (our pers. obs.).

Sampling of individuals and monitoring of incubation

Captured individuals were marked, equipped with radio-transmitters, measured and blood-sampled for molecular sexing. Full details of methods are

given in Bulla *et al.* (2014). To attach a radio-transmitter (PicoPip Ag392; Biotrack, <http://www.biotrack.co.uk/>; 1.18 g, which was 4.4% of the mean and 5.1% of the smallest bird's body mass) the feathers above the uropygial gland were trimmed, and the transmitter was glued to the skin and the short feather shafts with Loctite Super Glue. The behaviour of incubating parents was unaffected by the transmitter (Bulla *et al.* 2014). Culmen length was used as a proxy for body size (Ashkenazie & Safriel 1979b) because it correlates with other body size measures (Bulla *et al.* 2014).

The general procedures to monitor and extract incubation behaviour are described in detail elsewhere (Bulla *et al.* 2014). Based on a radio-frequency identification (RFID) system with an antenna around the nest, the length of each off-duty bout was determined as the time between a parent's departure from the nest and its subsequent arrival on the nest. An incubation bout was defined as the total time allocated to a single parent (i.e. the time between the arrival of a parent on the nest and its departure from the nest followed by incubation by its partner; Bulla *et al.* 2014).

Monitoring off-nest distance and behaviour

In 2011, we radiotagged 40 parents at 22 nests and aimed to obtain behavioural data from both parents during both the cold part (between 00:00 and 06:00 h) and warm part (between 09:00 and 20:00 h) of the day. The first observation session of a bird started as soon as possible after the radio-transmitter had been attached for 24 h. We tried to complete observation sessions within a short period (similar stage of incubation) but this was not always possible, due to pair-specific incubation patterns (e.g. day–night division of incubation among sexes; Bulla *et al.* 2014).

Each of two observers located parents using a Sika receiver (SIKARX4, Biotrack; www.biotrack.co.uk) and a customized yagi antenna (Luboš Peške; <http://peske.wz.cz/peske.htm>). The observers first identified the incubating bird and then searched for its off-duty partner. When the signal of the focal bird could not be detected or was weak, location was attempted 20–60 min later. Using this technique, the observers failed to locate the focal bird only eight times. Upon first location, the location of the observed bird was recorded by

Table 1. Behavioural categories noted during observations of off-duty parents.

Behaviour	Description
Ground feeding	Foraging on dry tundra, indicative of feeding on emerged adult insects
Water feeding	Foraging at the edge of water bodies, indicative of feeding on aquatic arthropod larvae
Resting	Staying motionless
Sleeping	Obvious signs of sleep: beak under the wing, eyes closed
Preening	Straightening and cleaning feathers, bathing
Flying	
Aerial display	Hovering and calling with typical motorboat-like sounds (Miller 1983)
Walking	Walking without foraging
Interaction	Interacting with another Semipalmated Sandpiper of same or opposite sex
Unknown	Bird out of sight

GPS (Garmin, Oregon 450, www.garmin.com). Further locations were automatically recorded whenever the observer following the bird moved at least 50 m. We calculated the straight-line distance from the nest for each recorded position using the *spDists* function from the *sp* package in R (Pebesma & Bivand 2005). The off-nest distances within each observation session were normally distributed, so means were used in the statistical analyses.

When the focal bird was located, the observer stayed about 100 m from the bird, kneeling in the tundra, and started observation after 1–3 min. There were no signs that the presence of the observer disturbed the birds' behaviour. Each individual was followed for 30 min unless it flew away earlier, and its behaviour was noted every 30 s (instantaneous sampling; Altmann 1974). Based on previous *ad hoc* observations, we defined 10 behavioural categories in advance (Table 1). For analyses, ground and water feeding were pooled. Whenever the bird was out of sight for longer than 5 min (two cases), a new observation session was started upon re-discovery of the bird.

Environmental variables

Surface tundra temperatures were recorded near each nest in vegetation similar to that surrounding the specific nest-cup (Bulla *et al.* 2014 describe the procedures in detail) and were used to confirm our definition of the warm and cold part of the day. Wind speed, measured 10 m above the

ground, was obtained from the NOAA Earth System Research Laboratory (<http://www.esrl.noaa.gov/>). In the analyses of the off-nest distance and behaviour we used the mean wind speed for each observation session.

Sample sizes

The dataset contained 89 observation sessions, conducted between 11 June and 12 July, from 17 active nests at which both parents took part in incubation (later verified by data from the incubation-monitoring system). We observed both parents from 15 nests, and a single parent from two nests (total $n = 32$ individuals). The median duration of an observation session was 30 min (range: 2.5–34 min; mean = 26 min) and the median number of observation sessions per nest was 6 (range: 1–10 sessions, mean = 5 sessions). As planned, the distribution of the observation sessions over the 24-h period was bimodal for both sexes. For analyses, we considered observation sessions that occurred between 00:00 and 06:00 h as 'night' observations (cold period; $n = 32$ sessions – 14 females and 18 males; with median tundra temperature of 1.7 °C; range: 0.2–5.4 °C) and observation sessions occurring between 09:00 and 20:00 h as 'day' observations (warm period; $n = 57$ sessions – 30 females and 27 males; with median tundra temperature of 18.4 °C; range: 5.4–27.6 °C).

Statistical analyses

Descriptive analyses

We calculated and visualized the mean off-nest distance per observation session and per individual, the proportion of time spent on each behaviour per individual, as well as the proportion of time spent feeding within observation session and individual. We used Pearson's correlation to assess whether mean off-nest distance and proportion of time spent feeding were correlated between pair members. In subsequent analyses, we only used the proportion of time spent feeding, which was the most abundant behaviour and the behaviour of interest in relation to the energy budget of the incubating birds.

Off-nest distance model

First, we assessed the effect of sex and time of day ('time': day or night) on off-nest distance

using a mixed model with ln-transformed off-nest distance as the dependent variable and with a Gaussian link-function. We included random intercepts (bird and nest identity) to account for repeated observations. Secondly, we assessed whether the estimated effects of sex and time changed when we controlled for potentially confounding variables, and we also explored the effects of these variables. We therefore included the following explanatory variables: bird size (culmen in mm; see Bulla *et al.* 2014) centred within sex (mean_{female} = 18.2 mm, mean_{male} = 17.2 mm), mean time since a bird left its nest (off-nest time; mean-centred; mean = 6.9 h), incubation day (1 = first day of incubation; mean-centred; mean = day 12.7; 1 = first day of incubation), mean wind speed within observation session (square-root-transformed and mean-centred; mean = 2.2 $\sqrt{\text{m/s}}$) in interaction with time of day (strong winds may be more relevant for energetic needs during the colder part of the day).

Off-nest behaviour models

First, we assessed the effect of sex and time on the proportion of time a bird spent feeding when off-duty using a generalized mixed model with a binomial link-function. The number of 30-s observations spent feeding (successes) within each observation session was the dependent variable, and the total number of 30-s observations within each session was the binomial denominator (unknown behaviour when bird was out of sight was excluded). We included the random intercepts (bird and nest identity) to account for repeated observations, and used an observation-session random intercept to account for overdispersion (Gelman & Hill 2007b). As for off-nest distance, we then investigated whether the sex and time estimates changed after controlling for potentially confounding variables (same as above, plus observer identity), and we explored the effects of these variables.

Off-duty bout and next incubation-bout models

We assessed whether the off-nest distance and the proportion of time spent feeding (predictors) were associated with the length of the off-duty bout or with the length of the next incubation bout (response variables). These models had a Gaussian link function and were controlled for the effects of sex and incubation day (Bulla *et al.* 2014), and for

pseudoreplication (bird and nest identities included as random intercepts).

Data imputation

The incubation monitoring system partly failed at one nest (during five observation sessions). Thus, for these five sessions, we imputed (following the procedure outlined in Nakagawa & Freckleton 2011) the time since the bird left the nest, the off-nest bout length and the next incubation bout-length. We used the *amelia* function in the R package *Amelia* (Honaker *et al.* 2011), specifying the minimum and maximum for a given parameter as priors (off-nest time: min = 20 min, max = 18.2 h; off-nest bout and next bout length: min = 3.4 min, max = 18.2 h; derived from current dataset and Bulla *et al.* 2014). We used the same procedure to impute the length of one 'off-duty bout' and of four 'nest incubation bouts', which could not be determined due to hatching or predation.

Software and procedures

We used R version 3.1.1 (R Core Team 2014) for all statistical analyses, and the *lme4* R package (Bates *et al.* 2014) for the mixed-effect modelling. Bayesian 95% credible intervals (CI) describe the uncertainty of the model estimates and of the predictions. Using the *sim* function from the R package *arm* and non-informative prior-distribution (Gelman & Hill 2007a, Gelman & Su 2013), we created a sample of 2000 simulated values for each model parameter; the 95% CIs of model estimates or predictions represent 2.5% and 97.5% percentiles of 2000 simulated or predicted values. The predictors in the models had low collinearity (all pairwise Pearson correlation coefficients $|r| < 0.24$). We assessed model fit through posterior model checking (e.g. by assessing whether simulated data from the fitted models resembled the original data; Gelman & Hill 2007a, Gelman & Shalizi 2013, Shirley & Gelman 2015) and Akaike's Information Criterion corrected for sample size (AICc; Anderson 2008). We further investigated the robustness of the estimates by removing all data for any one nest from the dataset, and then fitting these reduced datasets to the original models and visualizing the change in the effect sizes and their confidence intervals (the results of both, and also other model-checking procedures, can be replicated using the data and R script provided with the paper; Appendices S1 and S2).

RESULTS

Off-nest distance

The off-nest distance ranged from 19 to 1755 m (median = 140 m, mean = 224 m, $n = 89$ observations of 32 individuals from 17 nests; Fig. 2a, and Appendix S3, Fig. S1a). This might be an underestimate because in *c.* 10 instances parents were located only during the second location attempt (i.e. possibly when they were closer) and in eight instances the parents were not located at all (Fig. 2a). The mean distance the off-duty individual travelled from the nest tended to correlate positively between the members of a pair (Fig. 2b; Pearson's correlation coefficient (95% CI): $r = 0.39$ (-0.16 to 0.96), $n = 15$ pairs), suggesting that if one parent roamed far from the nest (compared with others in the population), so did its partner.

The distance the off-duty parent spent from the nest varied by sex and time of a day (Table 2a). Males stayed on average 0.47 times (95% CI: 0.19–0.66) closer to the nest than did females (Fig. 2b). Independent of sex, the off-duty parent stayed 0.32 times (0.02–0.53) closer to the nest at night than during the day (Table 2a). Both effects remained even when controlling for potentially confounding variables (Table 2b). The simple model with sex and time of a day fitted the data better (and based on AICc was three times more likely) than the complex model with confounding variables (Appendix S3, Table S1).

The complex model revealed that off-duty parents tended to move closer to the nest the longer they were off-nest (Table 2b) and that at night, but not during the day, off-duty parents tended to roam farther from the nest with increasing wind speed (Appendix S3, Fig. S2a). The evidence for the true effects to be zero or in the opposite direction was weak (Bayesian probability of 0.03 for the off-nest time and 0.04 for the time of day–wind interaction).

Off-nest behaviour

Parents spent on average 59% of their off-nest time feeding (Fig. 3a; 55% if unknown behaviour was included), and dedicated most of their non-feeding time to resting and preening.

The proportion of time spent feeding varied considerably between and within individuals (Fig. 4 and Appendix S3, Fig. S1b). Overall, males spent 31% (95% CI: 13–47) less time feeding than did females

(Fig. 4). The overall proportion of time spent feeding was not correlated between the members of a pair (Fig. 4; Pearson's correlation coefficient (95% CI): $r = 0.25$ (-0.31 to 0.85), $n = 15$ pairs).

The proportion of time spent feeding was similar during day and night (Fig. 3b, Table 3a). After controlling for potentially confounding variables, the sex effect remained, but a time-of-day effect emerged; the proportion of time spent feeding tended to be 11% (1–25%) lower at night than during the day (Table 3b), and the evidence for the true difference between night and day to be zero or in the opposite direction was weak (Bayesian probability of 0.04). The complex model fitted the data substantially better (and based on AICc was *c.* 31 times more likely) than the simple model with sex and time of day only (Appendix S3, Table S2).

The complex model revealed that the proportion of time spent feeding increased over the incubation period (by 3.6% per incubation day (1.9–5.3); Table 3b), and tended to increase with increasing wind speed during the night, but not during the day (Appendix S3, Fig. S2b). The evidence for the true effect to be zero or in the opposite direction was weak for the interaction between time of day and wind (Bayesian probability of 0.04).

Relationships with bout length

Neither the length of the off-duty bout nor the length of the next incubation bout could be explained by the off-nest distance of the off-duty bird or by the proportion of time the off-duty bird spent feeding (Table 4).

DISCUSSION

Although many bird species incubate biparentally (Deeming 2002), the behaviour of the off-duty parents has rarely been described in detail. Our observations reveal that in the Arctic-breeding Semipalmated Sandpiper, off-duty individuals moved on average 224 m from their nest and spent the majority of their off-nest time feeding, and most of the remaining time resting and preening. Males foraged closer to the nest and spent less time feeding than did females. Our data further suggest that there might be fewer feeding opportunities during the night, because off-duty parents were closer to the nest and tended to spend less

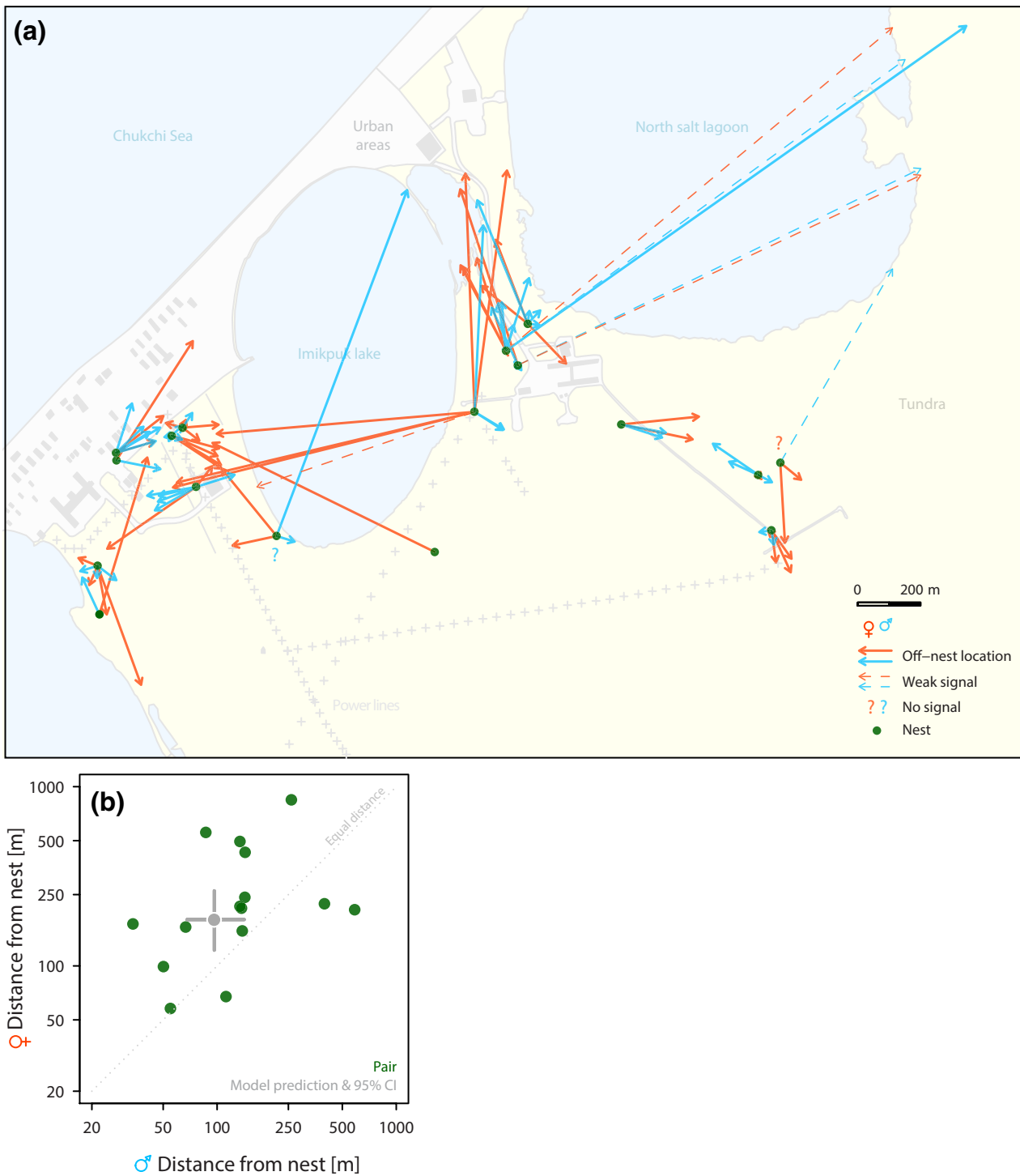


Figure 2. Map of the study site showing mean location of off-duty parents within each observation session (a), and within- and across-pair differences in the mean off-nest distance (b) (note the ln scale). In (a), thick arrows indicate the mean off-nest location within the observation session for ♀ (in red) and ♂ (in blue), dashed arrows indicate presumed off-nest location (i.e. the bird was not actually observed, but a weak radio signal came from the suggested direction); question marks indicate instances when we could not find the off-duty parent (no radio signal detected). In (b), each green dot represents one pair; the grey dot represents the mixed model prediction, and the grey cross its 95% CI (model summary is given in Table 2a).

Table 2. Mixed model estimates of the off-nest distance (ln-transformed) in relation to (a) sex and time of day and (b) culmen length^a, time since a bird left its nest^a, incubation day^a, date, sex^a, time of day, and wind speed^a within observation session.

Model	Fixed effects on off-nest distance	In-scale		Back-transformed (multiplicative scale ^b)	
		Estimate	95% CI	Estimate	95% CI
a	Intercept (♀ and day)	5.39	5.01 to 5.77	219	150–320
	Sex (σ)	−0.63	−1.07 to −0.21	0.53	0.34–0.81
	Time (night)	−0.38	−0.75 to −0.02	0.68	0.47–0.98
b	Intercept (♀ and day)	5.4	4.97 to 5.79	221	144–327
	Culmen	0.44	−0.04 to 0.86	1.55	0.96–2.37
	Off-nest time	−0.05	−0.1 to 0	0.95	0.91–1
	Incubation day	0.01	−0.03 to 0.06	1.01	0.97–1.06
	Sex (σ)	−0.58	−0.91 to −0.22	0.56	0.4–0.81
	Time (night)	−0.39	−0.74 to −0.03	0.68	0.47–0.97
	Wind	0.02	−0.53 to 0.56	1.02	0.59–1.75
	Time (night) × wind	0.78	−0.1 to 1.67	2.19	0.9–5.34
	Sex (σ) × culmen	−0.7	−1.3 to −0.05	0.5	0.27–0.96
	Variance				
Random effects		Model a		Model b	
Bird ID (intercept)		0.14		0	
Nest ID (intercept)		0.19		0.33	
Residual		0.56		0.56	

$n = 89$ observation sessions of 32 birds from 17 nests. If sex × time interaction was included in model (a), it had no effect (1.02 (0.48–2.23) on multiplicative scale). ^aTime since leaving the nest, incubation day and wind speed (square root) were mean-centred. Culmen was centred within sex. Similar results were obtained when culmen was not centred within sex or when the first principal component of culmen, head, tarsus, wing and cube-root of mass (centred within sex or not) was used instead of culmen. The first principal component was calculated with the R *princomp* function. The tarsus length of one individual was not measured, but its value was imputed using minimum (20.5 mm) and maximum (23.5 mm) tarsus length in our sample as priors (see Methods for details on imputation). Although mean wind speed during our observation session correlated with date (Fig. 1), the effect of wind remained even when we controlled for date by entering it in the model or using date and residual wind speed (wind speed regressed over the date); these models did not improve the model fit (see Appendix S3, Table S1 and posterior model checking in Appendix S2). ^bThe back-transformed intercept gives the estimated mean female off-nest distance during day (in metres); the remaining estimates are multiples (proportions) of the intercept, e.g. in model (b), the mean male off-nest distance (during day) was 116 m (221×0.56), the female off-nest distance (during day) decreased by 5% for every hour spent off-nest (i.e. from 221 to 210 m) and so on.

time feeding than during the day. In addition, during the night, when it is colder, the off-duty parents might be constrained by wind, because they tended to spend more time feeding when conditions were windy.

Consequences of roaming afar while off-nest

Despite extensive variation in the distance moved from the nest by off-duty parents (Fig. 2), in most cases they were probably outside the hearing range of their incubating partner (mean off-nest distance = 224 m). Indeed, the estimated maximum distance over which the loudest call of a parent is audible to its partner

in the open tundra habitat is 155 m (in optimal situations with low wind speeds, which are rare at our study site; details in Appendix S4). This is likely to have prohibited instantaneous communication among the parents, with three main implications.

First, it suggests an asymmetry in information acquisition between the two parents. Whereas both parents can communicate during the exchange on the nest, only the off-duty parent has the option to check upon its partner, as the location of the nest is known and fixed, whereas the location of the off-duty bird might be unknown to its partner. Of course, the incubating parent has the option to leave the nest. It can then use display flight and calling to attract its

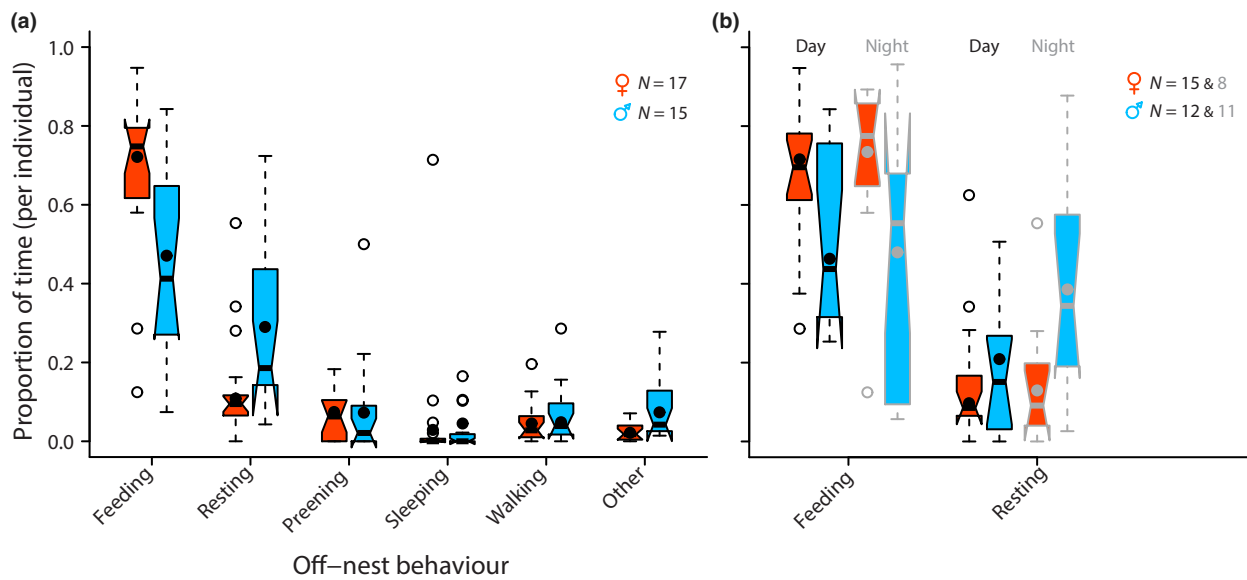


Figure 3. Distribution of the different off-nest behaviours for females and males (a), with feeding and resting further detailed for day and night (b). Unknown behaviour when the bird was out of sight was infrequent (weighted median_{female} = 5% of observed time, range_{female}: 0–22%; weighted median_{male} = 6%, range_{male}: 0–30%) and excluded from the calculations of depicted proportions. Box-plots give the median proportion of time spent on a given behaviour (horizontal line inside the box), the proportion of the time spent on the behaviour within the population (i.e. weighted mean; black dot), the 25th and 75th percentiles (box), the interquartile range or maximum/minimum value, whichever is smaller (dashed bars), and the extreme observations (open circles).

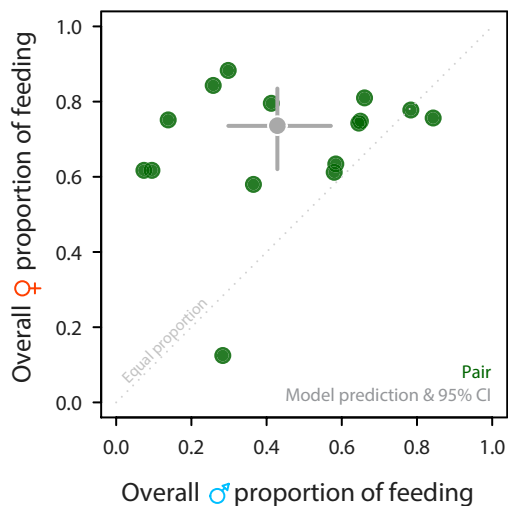


Figure 4. The overall proportion of time spent feeding (i.e. weighted means) within and across pairs. Each green dot represents one nest; the grey dot represents the mixed model prediction, and the grey cross its 95% CI (model summary is given in Table 3a).

off-duty partner, or actively search for the partner (e.g. in previously used common feeding grounds). Whereas calling the off-duty partner

back to the nest in case of danger is reported in some species (e.g. American Golden-Plover *Pluvialis dominica*; Johnson & Connors 2010), we rarely observed such behaviour in Semipalmated Sandpipers and related *Calidris* species. Moreover, when we visited the nest, the non-incubating bird rarely appeared nearby, even when the incubating bird alarmed loudly. Actively searching for the off-duty partner may be risky, because it leaves the eggs unattended and hence exposed to weather and predators. Indeed, incubating Semipalmated Sandpipers rarely leave their nests unattended within incubation sessions (incubation constancy is 95%; Bulla *et al.* 2014). Furthermore, our unpublished data from automated receivers and videos suggests that if the incubating parent leaves the nest during its bout, it stays nearby. That is, it does not search for its off-duty partner (not even 30 min prior to exchange on the nest). Such a general inability to communicate instantaneously with the partner (and hence an asymmetry in information acquisition) is typical among seabirds, in which the off-duty parents often forage far from the nest (Davis 1982, Chaurand & Weimerskirch 1994, Weimerskirch 1995, Gauthier-Clerc *et al.* 2001).

Table 3. Binomial mixed model estimates of the proportion of time spent feeding^a in relation to (a) sex and time of day and (b) time since a bird left its nest^b, incubation day^b, sex, time of day and wind speed^b within an observation session, with observer and culmen length^b as confounding variables.

Model	Fixed effects on feeding ^a	In-scale		Back-transformed (%)	
		Estimate	95% CI	Estimate	95% CI
a	Intercept (♀ and day)	0.99	0.44 to 1.54	72.9	60.8 to 82.3
	Sex (♂)	-1.31	-2.11 to -0.58	-30.8	-47.3 to -13.3
	Time (night)	0.07	-0.59 to 0.71	1.3	-12.2 to 13.3
b	Intercept (♀ and day and observer A)	1.04	0.39 to 1.67	73.9	59.6 to 84.2
	Observer (B)	0	-0.7 to 0.73	0	-15 to 13
	Culmen	-0.44	-1.17 to 0.29	-9.3	-26.9 to 5.2
	Off-nest time	-0.04	-0.11 to 0.03	-0.8	-2.3 to 0.7
	Incubation day	0.2	0.11 to 0.28	3.6	1.9 to 5.3
	Sex (♂)	-1.09	-1.63 to -0.57	-25.2	-36.8 to -12.7
	Time (night)	-0.49	-1.1 to 0.08	-10.5	-24.5 to 1
	Wind	0.05	-0.82 to 0.91	0.9	-18.7 to 14.4
	Time (night) × wind	1.26	-0.16 to 2.7	22	-3.3 to 46.1
	Sex (♂) × culmen	0.14	-0.9 to 1.19	3.4	-20.8 to 25.4

Random effects	Variance	
	Model a	Model b
Bird ID (intercept)	1.87	1.18
Nest ID (intercept)	0.40	0
Residual	0.06	1.05

$n = 89$ observation sessions of 32 birds from 17 nests. If sex × time interaction was included in model (a), it had no effect (-7% (-37 to 25)). ^aFeeding – the number of 30-s observations spent feeding (successes) within each observation session; the total number of 30-s observations within each session was the binomial denominator. ^bTime since leaving the nest, incubation day and wind speed (square root) were mean-centred. Culmen was centred within sex. Similar results were obtained if culmen was not centred within sex or if the first principal component of culmen, head, tarsus, wing and cube-root of mass (centred or not) was used instead of culmen. The first principal component was calculated with the R *princomp* function. The tarsus length of one individual was not measured, but its value was imputed using minimum (20.5 mm) and maximum (23.5 mm) tarsus length in our sample as priors (see Methods for details on imputation). The effects of incubation day and wind speed remained even when we controlled for date by entering it in the model or by using date and residual wind speed (wind speed regressed over the date); these models had poorer fit than the original complex model (see Appendix S3, Table S2, and posterior model checking in Appendix S2).

Secondly, the lack of instantaneous communication among partners implies that the off-duty parent determines when the changeover on the nest takes place, i.e. it cannot take place before the off-duty bird returns. However, two anecdotal observations suggest that the incubating parent also influences the time of changeover. First, the incubating parent does not always allow an exchange when its partner attempts it (Ashkenazie & Safriel 1979a). Secondly, the incubating parent sometimes leaves the nest before the return of its partner (Bulla *et al.* 2014). Such premature departures from the nest were mostly seen after an unusually long absence of the off-duty parent, as observed in other biparentally incubating species (Davis 1982, Chaurand & Weimerskirch 1994, Weimerskirch 1995, Gauthier-Clerc *et al.* 2001).

Thirdly, the lack of instantaneous communication leads to delayed information acquisition and reduced information accuracy about the state of the partner or the condition of the clutch, and hence a delayed response of individuals. If the off-duty parent rarely comes close to the nest (which typically seems to be the case), information about the state of both partners or of the brood can only be obtained during the change-over itself. For example, the off-duty parent cannot assess the condition of its incubating partner and would not know if its partner has left the nest. Consequently, in contrast to biparental offspring feeding (e.g. Wright & Cuthill 1990, Hinde 2006, Hinde & Kilner 2007, Harrison *et al.* 2009), optimization of incubation schedules cannot work via direct and immediate communication between the parents,

Table 4. Mixed model estimates of the off-duty bout length and the next incubation-bout length in relation to off-nest distance (ln-transformed)^a and proportion of time spent feeding within an observation session^a, with incubation day^a and sex as confounding variables.

Model	Response variable	Fixed effects	Estimate	95% CI
a	Off-duty bout length (h)	Intercept (♀)	11.43	10.45 to 12.35
		Incubation day	0.1	-0.03 to 0.22
		Sex (♂)	1.46	0.10 to 2.86
		Off-nest distance	0.23	-0.41 to 0.86
b	Next incubation-bout length (h)	Intercept (♀)	12.63	10.17 to 15.01
		Incubation day	0	-0.16 to 0.15
		Sex (♂)	-1.97	-3.56 to -0.33
		Off-nest distance	0.71	-0.12 to 1.50
c	Off-duty bout length (h)	Intercept (♀)	11.64	10.71 to 12.66
		Incubation day	0.11	-0.02 to 0.25
		Sex (♂)	1.03	-0.29 to 2.37
		Proportion of feeding	-1.21	-3.43 to 1.03
d	Next incubation-bout length (h)	Intercept (♀)	12.8	11.55 to 14.14
		Incubation day	-0.02	-0.19 to 0.16
		Sex (♂)	-2.33	-4.1 to -0.66
		Proportion of feeding	0.38	-2.57 to 3.26

Random effects	Variance			
	Model a	Model b	Model c	Model d
Bird ID (intercept)	1.08	1.09	1.09	1.02
Nest ID (intercept)	0	0.95	0	0.98
Residual	6.41	9.41	6.34	9.83

$n = 89$ observation sessions of 32 birds from 17 nests. ^aIncubation day, off-nest distance and proportion of feeding were mean centred ($\text{mean}_{\ln(\text{off-nest distance})} = 4.9$; $\text{mean}_{\text{proportion}} = 0.58$).

and parents cannot immediately adjust their behaviour to the needs of the partner or the brood. Thus, the species might have evolved mechanisms to enhance the optimization of incubation schedules, e.g. improved cognitive skills to assess the partner's condition or willingness to invest. Such mechanisms would enable individuals to make better predictions about the state of their mate even when not physically present. We then expect that the longer parents stay together, the better they are at assessing their partner's condition or willingness to invest. Indeed, 80% of Semipalmated Sandpiper pairs that return each year reunite (Gratto-Trevor 1991), but to date the evidence for higher hatching success of faithful pairs (e.g. as a consequence of improved coordination on the nest) is lacking. Alternatively, if no useful information can be acquired during the exchange, individuals might be selected to use simple rules (e.g. come back after a more or less fixed amount of time). This scenario is plausible in Semipalmated Sandpipers, because incubation is continuous with smooth exchanges on the nest (Bulla *et al.* 2014) and not energetically

constrained (i.e. it is unlikely that the state of the incubating bird drives the length of an incubation bout; Bulla *et al.* 2015).

Possible explanations for sex differences in off-nest behaviour

Although off-nest distance of a pair (unlike time spent feeding) tended to be positively correlated among pair members, males stayed closer to the nest and spent less time feeding than did females (Figs 2 and 4). Sex differences in the off-nest distance and behaviour have also been reported in other species, where they may be explained by sex-specific foraging strategies related to sexual size dimorphism (González-Solís *et al.* 2000, Lewis *et al.* 2005). However, Semipalmated Sandpipers lack pronounced sexual size dimorphism (Bulla *et al.* 2014), and the sex-specific effects remained even when controlling for body size (Tables 2b and 3b).

The observed sex difference in the off-nest distance was also unlikely to be due to different for-

aging strategies, given that females and males fed in the same general feeding areas (Fig. 2a). One could hypothesize that males stayed closer to the nest because they are the more territorial sex (Ashkenazie & Safriel 1979a). However, males still roamed far from their nests (Fig. 2), which makes efficient nest defence against intruders unlikely. In theory, males could also be the more active sex in defending the nest against avian predators, but incubating Semipalmated Sandpipers predominantly rely on crypsis and not on direct attack of predators (Ashkenazie & Safriel 1979a). Hence, it is unclear why off-nest males remained closer to the nest than off-nest females.

The observation that female Semipalmated Sandpipers spent more time feeding than males might reflect their energy deficit after egg-laying. This is plausible because females typically lay four eggs in 5 days (Sandercock 1998) and the mass of the clutch is remarkably similar to female body mass (Hicklin & Gratto-Trevor 2010). Moreover, females had *c.* 10% longer incubation bouts than males (Bulla *et al.* 2014) and hence may have needed more feeding time. Also, females were usually off-nest during the warmer parts of the day, when prey is more available (Bulla *et al.* 2014), but this could also lead to more efficient foraging and therefore less time needed to refuel. Indeed, our study measured the time parents dedicated to feeding, and not feeding rate, number of successful prey captures or prey size. Hence, differences in the time spent foraging may not directly relate to energy intake.

Off-nest behaviour in a fluctuating environment: feeding with time for a rest

Our observations revealed that parents dedicated *c.* 60% of their off-nest time to feeding and much of the remaining time to resting and preening (Fig. 3). The finding that feeding dominates the off-nest activity confirms previous results (based on observation of two individuals; Ashkenazie and Safriel 1979b) and is in line with observations of other species (e.g. Whittingham *et al.* 2000, Lewis *et al.* 2005, Pinet *et al.* 2012). The predominance of feeding is not surprising given that the 22–32 g Semipalmated Sandpiper incubates continuously for on average 11.5 h (Bulla *et al.* 2014) and will thus need to replenish its energy stores. Moreover, being active in the extreme high-Arctic environment is energetically stressful

(Piersma *et al.* 2003). Hence, extensive feeding might be necessary to avoid an energetic deficit, even independent of incubation. However, parents still dedicate *c.* 40% of their off-duty time to other activities. This may indicate that the Arctic environmental conditions are less energetically stressful than believed, that the quality or amount of available food is such that foraging is highly efficient, or that individuals avoid feeding during unfavourable foraging conditions. Two of our findings provide some support for the last of these. First, during cold night conditions, Semipalmated Sandpipers tended to spend less time feeding than during the day (Table 3b), which might also explain why they stayed closer to the nest at night (Table 2). It is unlikely that reduction in night feeding-time was compensated for by higher feeding efficiency, because data on defecation rate (obtained in a different year) suggested that birds did not feed more at night (Fig. S2c and Appendix S5, Table S3). However, to replenish their reserves under energetically stressful times (high winds during cold night), parents might have been forced to feed. Indeed, the time spent feeding (as well as defecation rate) tended to increase when it was windy at night (Appendix S3, Fig. S2). Night temperatures are usually below the thermo-neutral zone of sandpipers and windy conditions increase conductance; both increase the need for thermoregulation (Bakken 1990, 1991) and hence for energy. Off-duty parents may reduce the effects of adverse weather by adjusting their behaviour (Wiersma & Piersma 1994), e.g. by foraging in wind shade. However, this might not be possible given that preferred feeding grounds are at the edges of larger water bodies (Fig. 2a). Secondly, the time spent feeding increased over the incubation period (Table 3b), which might reflect the cumulative stress of incubation, increasing prey-availability (Corbet 1966, MacLean & Pitelka 1971, Danks & Oliver 1972, Schekkerman *et al.* 2003, Tulp & Schekkerman 2008), or both. There is some evidence that prey availability drives the increase in time spent feeding, because our *ad hoc* observations from the early breeding season reveal no or rare defecation under severe environmental conditions (frozen tundra), and because minimum temperatures (Fig. 1), as well as time spent feeding, increased over the breeding season (result not shown, but data and R-script of the analyses are available online in Appendices S1 and S2).

CONCLUSION

The finding that off-duty Semipalmated Sandpipers spent their time far from the nest implies that the length of incubation bouts must generally be driven by the off-duty parent's decision to return to the nest and relieve its incubating partner; however, we still do not understand the factors that influence such decision. The observation that parents spent more time feeding during the day and during windy conditions at night suggests that there might be a conflict over who is off-duty during times that are most favourable for foraging. This highlights the need to consider the fluctuating environment when addressing individual costs of parental care.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Mean off-nest distance and the proportion of time spent feeding during each observation session.

Figure S2. Estimated change in the distance the off-duty bird spent away from its nest, in the proportion of time the off-duty bird spent feeding,

and in the defecation rate with increasing wind speed during the day and night.

Table S1. Results of AICc analyses for the simple and complex off-nest distance models.

Table S2. Results of AICc analyses for the simple and complex off-nest behaviour models.

Table S3. Poisson mixed model estimates of defecation rate in relation to time of day, and wind speed within observation session.

Appendix S1. Data.

Appendix S2. R-script.

Appendix S3. Off-nest distance and behaviour – additional figures and tables.

Appendix S4. Estimated audibility of alarm calls.

Appendix S5. Defecation: data and analyses.

SUPPORTING INFORMATION

Bulla, M. et al. 2015. Off-nest behaviour in a biparentally incubating shorebird depends on sex, time of a day, and weather. IBIS.*

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APPENDIX S1 – DATA

Data are available at figshare.com digital repository:

[http://figshare.com/articles/Data from Off nest behaviour in a biparentally incubating shorebird depends on sex time of a day and weather/1248902](http://figshare.com/articles/Data_from_Off_nest_behaviour_in_a_biparentally_incubating_shorebird_depends_on_sex_time_of_a_day_and_weather/1248902)

APPENDIX S2 – R-SCRIPT

The R-script (of the statistical analyses, model fits and checks, tables and figures) is available at figshare.com digital repository:

[http://figshare.com/articles/R script from Off nest behaviour in a biparentally incubating shorebird depends on sex time of a day and weather/1248905](http://figshare.com/articles/R_script_from_Off_nest_behaviour_in_a_biparentally_incubating_shorebird_depends_on_sex_time_of_a_day_and_weather/1248905)

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APPENDIX S3 – OFF-NEST DISTANCE AND BEHAVIOUR: ADDITIONAL FIGURES AND TABLES

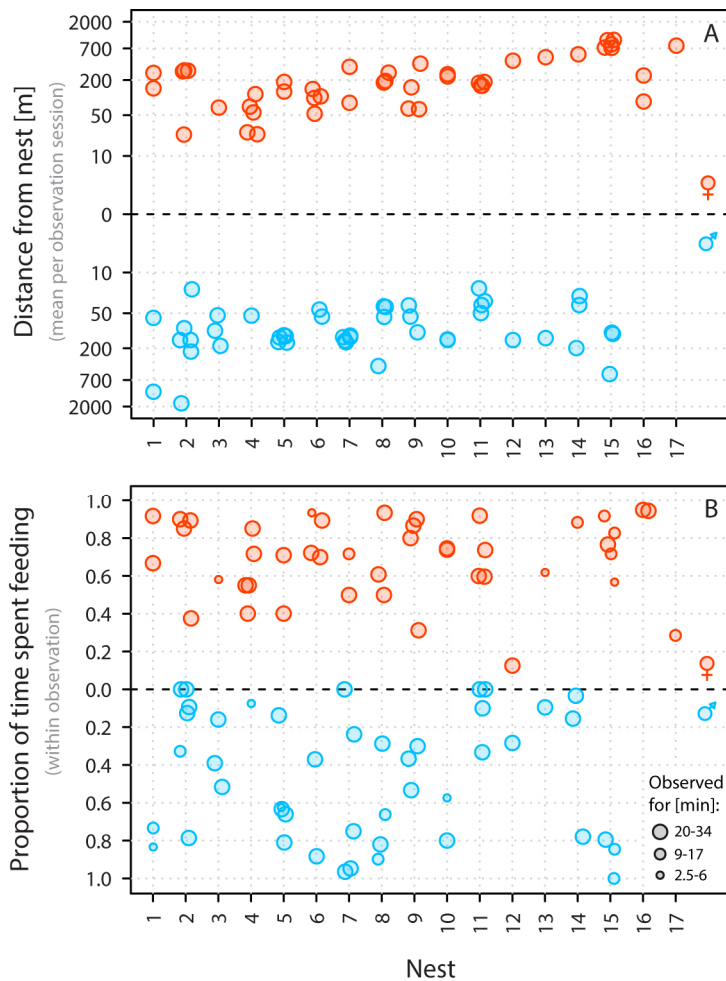


Figure S1. Mean off-nest distance **A** (note the ln scale) and the proportion of time spent feeding **B** during each observation session. In **B**, the size of dots approximates the time (in minutes), for which the bird was effectively observed.

Table S1. Results of AICc analyses for the simple and complex off-nest distance models.

Model	Fixed effects	K ^a	AICc	ΔAICc ^b	w _i ^c	ER ^d
Simple	sex + time	6	239	0	0.7167	
Complex	off-nest time + incubation day + sex*cul+ time*wind	12	242	3	0.1423	3
Date	off-nest time + incubation day + sex*cul+ time*wind + time*date	14	243	5	0.0705	5
Residual	off-nest time + incubation day + sex*cul+ time*residual wind + time*date	14	243	5	0.0705	5

In all four models random intercepts (bird and nest identity) accounted for repeated observations.

^a Number of parameters in the fitted model

^b The difference in AICc between the first-ranked model and the given model.

^c Akaike weight – the weight of evidence that a given models is the best approximating model.

^d Evidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

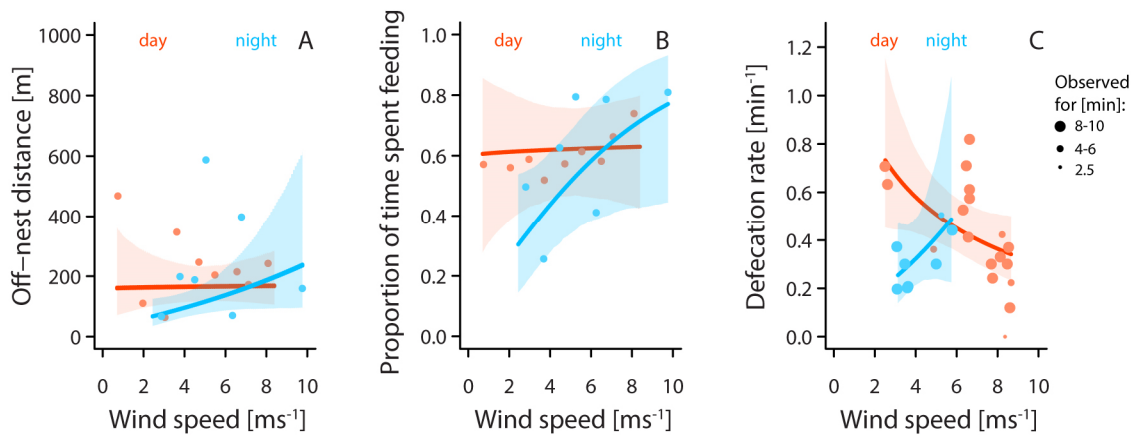


Figure S2. Estimated change in the distance the off-duty bird spent away from its nest (A), in the proportion of time the off-duty bird spent feeding (B), and in the defecation rate (C) with increasing wind speed during the day (● warm part of the day) and night (● cold part of the day). Lines represent the model predictions, shading their 95% CIs (model summaries are in Table 2A, 3A & S3). The predictions are for the range of mean wind speeds during day or night observations in 2011 (A, B) and 2013 (C). In A and B, dots represent means for intervals spread evenly across the range of the x-variable for day and night; in C, dots represent raw data and their size approximates the time (in minutes) for which the bird was effectively observed.

Table S2. Results of AICc analyses for the simple and complex off-nest behaviour models.

Model	Fixed effects	K ^a	AICc	ΔAICc ^b	w _i ^c	ER ^d
Complex	off-nest time + incubation day + sex*cul+ time*wind	13	663	0	0.7043	
Date	off-nest time + incubation day + sex*cul+ time*wind + time*date	15	666	3	0.1365	5
Residual	off-nest time + incubation day + sex*cul+ time*residual wind + time*date	15	666	3	0.1365	5
Simple	sex + time	6	670	7	0.0227	31

In all four models random intercepts (bird and nest identity) accounted for repeated observations and observation-session random intercept for over-dispersion.

^a Number of parameters in the fitted model.

^b The difference in AICc between the first-ranked model and the given model.

^c Akaike weight – the weight of evidence that a given models is the best approximating model.

^d Evidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

APPENDIX S4 - ESTIMATED AUDIBILITY OF ALARM CALLS

Being away from the nest prohibits instantaneous communication only if the alarm calls or display calls of the incubating parent are not audible to the off-duty parent. We thus estimated the maximum transmission distance of these calls, as follows.

Monitoring. In 2014, using a Voltcraft SL 400 sound level measuring meter, we measured the maximum sound pressure of 4 alarm/display calls of an incubating parent from a distance of 5 m, by approaching its nest. Before and after this measurement we also measured the sound pressure of the background noise, i.e., of the wind. All measurements were done using the A filter and dB values refer to 20 μ Pa.

Estimation. We estimated the maximum transmission distance for the loudest call, i.e., the call with the highest peak amplitude, which had a sound pressure level of 69.5 dB(A) at 5 m. We based the estimation on sound transmission models of bird vocalizations (Nemeth and Brumm 2010; Nemeth and Zollinger 2013) with peak frequency of 1.5kHz (an average peak frequency of semipalmated sandpiper call; Miller 1983), and spectrum level of the background noise of 10 dB at 2.5 kHz (estimated from our highest background noise measurement, which corresponds to low winds, of 42 dB(A) and spectra of wind noise profiles; Boersma 1997). To our knowledge, the auditory thresholds in noise are missing for sandpipers. Hence, as a proxy we used a critical ratio of 25dB – an average across birds (Nemeth and Brumm 2010). Because the calls were uttered in an open tundra habitat with no obstacle between the calling bird and the receiver, the majority of sound attenuation during transmission resulted from spherical spreading loss. Thus, we further added an excess attenuation of 2 dB/100m, which represents sound transmission in open fields (Marten and Marler 1977)

Results. The maximum estimated communication distance was 155 m.

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APPENDIX S5 - DEFECATION: DATA AND ANALYSIS

Time spent feeding is not necessarily linked to food intake, because of variation in foraging efficiency. Hence, we obtained data on defecation rate (two years later) and used it as a proxy of intake rate. We then assessed whether the time of day and wind speed correlated with defecation rate, same as they and correlated with time spent feeding (Table 3A).

Monitoring. In 2013 we observed defecation data of banded individuals during the cold and warm part of the day. A single observer located foraging individuals and observed them for 10 min (unless they flew away earlier), while noting the time of the bird's first defecation, the number of defecations, and the amount of unobservable time (e.g., time when the bird faced the observer such that observing its defecation was impossible).

Sample size. In total, we observed 23 banded individuals during 26 observation sessions between 1 and 9 July 2013. The median duration of an observation session was 10 min (range: 2.5–10 min; mean = 8.7 min) and the median duration for which we effectively observed the bird was 9.3 min (range: 2.5–10 min; mean = 8.3 min). For analyses, we considered observations that occurred between 0000 and 0600 hours as “night” observations ($N = 8$ sessions; with median tundra temperature: 6.1 °C; range: 5.4–6.7 °C) and observations occurring between 0900 and 1930 hours as “day” observations ($N = 18$ sessions; with median tundra temperature: 13.5 °C; range: 8.9–20.4 °C).

Model. Variation in defecation rate was analysed using a generalized linear model with time of day as explanatory variables, with a Poisson link function, and with the offset specified as time during which the bird was effectively seen within the observation session (\ln transformed). We further tested for the effect of mean wind speed 30 min prior to each observation session until the start of the session (square root transformed and mean centred; mean = 2.4 $\sqrt{[m\ s^{-1}]}$) in interaction with time of day.

Results. The median defecation rate was 0.37 defecations min^{-1} (range: 0–0.82, mean = 0.39). The defecation rate tended to be lower (0.3 times, CI: -0.11–0.58) at night than during the day ($N = 26$ observations of 23 individuals). Similar to the time spent feeding, during the night the defecation rate increased with increasing wind speed, while during the day it decreased with increasing wind speed ([Fig. S1C](#); [Table S1](#)). This complex model fitted the data better (according to AICc was twice more likely) than a model without wind speed.

Discussion. The finding that defecation positively correlated with wind speed during the night mirrors the finding that the time dedicated to feeding increased as wind speed increased during the night. These results suggest some limitation to foraging at night and that during adverse conditions birds might attempt to increase their foraging effort or success. Nevertheless, such speculations deserve further testing. Essentially, it remains to be tested whether defecation rate of arctic breeding sandpipers is the proper proxy for foraging success and intake rate.

Table S3. Poisson mixed model estimates of defecation rate in relation to time of day, and wind speed^a within observation session.

Fixed effects on defecation	Log-scale		Back-transformed (multiplicative scale ^b)	
	Estimate	95% CI	Estimate	95% CI
Intercept (day)	-0.73	(-0.97--0.49)	0.48	(0.38-0.62)
Time (night)	-0.06	(-0.8-0.69)	0.95	(0.45-2)
Wind	-0.56	(-1.07--0.06)	0.57	(0.34-0.94)
Time (night) × Wind	1.6	(-0.22-3.45)	4.96	(0.8-31.56)

N = 26 observation sessions of 23 birds. Time for which the bird was effectively seen was fitted as an offset. Model with individual specified as random intercept gave exactly the same results.

^a Wind speed (square root) was mean centred.

^b The back-transformed intercept gives the estimated mean defecation rate (min^{-1}) during the day, the remaining estimates are multiples of the intercept, e.g., the defecation rate decreased during the day by 0.27 (0.48 times 0.57) as wind speed (square root) increased by $1 \sqrt{\text{m s}^{-1}}$. Back-transformed estimates with credible intervals (CIs) including 1 suggest no significant difference.

Chapter 3

Parental cooperation: diverse response to temporary absence of partner's care in biparentally incubating shorebird

Martin Bulla, Mihai Valcu, Anne Rutten, Bart Kempenaers

Biparental care for offspring requires cooperation, but it is often also a source of conflict, since caring less today saves energy for tomorrow. How do parents cooperate despite this temptation to cheat? Theoretical models predict that chick feeding parents in passerine birds should achieve cooperation by partially compensating for the reduced care of their partner. However, partial compensation is unlikely during incubation, when the entire brood can fail with reduced care. Here, in a biparentally incubating shorebird, the semipalmated sandpiper, we removed an incubating parent for 24 hours to investigate how its partner responds. We then investigated population level response, individual differences in response, and explored the correlates of the response and of how incubation changed when the removed parent returned. On average the parents compensated partially for the absence of their partner's care (59%; 95%CI: 49-70%), but the individual responses (irrespective of sex) span the entire range of what is possible (2-101%; no, partial and full compensation). Essentially, as incubating parents do not feed, even the fully compensating parents later left the nest unattended. In contrast to undisturbed situation and uniparental species, nest attendance during compensation tended to be higher during the warm times of day. In 7 nests, where a removed parent never returned, the widowed parent attended the nest for 4 days (median; range: 0-10 days). Although compensation was not related to the pre-experimental share of incubation, shy (responsive) parents compensated more. Finally, the quality of incubation in post-experimental period was lower than usual, but improved with time. Our findings suggest that some parents may lack the energy for full compensation or are less responsive to their partner's absence, but are nevertheless able to adjust their subsequent behaviour to take full responsibility for the nest when widowed for good. The previously undescribed link of compensation to 'personality' opens up exciting areas for future research in parental cooperation.

Introduction

Biparental care is a complex social behaviour where females and males cooperate in the rearing of their offspring. Whereas both parents gain from parental care provided by either of the parents, each parent only pays the costs of its own care. Consequently, each parent would have higher overall reproductive success if the other parent provided a larger share of the care (Trivers 1972; Lessells 2012). How do parents achieve cooperation in face of this conflict?

Established theoretical models have predicted (reviewed by Lessells 2012) that parents should partially compensate for change in their partner's care when breeding success continuously increases (in a decelerating fashion) with increased parental care (Houston & Davies 1985; McNamara et al. 1999; McNamara et al. 2003). However, although partial compensation prevails during chick feeding in passerine birds (Harrison et al. 2009), a context for which the models were initially developed, partial compensation is unlikely when breeding attempts fail due to a small decrease in parental care, i.e. where the return of investment is zero unless a threshold amount of care is delivered. Such a situation is typical for biparental incubation of eggs in birds, especially in a species where both parents are essential for successful breeding attempts and in extreme environments where unattended eggs are subject to severe predation pressure, as in gull or frigatebird colonies (Dearborn 2001; Jones et al. 2002); overheating, as in deserts (AlRashidi et al. 2011); or cooling, as in the Arctic or Antarctica (Gauthier-Clerc et al. 2001; Hicklin and Gratto-Trevor 2010). Here, a theoretical model has predicted that parents should compensate fully or not at all (Jones et al. 2002).

To test this full or no compensation prediction, the experiment needs to be short term as parents of biparental species incubate their clutch nearly continuously and hence are unable to compensate indefinitely (Deeming 2002). Also, the experiment needs to be evaluated on the individual level, because if some individuals compensate fully and some not at all, the evaluation on the population level (i.e., its mean response) would blur this dichotomy.

Although biparental incubation of eggs prevails in 50% of avian families (and in 80% of non-passerine ones; Deeming 2002), the experimental studies that targeted cooperation during biparental incubation are dominated by two approaches, both with long-term effects that are irreversible within one breeding attempt. The first approach created a situation of no care (permanent nest desertion) by completely removing a parent (Burley 1980; Erckmann 1981; Bowman & Bird 1987; Brunton 1988; Duckworth 1992; Pinxten et al. 1995). The second created a situation of reduced care by handicapping the male by testosterone implants (De Ridder et al. 2000; Alonso-Alvarez 2001; McDonald et al. 2001; Schwagmeyer et al. 2005), or by handicapping one parent by attaching extra weights (Wiebe 2010). In contrast, short-term reversible manipulations of female and male incubation effort (e.g. by supplemental feeding or temporary removal of one parent) are scarce and the evaluation of individual differences in response to such short-term change in parental care even more so (Gibbon et al. 1984; Kosztolányi et al. 2003; Kosztolányi et al. 2009). Apart from testing for

full or no compensation, the study of cooperation (and solutions to conflict) over short-term has an additional advantage. It mimics the response of parents to natural short-term deficiencies in their partner's care, and it sheds light on whether such a response also affects subsequent bouts of care (i.e. it has carry over effects).

Here, we investigate the mean response of parents in the population, as well as the individual differences in response to the temporary absence of a partner's care during the biparental incubation of a small shorebird (23-32 g), the semipalmated sandpiper (*Calidris pusilla*). This sandpiper breeds in an extreme High Arctic environment and successful incubation is thought to require the participation of both sexes (Hicklin & Gratto-Trevor 2010). The sandpipers attend their nest 95% of time (Bulla et al. 2014). To achieve such a continuous nest attendance, the incubating parent is not feeding throughout its incubation bout, which is on average 11.5 hours for females and 10.7 hours for males (Bulla et al. 2014).

We removed a parent at the end of its regular incubation bout and released it 24-hours later. In this way, we made a temporarily widowed bird responsible not only for its own incubation bout (control period), but also for the following incubation bout of its partner (treated period). We then investigated the change in the nest attendance between control and treated period, whether this change differed between females and males, and how variable the change was between individuals.

Based on the theoretical full or no compensation model, we anticipated four possible scenarios for how the temporarily widowed parent would respond (Figure 1). (a) It may leave the nest and not return for the supposed incubation bout of its partner (no compensation). Such behaviour may either reflect no immediate response to the partner's absence, or a lack of knowledge about the partner's absence - the bird may leave the nest because it has reached its energetic limits, not knowing that its partner would ever return. (b) The bird may continue incubating for the entire supposed incubation bout of its partner (full compensation and immediate response to partner's absence). In addition, the bird may attempt full compensation (i.e. continue incubating), but when its energy reserve is depleted (c) may leave the nest (partial compensation and response to partner's absence), or (d) may continue incubating, but with decreasing nest attendance that is leave the nest for short feeding bouts like uniparental species do (partial compensation, response to partner's absence).

We further tested three possible drivers of the diverse compensation responses: (a) the time of day, as it is easier to incubate and forage when it is warm (Cartar & Montgomerie 1985; Løfaldli 1985; Reneerkens et al. 2011); (b) the share of incubation prior to the removal, as individuals that invest relatively less in parental care may be also reluctant to compensate (Bowman & Bird 1987; Duckworth 1992); and (c) the median escape distance from the nest upon approach of a human, as bold individuals are expected to be less responsive and hence less prone to compensate (Koolhaas et al. 1999; Coppens et al. 2010). Last, we explored how incubation of the two parents changed after the removed parent returned.

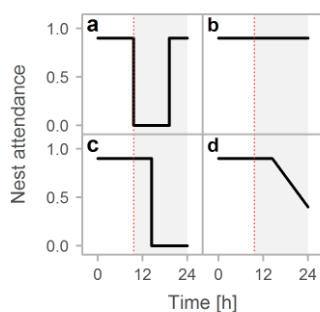


Figure 1 | Possible compensation strategies for temporal absence of partner's care. **a-b**, Red dotted line indicates the time when one parent is experimentally removed and grey are the time for which the partner is removed. **a**, No compensation – an individual leaves the nest at the end of its incubating bout and returns when its next bout is supposed to start. **b**, Full compensation – an individual continuously incubating for the entire supposed bout of its partner. **c-d**, Partial compensation – an individual continues incubating, but then leaves (**c**) or continues incubating, but with decreasing nest attendance (**d**).

Methods

Study site

The experiment took place in a population of semipalmated sandpipers near Barrow, Alaska (71.32° N, 156.65° W), between 1 June and 4 July 2013. The study area and species are already described in detail elsewhere (Ashkenazie and Safriel 1979; Bulla et al. 2014a). Barrow has continuous daylight throughout the breeding season, but environmental conditions show consistent and substantial diurnal fluctuations; ambient temperatures are generally low, below 5 °C, but surface tundra temperatures can reach up to 28 °C (Supplementary Figure S1 in Bulla et al. 2014a).

Recording incubation

The general procedure of monitoring incubation is described in detail elsewhere (Bulla et al. 2014; Bulla et al. 2015b). In short, the presence of parents, banded with a plastic flag containing a glass passive tag (9.0 mm × 2.1 mm, 0.08 7g, <http://www.biomark.com/>), was registered every 5 s by a custom made radio frequency identification device (RFID; Bulla et al. 2014), with a thin antenna loop around the nest cup connected to a reader. Incubation was further determined by comparing nest temperature, measured by high resolution temperature-probe, and surface tundra temperature, measured by the MSR® 145 data logger placed next to the nest (Bulla et al. 2014; Bulla et al. 2015b). The probe connects with the logger by a thin wire (<http://www.msr.ch/en/>; see Supplementary Pictures in Bulla et al. 2014). In addition, 12 nests were equipped with a video recording system for some days (Bulla et al. 2014), and 15 nests were protected against avian predators using enclosures made of mesh wire (Supplementary Figure 1a).

Experimental procedure

At 29 nests we attempted to temporarily remove one parent (henceforth, the 'removed parent') around the 11th day of the 19-21 day incubation period, that is shortly before we expected its partner (henceforth, the 'focal parent') to return to incubate. This we assessed

by downloading the RFID data and visualizing the incubation pattern on the previous day. Males and females were captured alternately, starting with the male at the first experimental nest. The sex of individuals was known from previous years, or estimated from body measurements and later confirmed by molecular analyses (Bulla et al. 2014; Bulla et al. 2015b).

We held the removed parent in captivity for 24 hours and then released it in the vicinity of the nest. In this way, the focal parent incubated its 'natural' incubation bout (henceforth, the 'control period'), which at this stage of incubation typically lasts about 10-11 hours (Bulla et al. 2014). Then, the focal parent was treated for the rest of the removal period (henceforth, the 'treated period'), i.e., for about 13 hours.

We have tested whether and how the focal parent compensated for the absence of its partner by comparing the nest attendance between the control and treated periods during the 24 hours when a removed partner was absent. We defined nest attendance as the proportion of time a bird actually incubated during a given time period (Bulla et al. 2014). We defined control period as the time span that lasted from the arrival of the focal bird to the nest (after removal of its partner) until the length of median bout (estimated from the three pre-experimental incubation bouts of the focal bird). We further defined the treated period as the time span between the end of the control period and the release of the partner from the captivity.

Nest attendance was derived from temperature data (Bulla 2014; Bulla et al. 2014) in all but one nest, where temperature measurements failed. In this nest, the nest attendance was derived from RFID readings, since temperature based attendance correlates with RFID based attendance: $r = 0.79$, $N = 1584$ incubation bouts from 2011 (Bulla et al. 2013a; Bulla et al. 2013b).

Four nests were unsuitable for analyses of compensation because: (a) a focal parent deserted the nest prior to treatment (one nest); (b) because of depredation (two nests); and (c) because the wrong bird was removed (one nest). Thus, 25 nests with 12 females and 13 males as focal parents were used in this analysis.

Captivity

The removed parent was kept in a cardboard box (21 cm × 30 cm × 25 cm) in a shed which was sheltered from the elements (Supplementary Figure 1b). The bottom of the box was lined with tundra (fresh for every bird) and contained water and a feeding tray (Supplementary Figure 1c).

Because we also wanted to approximate the mass loss during an incubation bout, the first eight birds were starved for the first 12 hours in captivity and then provided with ad libitum food for the remaining 12 hours. After two females died on this regimen, the remaining birds were kept on ad libitum food throughout.

Initially, the ad libitum food consisted of 100 meal worms (~7.5 g) per 12 hours. The energetic content that birds can metabolize from meal worms is ~24.2 kJ/g (Bell 1990). Thus,

~7.5g of worms provided ~181 kJ, which should be more than adequate to cover the estimated daily energetic requirement of semipalmated sandpipers during the incubation period (19-59 kJ/day; Ashkenazie & Safrieli 1979), or while resting (123 kJ/day using equation for resting metabolic rate from Norton 1973 and assuming 27 g bird, median Barrow tundra temperature of 6.2 °C and one liter of oxygen equals 20.1 kJ). However, the first two captive birds ate nearly all of the provided mealworms. Hence we supplemented meal worms with cat food (for six birds, four of which rejected the cat food entirely) and increased the amount of meal worms to 125-200 per 12 hours (for all remaining birds).

Statistical analyses

Compensation for absence of parental care - To test for the difference in nest attendance between control and treated period we used linear mixed effect models. We specified nest attendance as the dependent variable and the type of period (control or treated) as a categorical predictor. To account for the paired (within individual) design of the experiment, we included bird ID as random intercept. As nest attendance is a function of period length, we first investigated whether controlling for the length of period improved the model fit. It did not. The model with period length was twice less likely than the simple model (Supplementary Table 1). Hence here, and in the subsequent analyses, we made the inference from simpler models without period length.

Next we tested whether the compensation was sex specific by specifying a model with the type of period in interaction with sex, and by comparing it with the initial model without the interaction (Supplementary Table 1).

Explaining the diversity in compensation - To explore the possible drivers of the diversity in compensation, we further tested in the three linear models whether: (a) nest attendance during the treated period correlated with the time of day (defined as mid-point of treated period, transformed to radians and represented by a sine and cosine); (b) escape distance from the nest upon approach of a human (estimated as median escape distance from all escape distances of an individual prior to the experiment (for estimations of escape distance see Bulla et al. 2016); and (c) the proportion of time the focal bird was responsible for incubation prior to the experimental treatment (estimated as median share of daily incubation, without exchange gaps, from three days prior to treatment). We further assessed the relative importance of the three variables by comparing the three models (Supplementary Table 2). We used nest attendance (instead of compensation) because attendance correlated strongly with compensation ($r = 0.997$), and because the nest attendance findings are directly comparable to the nest attendance findings from natural conditions. Since for one individual we had no escape distance estimate, we imputed this value (following the procedure outlined in Nakagawa & Freckleton 2011) as a median of 1,000 imputations generated by an 'amelia' function in the 'Amelia' R package (Honaker et al. 2011), while specifying the range of likely escape distances (0 – 80 m) as a prior.

Post treatment effects – We explored how incubation changed after the removed parent returned to the nest (post-experiment period) by comparing the nest attendance and length

of the last three before-experiment incubation bouts with the first three post-experiment bouts (of each parent). In these bouts we also compared the presence and length of exchange gaps. To this means we have constructed descriptive plots and specified mixed effect models with nest attendance (proportion), bout length (in hours), presence of exchange gap (binomial response: 0 – no gap, 1 – gap present), and the length of detectable exchange gap (in minutes) as the response. We entered the period (before or post) in interaction with the day in incubation period (day) as predictors. Day was mean-centred within each nest, so that negative values represent before, and positive values post experimental period. To control for non-independence of data-point we entered bird ID as a random intercept and day as a random slope. Results of the models with and without interactions, as well as those containing parents (focal or removed) are shown in Supplementary Table 4 and 5.

In addition, we explored whether the post-experiment nest attendance and bout length of the removed parent were related to its mass loss while in captivity, and whether the post-experiment nest attendance and bout length of the focal parent were related to its percentage of compensation during the treated period. We furthermore investigated whether these relationships were sex specific. Bird ID was entered as a random intercept, and mass loss or compensation as random slopes (Supplementary Table 6 and 7).

General procedures - R version 3.3.0 (R-Core-Team 2016) was used for all statistical analyses and the 'lme4' R package (Bates et al. 2015) for fitting the mixed-effect models. The models were fitted with maximum likelihood. We used the 'sim' function from the 'arm' R package and non-informative prior-distribution (Gelman & Hill 2007; Gelman & Su 2015) to create a sample of 2,000 simulated values for each model parameter (i.e. posterior distribution). We report effect sizes and model predictions by the medians, and the uncertainty of the estimates and prediction by the Bayesian 95% credible intervals represented by 2.5 and 97.5 percentiles (95% CI) from the posterior distribution of 2,000 simulated or predicted values. We estimated the variance in the random effects by 'lmer' or 'glmer' function from the 'lme4' R package (Bates et al. 2015).

In models with control and treated period, or with before- and post-experimental period, the dependent variables for treated and post-experimental period were necessarily more variable than for control or before-experimental period (heteroscedascity). Thus, we have specified a set of models where we controlled for the heteroscedascity by scaling the dependent variable within period (control or treated, or before or post-experimental). These models generated similar results as the original models. Because the original models are on original scale, and hence easier to interpret, we report only the outcomes of the original models.

In all model comparisons we assessed the model fit by Akaike's Information Criterion corrected for sample size (AICc; Anderson 2008) generated by the 'AICc' function from the 'AICcmodavg' R package (Mazerolle 2016).

Results

Compensation for absence of parental care

Overall the focal parents partially compensated for the absence of their partner's care (Figure 2a). The nest attendance (proportion) in the treated period was on average by 0.38 (95%CI: 0.27-0.50) lower than in the control period (Figure 2b; Supplementary Table 1; $N = 25$ nests each with one control and one treated period). This translates to 59% (49-70%) compensation for the absence of the partner's care. There was a 0.65 probability that the true mean compensation of the population was between 55% and 65%. The compensation was similar for females and males (Figure 2b, Supplementary Table 1; the model containing sex in interaction with treatment was ~ 8.5 times less likely than the model without this interaction).

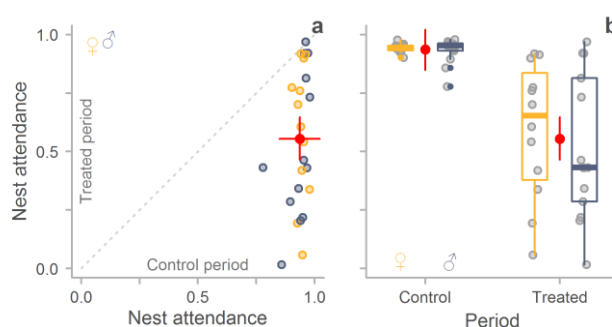


Figure 2 | Compensation for a temporary absence of care. **a-b**, Control period reflects regular incubation bout of the focal parent, treated period the temporary absence of care from the focal parent's partner, i.e. the period, during which the removed partner should have incubated, but could not because we held it in captivity. Yellow indicates ♀, blue-grey ♂, points represent nest attendance for each individual, red dots with bars indicate model predictions with 95%CI (Supplementary Table 1). **a**, Compensation of each individual ($N = 25$). Grey dashed line indicates full compensation. Points below the line represent various degrees of partial compensation or no compensation; points above the line represent over-compensation. **b**, Overall difference in nest attendance between control and treated period and between female and male ($N = 25$ individuals, 12 females and 13 males, each with one control and one treated period). Box plots depict median (horizontal line inside the box), the 25th and 75th percentiles (box), 25th percentiles minus 1.5 times interquartile range and 75th percentile plus 1.5 times interquartile range or minimum/maximum value, whichever is smaller (bars), and the outliers (yellow and blue-grey dots).

The compensation response of the individual parents span the entire range of what is possible from no to full compensation (Fig 2a; median [range] compensation = 57% [2-101%], $N = 25$ nests). Birds achieved similar levels of partial compensation by various strategies (Figure 3). Some gradually decreased the nest attendance over the experimental period; some compensated fully for a part of the experimental period and then reduced the nest attendance, left the nest unattended, or left the nest unattended but came back later. Remarkably, the individuals with nearly no compensation during the treated period, returned to the nest for their next incubation bout and continued with their incubation routine (Figure 3, top row). Similarly, the fully compensating parents could not sustain full compensation for ever and hence left the nest unattended after continuously incubating for more than 24 hours (Figure 3, panels in two bottom rows).

Explaining the diversity in compensation

Contrary to the natural situation, in which nest attendance slightly decreases during the warmer part of a day (Figure 4a, in blue-grey and green), the parents compensating during the warmer part of a day tended to have higher nest attendance (Figure 4a, in yellow). Compensation seemed unrelated to the proportion of the focal parent's care during the pre-treatment period (Figure 4b), which may be due to a lack of variation in the proportion of focal parent's care (range: 0.42-0.55). There was a tendency for parents with long escape distance (that is sensitive parents) to compensate more (Figure 4c). The escape distance model had greatest support of the three models (time of day, proportion of care and escape). The probability of the escape model was 0.87 and the model was 18 times more likely than the proportion of care model and 11 times more likely than the time of day model (Supplementary Table 2).

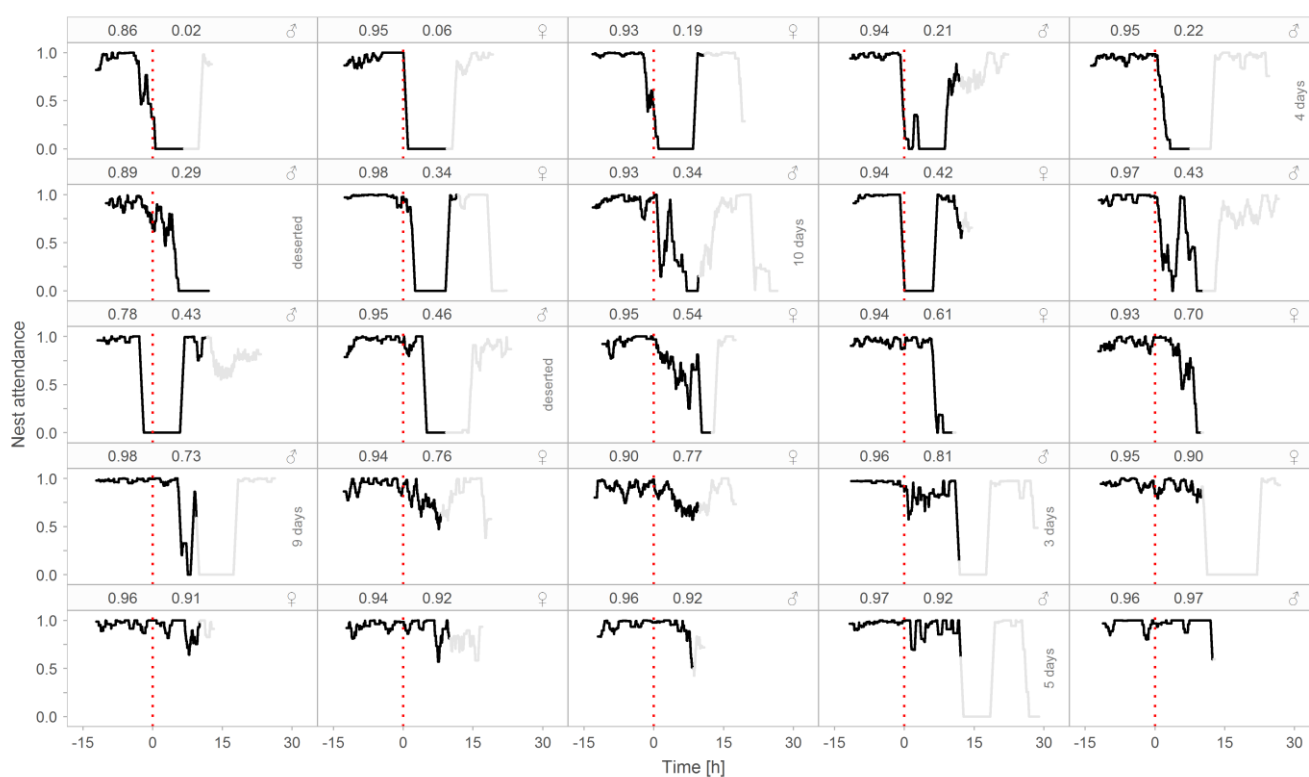


Figure 3 | Diverse compensation response for an absence of care. Each panel represents one of 25 focal individuals. Panels are ordered according to nest attendance within the treated period; the individual with the lowest nest attendance is in the top-left panel, the individual with the highest nest attendance in the bottom-right panel. Black lines demarcate the nest attendance during the experimental period (i.e., time from return of the focal parent until the release of the removed parent). Red dotted line indicates the end of the control period (i.e. regular incubation bout; negative values) and the start of the treated period (compensation period, positive values). Grey line indicates the nest attendance from release of the removed parent until its return to the nest. In seven nests where the removed parent never returned, we show a maximum of 30 hours of post-experimental period (grey line) and note whether the incubating parent deserted within this period, or for how many days the individual continued incubating uniparentally.

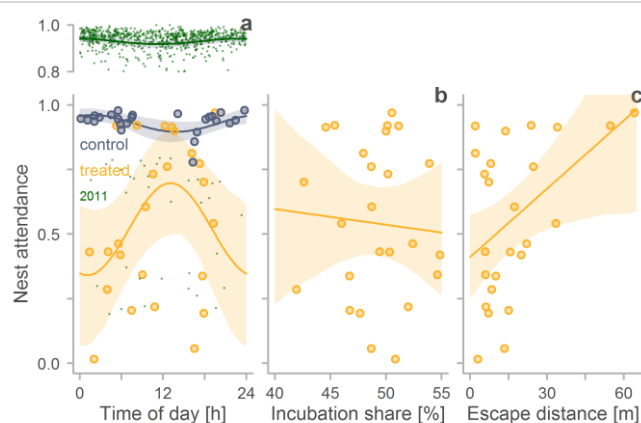


Figure 4 | Correlates of compensation. **a-c**, Relationships between nest attendance and the mid-time of the treated period, for which the focal parent compensated (**a**), the focal parent's share of incubation (**b**) and its escape distance from the nest (**c**) prior to the experiment. Yellow points represent individual observations ($N = 25$) and yellow lines with yellow-shaded areas indicate model predictions with 95%CI for the treated period (Supplementary Table 2). **a**, To emphasize how the relationship of nest attendance with time differs between treated period and undisturbed situation, we also added in blue-grey the observations and predictions for the control period and in green observations and predictions from the year 2011 (Supplementary Table 3; the 2011 data come from Bulla et al. 2013b; Bulla et al. 2014).

Post-experimental effects

In five out of 25 experimental nests the removed parent never returned upon release. All five birds were females. Also in an additional two nests (excluded from the main analyses, as one was partially depredated during the incubation bout prior to removal and another deserted by the focal bird prior to treatment), the removed females never returned.

The five widowed males and the additional two experimentally widowed males (see Methods) continued incubating for another 4 days (median; range: 0-10 days). They then deserted the nest ($N = 5$), possibly hatched one egg and deserted the remaining three eggs ($N = 1$), or the nest was depredated ($N = 1$).

In the 18 nests where the removed parent returned to incubate, parents differed markedly in how long it took them to return (median [range] = 7.36 hours [0.26-16.85 hours]). In these 18 nests, the overall quality of incubation during the post-experimental period was lower than during before-experimental period (Figure 5; Supplementary Table 4 and 5); nest attendance decreased, length of incubation bouts shortened and non-zero exchange gaps, although their probability was similar across periods, prolonged (at least immediately after the end of the experiment; figure 5c). However, parents recovered from the effect of treatment with time, as the nest attendance tended to increase, bouts prolonged, and gaps shortened with days after experimental period (Figure 5c).

The length, but not nest attendance, of post-experimental incubation bouts might have been related to the mass loss of the removed parent while in captivity (Figure 6a), or by how much the focal parent compensated during treated period (Figure 6b).

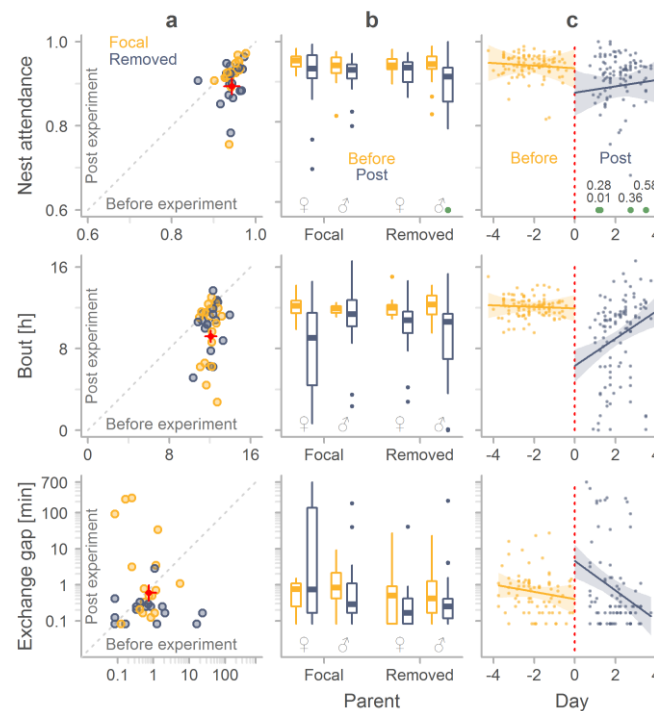


Figure 5 | Differences in quality of incubation before and post experimental period. **a**, Relationships between before- and post-experimental period for median nest attendance, median bout length and median non-zero exchange gap. Points represent medians for focal parents (in yellow) and for removed parents (in blue-grey; $N_{\text{nest attendance}} = 36$ individuals, $N_{\text{bout}} = 36$ individuals, $N_{\text{gap}} = 33$ individuals). Red dots with red crosses indicate model predictions with 95%CI (Supplementary Table 4 and 5, 'simple model'). **b**, Distribution of constancies, bouts and gaps across parents (focal, removed), sex and period (before experiment – in yellow, post experiment – in blue-grey; $N_{\text{nest attendance}} = 214$ bouts, $N_{\text{bout}} = 214$ bouts, $N_{\text{gap}} = 164$ gaps; for description of boxplots see Figure 2). Four outliers outside the y-axis range in the outer-right nest attendance boxplot are depicted by green point and their actual value is indicated in **c**. **c**, Relationship between nest attendance, bout or gap and number of days before- (in yellow) and post-experimental period (in blue-grey). N and color-coding is same as in **b**. Dots represent individual observations and lines with shaded areas indicate model predictions with 95%CI (Supplementary Table 6 and 7, 'day model'). Red dotted line indicates the experimental period (i.e. end of before-experimental and start of post-experimental period). In the nest attendance graph, nest attendance values of four points (in green) are outside the y-axes range; numbers above the points indicate their actual nest attendance value. In case of nest attendance the day model (predictions in **c**) was 2.6 less more likely than the simple model (predictions in **a**). In case of bout length, the day model (**c**) was nearly 10,000 times more likely than the simple model (**a**), and in case of exchange gap, the day model (**c**) was ~580,000 times more likely than the simple model (**a**), but model containing also parent (focal, removed) was even more likely (Supplementary Table 5).

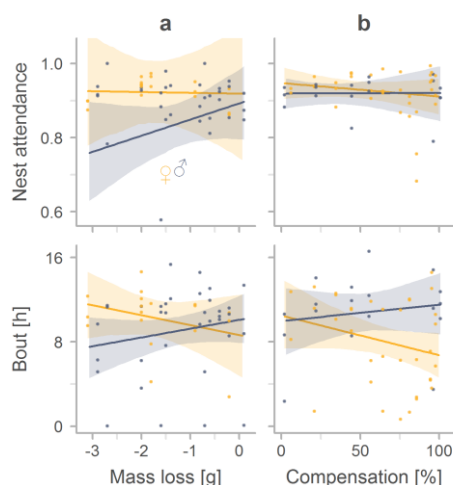


Figure 6 | Mass loss and compensation as predictors of nest attendance and bout length in the post-experimental period. a, Relationship between mass loss of the removed parent (while in captivity) and its bout attendance and length during post-experimental period. **b**, Relationship between amount of compensation of the focal parent during treated period and its bout attendance and length during post-experimental period. **a-b**, Yellow indicates ♀, blue-grey ♂, dots represent individual observations and lines with shaded areas indicate model predictions with 95%CI (Supplementary Table 6 and 7, 'sex model'). In all four cases the model with sex was far more likely than model without sex (Supplementary Table 6 and 7).

Discussion

Diverse compensation

Our result, that parents of semipalmated sandpipers on average partially compensate for temporal absence of care from their partner, seems to defy the prediction of the incubation model (Jones et al. 2002), but seems in line with the general predictions of established parental care models (Houston & Davies 1985; McNamara et al. 1999; McNamara et al. 2003). However, contrary to the later model, partial compensation was not the dominating response. That is, parents varied greatly in how they responded (Figure 3): some parents did not compensate, some showed various degrees of partial compensation, and some compensated fully. Essentially, the distribution of the compensation responses was uniform (Figure 2a). We discuss two possible explanations of this uniform diversity.

(1) Both parents of semipalmated sandpipers were thought to be needed for successful incubation (Hicklin & Gratto-Trevor 2010). Thus, according to this theory, parents faced with a temporal decrease in incubation from their partner should fully compensate, or desert the nest (Jones et al. 2002). However, under certain circumstances (e.g. warmer breeding season, nearing end of incubation period, or a parent with large energy reserves) a reduction in incubation effort may not lead to complete loss of breeding attempt and thus parents may have some room to exploit one another. Indeed here, one permanently widowed parent incubated uniparentally for 10 days (see Supplementary Actograms in Bulla 2016) and some non-experimental nests hatched after 14 days of uniparental incubation (**Chapter 4** & Supplementary Actograms in Bulla & Kempnaers 2016). Thus the varying circumstances among nests could translate into various compensation levels.

Alternatively, (2) parents always attempt to compensate fully, but sometimes fail to do so as (2a) their energy reserves get depleted (Figure 3), and/or because (2b) they are less responsive to the temporal absence of their partner's care (Figure 4c).

(2a) Parents of biparental species with continuous incubation (i.e. with close to 100% nest attendance) starve while incubating (Chaurand & Weimerskirch 1994; Weimerskirch 1995; Dearborn 2001; Bulla et al. 2014; Bulla et al. 2015a). Parents are then unable to incubate forever, that is, full compensation is possible as long as the energetic reserves last. We find some support for this explanation. As we demonstrate, even the parents that compensated fully at some point (likely when their body mass reached a threshold) left the nest unattended (Figure 3). The fully compensating parents differed from the not- or partially-compensating parents by 'deserting' the nest considerably later.

Also, parents treated during the warmer part of a day (when incubation is less demanding) tended to compensate more (i.e. had higher nest attendance) than parents treated during the colder part of a day. This contrasts with the nest attendance when both parents are present (Figure 4), as well as with the nest attendance of uniparentally incubating species (Cartar & Montgomerie 1985; Løfaldli 1985; Reneerkens et al. 2011). Their nest attendance drops during the warmer part of a day because the demands to warm the eggs are lower and food availability higher. Thus, the compensating parents might have tried but could not compensate fully when it was cold.

(2b) The level of compensation may depend solely on the perceived absence of the partner's care. Unlike chick feeding, where parents feed chicks simultaneously, incubation is a mutually exclusive behaviour, so that only a single parent can incubate at a time. However, as the off-nest parent is often out of the hearing range of the nest, the incubating and the off-nest parent communicate only during the brief period while exchanging on the nest. Thus, sometimes the off-nest partner is delayed and incubating parent leaves the nest before its partner returns to incubate (Ashkenazie & Safriel 1979; Bulla et al. 2014; Bulla et al. 2015a). Consequently, an incubating parent may be unable to realize immediately that its partner is truly missing. We can imagine a situation where a parent leaves the nest unattended and simply assumes that the partner will come back and incubate. The variation in how long a parent is willing to wait for its partner, or in responsiveness to the absence (Figure 4c), would then mirror the level of compensation. Indeed, some permanently widowed parents seemed to take several days to realize that their partner has deserted. They incubate their regular bout and leave the nest unattended for the supposed bout of their partner; after several days they take full responsibility for the nest and usually switch to uniparental incubation pattern (see **Chapter 4** & Supplementary Actograms in Bulla & Kempnaers 2016 and Bulla 2016).

Also, shy individuals are in general more responsive than bold ones (Koolhaas et al. 1999; Coppens et al. 2010). Indeed, our results suggest that shy individuals (those with longer escape distance) compensated more than bold ones (those with short escape distance; Figure 4c).

In sum, energetic constraint and responsiveness likely act together. Those parents that are responsive to the absence of their partner, and have the resources to wait for their partner's delayed return, will do so. Those parents that are less responsive to their partner's absence, or do not have the resources for full compensation, will compensate partially or not at all. Such an explanation is in line with the recent predictions of parental care models: parents are likely to vary in their compensation response based on the likelihood of the brood to fail in the absence of the care, parent's current condition and knowledge about (we add responsiveness to) their partner's condition or broods need (Jones et al. 2002; Johnstone & Hinde 2006).

Post-experimental effects

All parents that never returned to incubate upon release from captivity were females, which is similar to other species (Wiebe 2010). Given the stress of laying the eggs (a four-egg clutch is laid in five days and has a similar total mass as an average female's body mass; Hicklin & Gratto-Trevor 2010) females might be more sensitive to additional stressors. Indeed, females tend to desert the brood after hatching (Hicklin & Gratto-Trevor 2010). Nevertheless, we found no marked differences between females and males in compensation (Figure 2), or in post-experimental quality of incubation (Figure 5).

The quality of incubation in post-experimental period was lower than in before-experimental period, but improved with time (Figure 5); three days post-experimental period, the parents incubated as usual. As the post-experimental effects were generally similar for the focal and removed parent (Supplementary Table 4 and 5), the results suggest that the stress of compensation was likely similar to the stress of captivity. Furthermore, the mass loss of the removed parent while in captivity and the amount of compensation of the focal parent during experiment were poor predictors of post-treatment effects (Figure 6): they were unrelated to the nest attendance and unconvincingly related to the bout length in the post-experimental period.

Conclusions

Our finding that biparentally incubating shorebirds partially compensate, on average, for the temporal absence of parental care corroborates the predictions of established models (Houston & Davies 1985; McNamara et al. 1999; McNamara et al. 2003) and results of a meta-analysis (Harrison et al. 2009). However, the unprecedented uniform-distribution of diverse individual responses suggests no dominant compensation response in the population, i.e., it defies the predictions of the very same models. We speculate that all individuals attempt full compensation, but some fail because their energy reserves get depleted, or because they are less responsive to the absence of their partner, for which we provide some correlational evidence. To test whether energy reserves truly drive the compensation, saving energy (e.g. by supplemental feeding) during treatment should reduce the diversity in compensation responses, with all individuals compensating nearly fully. Although tricky, an alternative would be to repeat the very same experiment presented here, but with scales under the nest cups to continuously measure body mass of the

incubating birds. To verify whether responsiveness of the parents drives the compensation, the experiment should be repeated with the same and with other taxa. The diversity of compensation responses, their possible energetic constraint, as well as the possible link of responses to the responsiveness ('personality') of the parents deserves theoretical and mathematical modelling.

Author's contributions: M.B. and B.K. conceived the study; M.B. with help of A.R. collected the data; A.R. and M.B. managed the database; M.B. coordinated the study, analysed the data with help from M.V. and drafted the manuscript. All authors wrote the final paper.

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Data accessibility - All statistical analyses are replicable with the open access data and r-code available from <https://osf.io/mx82q/>, which also contains all supporting information.

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Supplementary information



Supplementary Figure 1 | Enclosure for nest-protection, boxes and shed for removed parents. **a**, Enclosure that protected the nest against avian predators (approximate size $0.8 \times 0.7 \times 0.5$ m) was a modification of an earlier design (Bulla et al. 2015b) and was made by cutting and bending a chicken wire (mesh size 5×5 cm and 5×10 cm where the cage touched the ground; wire ϕ 1.9 mm). The sharp parts sticking out into the air prohibit avian predators to land on the enclosure. **b**, Removed parents were brought to the shed where they were kept in cardboard boxes (21 cm \times 30 cm \times 25cm; with holes on the sides). **c**, Each box was lined with tundra and contained water and feeding tray.

Supplementary Table 1 | Effects of treatment on incubation constancy.

Model	AIC	Δ AICc ^a	w_i^b	ER ^d	Response	Effect type	Effect	Estimate	95% CI	
									Lower	Upper
minimal	-5.64	0	0.624	1	Incubation constancy (proportion)	Fixed	Intercept (control)	0.939	0.854	1.024
							Period (treated)	-0.384	-0.494	-0.266
							Random (variance)	0.004		
							Residual	0.04		
with period length	-4.19	1.45	0.302	2.06	Incubation constancy (proportion)	Fixed	Intercept (control)	0.915	0.823	1.011
							Period (treated)	-0.338	-0.484	-0.206
							Period length	0.035	-0.034	0.106
							Random (variance)	0.005		
with sex	-1.36	4.28	0.074	8.48	Incubation constancy (proportion)	Fixed	Intercept (control, ♀)	0.942	0.811	1.063
							Period (treated)	-0.345	-0.517	-0.179
							Sex (♂)	-0.012	-0.183	0.156
							Period \times Sex	-0.066	-0.304	0.165
						Random (variance)	Bird (intercept)	0.004		
							Residual	0.039		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 2,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015). $N = 25$ individual each with one control and treated period ($N = 50$ periods). We used 50 as the number of independent observations for AICc computation.

Period length was z-transformed (mean-centered and divided by SD).

^aThe difference in AICc between the first-ranked model and the given model.

^bAkaike weight – the weight of evidence that a given models is the best approximating model (i.e., probability of the model).

^dEvidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

Supplementary Table 2 | Predictors of incubation constancy during compensation.

Model	AIC	ΔAICc^a	w_i^b	ER ^d	Response	Effect	Estimate	95% CI	
								Lower	Upper
Time	15.71	4.74	0.08	11	Incubation constancy (proportion)	Intercept	0.518	0.391	0.645
						sin (time)	-0.051	-0.212	0.111
						cos (time)	-0.169	-0.381	0.028
Proportion	16.74	5.78	0.05	18	Incubation constancy (proportion)	Intercept	0.832	-1.145	2.725
						Proportion of incubation	-0.551	-4.411	3.484
Escape	10.97	0	0.87	1	Incubation constancy (proportion)	Intercept	0.405	0.245	0.569
						Escape distance (m)	0.009	0.001	0.016

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 2,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). $N = 25$ incubation constancies of treated periods of 25 individuals. We used 25 as the number of independent observations for AICc computation.

^aThe difference in AICc between the first-ranked model and the given model.

^bAkaike weight – the weight of evidence that a given models is the best approximating model (i.e., probability of the model).

^dEvidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

Supplementary Table 3 | Relationship of incubation constancy and time under un-manipulated conditions.

Model	Response	Effect type	Effect	Estimate	95% CI	
					Lower	Upper
Control	Incubation constancy (proportion)	Fixed	Intercept	0.929	0.911	0.947
			sin (time)	0.015	-0.005	0.035
			cos (time)	0.028	-0.003	0.058
2011 data	Incubation constancy (proportion)	Fixed	Intercept	0.929	0.918	0.939
			sin (time)	0.015	-0.011	0.007
			cos (time)	0.028	0.003	0.021
		Random (variance)	Bird (intercept)	0.00181		
			sin (time)	0.00008		
			cos (time)	0.00007		
			Residual	0.00617		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 2,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015).

$N_{\text{Control}} = 25$ incubation constancies of control periods of 25 individuals.

$N_{\text{2011 data}} = 832$ incubation constancies of 832 incubation bouts from 47 nests (the data come from Bulla et al. 2013b; Bulla et al. 2014)

Supplementary Table 4 | Difference in incubation constancy and bout length in before- and post-experiment period.

Model	AIC	$\Delta AICc^a$	w_i^b	ER ^d	Response	Effect type	Effect	Estimate	95% CI		
									Lower	Upper	
day	-388.3	1.92	0.268	2.61	Incubation constancy (proportion)	Fixed	Intercept (before)	0.937	0.891	0.982	
							Period (post)	-0.057	-0.128	0.011	
							Day	-0.003	-0.023	0.016	
							Period × Day	0.01	-0.021	0.04	
							Random (variance)	Bird (intercept)	0.001		
							Residual	0.008			
simple	-390.2	0	0.701	1	Incubation constancy (proportion)	Fixed	Intercept (before)	0.943	0.925	0.962	
							Period (post)	-0.049	-0.076	-0.025	
							Random (variance)	Bird (intercept)	0		
							Residual	0.009			
complex	-383.9	6.27	0.03	22.98	Incubation constancy (proportion)	Fixed	Intercept (before, removed)	0.94	0.875	1.009	
							Period (post)	-0.108	-0.206	-0.012	
							Parent (focal)	-0.007	-0.093	0.079	
							Day	-0.001	-0.027	0.025	
							Period × Parent	0.105	-0.034	0.242	
							Period × Day	0.017	-0.028	0.061	
							Parent × Day	-0.005	-0.042	0.033	
							Period × Parent × Day	-0.016	-0.077	0.041	
							Random (variance)	Bird (intercept)	0.001		
							Day (slope)	0			
							Residual	0.008			
day	1045.7	0	0.992	1	Bout length (hours)	Fixed	Intercept (before)	11.94	10.74	13.15	
							Period (post)	-5.64	-7.5	-3.71	
							Day	-0.07	-0.6	0.46	
							Period × Day	1.39	0.57	2.22	
							Random (variance)	Bird (intercept)	0.65		
							Day (slope)	0.1			
Residual	6.28										
simple	1064	18.3	0	9918	Bout length (hours)	Fixed	Intercept (before)	12.08	11.52	12.64	
							Period (post)	-2.85	-3.62	-2.1	
							Random (variance)	Bird (intercept)	0.24		
Residual	7.89										
complex	1055.3	9.63	0.008	122.44	Bout length (hours)	Fixed	Intercept (before, removed)	11.64	9.77	13.63	
							Period (post)	-4.92	-7.86	-2.06	
							Parent (focal)	0.48	-2	3.08	
							Day	-0.2	-0.97	0.56	
							Period × Parent	-1.51	-5.42	2.36	
							Period × Day	1.48	0.2	2.68	
							Parent × Day	0.26	-0.8	1.41	
							Period × Parent × Day	-0.13	-1.9	1.69	
							Random (variance)	Bird (intercept)	0.61		
							Day (slope)	0.1			
							Residual	6.26			

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 2,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015).

$N = 214$ incubation bouts from 36 individuals from 18 nests (three before- and three post-experimental bouts for each individual with exception of one nest where due to depredation both parents have only two post-experimental bouts). We used 72 as the number of independent observations for AICc computation, i.e., 36 individuals with before- and with post-experimental period.

^aThe difference in AICc between the first-ranked model and the given model.

^bAkaike weight – the weight of evidence that a given models is the best approximating model (i.e., probability of the model).

^dEvidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

Supplementary Table 5 | Difference in probability and length of exchange gap in before- and post-experiment period.

Model	AIC	ΔAICc^a	w_i^b	ER ^d	Response	Effect type	Effect	Estimate	95% CI		
									Lower	Upper	
day	236.4	6.92	0.03	31.82	Exchange gap (binomial scale)	Fixed	Intercept (before)	1.54	0.4	2.77	
							Period (post)	0.91	-0.85	2.64	
							Day	0.04	-0.46	0.6	
							Period × Day	-0.51	-1.35	0.3	
							Random (variance)	Bird (intercept)	1.19		
Day (slope)	0.01										
simple	229.4	0	0.964	1	Exchange gap (binomial scale)	Fixed	Intercept (before)	1.33	0.77	1.92	
							Period (post)	0.21	-0.46	0.89	
							Random	Bird (intercept)	1.06		
complex	239.8	10.3	0.006	172.16	Exchange gap (binomial scale)	Fixed	Intercept (before, removed)	1.09	-0.28	2.66	
							Period (post)	-0.18	-2.39	2.1	
							Parent (focal)	1.64	-1.33	4.45	
							Day	-0.02	-0.76	0.7	
							Period × Parent	2.15	-2.11	6.24	
							Period × Day	0.32	-0.81	1.46	
							Parent × Day	0.4	-0.81	1.57	
							Period × Parent × Day	-2.08	-3.76	-0.34	
							Random (variance)	Bird (intercept)	1.29		
							Day (slope)	0.01			
day	1862.9	5.61	0.057	16.51	Exchange gap (minutes)	Fixed	Intercept (before)	8.68	-23.7	42.25	
							Period (post)	100.1	53.72	147.7	
							Day	2.58	-11.82	16.68	
							Period × Day	-40.62	-64.01	-17.99	
							Random (variance)	Bird (intercept)	1444.33		
Day (slope)	131.97										
Residual	3385.53										
simple	1889.4	32.15	0	9586519	Exchange gap (minutes)	Fixed	Intercept (before)	2.62	-15.63	21.73	
							Period (post)	33.04	10.85	54.5	
							Random (variance)	Bird (intercept)	860.57		
Residual	4936.25										
complex	1857.3	0	0.943	1	Exchange gap (minutes)	Fixed	Intercept (before, removed)	3.04	-38.43	43.71	
							Period (post)	24.93	-37.64	91.44	
							Parent (focal)	2.05	-63.35	67.22	
							Day	0.25	-20.89	19.97	
							Period × Parent	150.82	55.66	242.48	
							Period × Day	-11.22	-43.8	20.99	
							Parent × Day	1.32	-27.78	31.18	
							Period × Parent × Day	-51.71	-94.35	-7.46	
							Random (variance)	Bird (intercept)	1178.04		
							Day (slope)	106.85			
Residual	3111.94										

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 2,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015).

$N_{\text{binomial}} = 214$ exchange gaps from 36 individuals from 18 nests (three before- and three post-experimental gaps for each individual with exception of one nest where due to depredation both parents have only two post-experimental gaps). We used 72 as the number of observations for AICc computation, i.e., 36 individuals with before- and with post-experimental period.

$N_{\text{minutes}} = 164$ non-zero exchange gaps from N_{binomial} from 35 individuals from 18 nests. We used 68 as the number of observations for AICc computation, i.e., 34 individuals with before and 34 individuals with post period (out of 35 individuals one individual had not before and another individual no post non-zero exchange gap).

^aThe difference in AICc between the first-ranked model and the given model.

^bAkaike weight – the weight of evidence that a given models is the best approximating model (i.e., probability of the model).

^dEvidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

Supplementary Table 6 | Effect of mass loss of the removed parent on its incubation constancy and bout length in the post-experiment period.

Model	AIC	ΔAICc^a	w_i^b	ER ^d	Response	Effect type	Effect	Estimate	95% CI		
									Lower	Upper	
sex	-15.2	0	0.98	1	Incubation constancy (proportion)	Fixed	Intercept (♀)	0.925	0.838	1.01	
							Mass loss	-0.005	-0.09	0.082	
							Sex (♂)	-0.094	-0.19	0.008	
							Mass loss × sex	0.044	-0.06	0.153	
							Random (variance)	Bird (intercept)	0		
							Residual	0.028			
simple	-7.4	7.81	0.02	49.55	Incubation constancy (proportion)	Fixed	Intercept	0.866	0.815	0.917	
							Mass loss	0.015	-0.03	0.064	
							Random (variance)	Bird (intercept)	0		
							Mass loss (slope)	0			
							Residual	0.03			
sex	309.9	0	0.988	1	Bout length (hours)	Fixed	Intercept (♀)	9.917	8.024	11.77	
							Mass loss	-0.871	-2.75	0.985	
							Sex (♂)	-1.004	-3.18	1.221	
							Mass loss × sex	1.676	-0.6	3.849	
							Random (variance)	Bird (intercept)	0.66		
							Mass loss (slope)	0.074			
Residual	12.862										
simple	318.8	8.86	0.012	83.88	Bout length (hours)	Fixed	Intercept	9.446	8.385	10.55	
							Mass loss	0.073	-0.98	1.179	
							Random (variance)	Bird (intercept)	0.197		
							Mass loss (slope)	0.002			
							Residual	13.859			

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 2,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015).

$N = 53$ incubation bouts from 18 individuals (three post-experimental bouts for each individual with exception of one where due to nest the parent has only two post-experimental bouts). We used 18 as the number of independent observations for AICc computation.

Mass loss (g) was z-transformed (mean-centered and divided by SD), except for random slope in bout models as non-transformed mass loss improved convergence.

^aThe difference in AICc between the first-ranked model and the given model.

^bAkaike weight – the weight of evidence that a given models is the best approximating model (i.e., probability of the model).

^dEvidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

Supplementary Table 7 | Effect of compensation on focal parent's incubation constancy and bout length in the post-experiment period.

Model	AIC	$\Delta AICc^a$	w_i^b	ER ^d	Response	Effect type	Effect	Estimate	95% CI		
									Lower	Upper	
sex	-147.7	0	0.996	1	Incubation constancy (proportion)	Fixed	Intercept (♀)	0.925	0.9	0.95	
							Compensation	-0.012	-0.037	0.012	
							Sex (♂)	-0.007	-0.051	0.04	
							Compensation × sex	0.012	-0.03	0.053	
							Random	Bird (intercept)	0.001		
							(variance)	Compensation (slope)	0		
simple	-136.5	11.26	0.004	279.31	Incubation constancy (proportion)	Fixed	Intercept	0.923	0.902	0.943	
							Compensation	-0.005	-0.025	0.014	
							Random	Bird (intercept)	0.001		
							(variance)	Compensation (slope)	0		
								Residual	0.002		
sex	317.8	0	0.918	1	Bout length (hours)	Fixed	Intercept (control, ♀)	8.217	6.939	9.553	
							Compensation	-1.248	-2.827	0.22	
							Sex (♂)	2.724	0.305	5.019	
							Compensation × sex	1.806	-0.281	4.076	
							Random	Bird (intercept)	0		
							(variance)	Compensation (slope)	0		
simple	322.7	4.84	0.082	11.27	Bout length (hours)	Fixed	Intercept	9.06	7.896	10.277	
							Compensation	-0.67	-1.891	0.501	
							Random	Bird (intercept)	0.783		
							(variance)	Compensation (slope)	0.337		
								Residual	15.273		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 2,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015).

$N = 53$ incubation bouts from 18 individuals (three post-experimental bouts for each individual with exception of one where due to nest predation the parent incubated only for two post-experimental bouts). We used 18 as the number of independent observations for AICc computation.

Compensation (proportion) was z-transformed (mean-centered and divided by SD).

^aThe difference in AICc between the first-ranked model and the given model.

^bAkaike weight – the weight of evidence that a given models is the best approximating model (i.e., probability of the model).

^dEvidence ratio – model weight of the first-ranked model relative to that of the given model (i.e., how many times is the first-ranked model more likely than the given model).

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Chapter 4

Flexible parental care: Uniparental incubation in biparentally incubating shorebirds

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Parental care comes in various forms. Recent theory and empirical findings suggest that the adult sex-ratio of a population should drive its specific form of care (e.g. all else being equal, if the sex ratio is male skewed, males should be the more caring sex). Whether such outcomes are evolutionary fixed to the typical sex-ratio of the species, or arise through flexible response of individuals to the current sex-ratio, remains unclear. Nevertheless, the flexible response might be limited by evolutionary history (e.g. males of avian species that have lost the brood patch are unlikely to incubate, or uniparental incubation in biparental birds might be unlikely if embryos die under fluctuating temperatures, or if parents are unable to maintain their energetic balance). Here, we demonstrate that after desertion of a parent, 8 out of 15 biparentally incubating shorebird species were able to incubate uniparentally, at least for some time (median = 3, range: 1-19 days, $N = 69$ cases). Such uniparental incubation resembled the incubation of uniparental species. Contrary to the prior belief that females of some shorebirds desert their brood after hatching, our findings demonstrate that either sex sometimes deserts even prior to hatching. Strikingly, in 5 species we document cases where uniparentally incubating parents brought their clutch to hatching. These findings reveal a potential for a flexible switch from biparental to uniparental care.

Introduction

Parental care is a tremendously diverse social trait; the amount of parental cooperation varies along continuum, from equal share of care by the female and male, to uniparental care in which only one of the two provides all care (Clutton-Brock 1991; Royle et al. 2012). A recent theory and between-species empirical data suggest that the sex that is in short supply in the population has an increased mating opportunity, and is thus less likely to provide care than the more abundant sex (Forsgren et al. 2004; Kokko & Jennions 2008; Kokko & Jennions 2012; Liker et al. 2013; Parra et al. 2014; Remes et al. 2015). Although these empirical data provide some support for the role of the adult sex-ratios in shaping the parental care system on the evolutionary time-scale, it is less clear whether species and populations flexibly adjust their form of parental care to the current sex-ratios. Essentially, this potential flexibility might be limited by the species' evolutionary history.

We take incubation of eggs in birds as an example. Whereas in some species parents can switch flexibly between years from biparental to uniparental care and vice versa (Reneerkens et al. 2014), in others such flexibility is unlikely because, for example, males have already lost their brood patch and hence cannot incubate effectively (Hawkins 1986). Similarly, species that typically incubate biparentally (i.e. parents share incubation roughly equally and both parents possess brood-patch) might be evolutionary constrained to incubate uniparentally because embryos might not withstand fluctuating temperatures, or single parents may not be able to work hard enough to bring the clutch to hatching (Erckmann 1981; Martin Bulla 2016).

Here, we investigated in 15 biparentally incubating shorebird species (1) whether uniparental incubation is possible. If so, we used daily nest attentiveness (incubation constancy) and its temporal distribution over the day to demonstrate (2) how biparental incubation rhythm changed to uniparental one, and to compare this uniparental incubation rhythm with the incubation rhythm of uniparental shorebird species with female-only incubation (pectoral sandpiper, *Calidris melanotos*) and male-only incubation (red-necked phalarope, *Phalaropus lobatus*). Then, we investigated (3) whether the uniparental nests succeeded and, if so, whether the nest success was related to when within the incubation period the uniparental incubation started and for how long the uniparental incubation lasted.

Methods

Data collection

Between 2011 and 2014, we recorded biparental incubation with radio frequency identification (RFID) in combination with nest and surface (next to the nest) temperature probes (Bulla et al. 2014; Bulla et al. 2015a) at hundreds of nests from 19 populations of 15 shorebird species (for list of populations and species see Data (Bulla & Kempenaers 2016));

eight populations come from Alaska, seven from Iceland, one from the Czech Republic and two from the Neatherlands (for site information see (Bulla et al. 2015b; Bulla et al. 2016a)).

In 2008 and 2009, we recorded uniparental incubation of 13 female pectoral sandpipers (*Calidris melanotos*) from Alaska (71.32°N, 156.65°W) by automated tracking system (Lesku et al. 2012).

In 2015, we recorded uniparental incubation of 9 male red-necked phalaropes (*Phalaropus lobatus*) from Chukotka (64.75°N, 177.67°E) with nest and surface temperature probes (Bulla et al. 2014; Bulla et al. 2015a).

If a nest was found during laying, we estimated the start of incubation from the visualized raw data (actograms) or by assuming that females laid one egg per day. If nests were found with a full clutch (usually four, rarely three eggs), we estimated the start of incubation by subtracting the average incubation period of the species (derived from the literature (Bulla & Kempenaers 2016)) from the hatching date, or as the median start of incubation based on the height and inclination of the eggs floated in water (Liebezeit et al. 2007). For one nest we lacked any of this information and hence the start of incubation was estimated as the median start of incubation of the species in the given year.

Extraction of incubation

In nests with temperature recordings, constant incubation-temperatures higher than surface temperatures were interpreted as continuous incubation; the start of incubation was determined from a steep increase in nest temperatures, the interruption of incubation from a steep decrease (Bulla 2014; Bulla et al. 2014; Bulla et al. 2015a; Bulla & Kempenaers 2016)

For nests with automated tracking, the signal strength of a radio-tag attached to the rump of a female was nearly constant when the female was incubating (Lesku et al. 2012; Bulla & Kempenaers 2016).

We define uniparental incubation in biparental species as the incubation of a single parent after it incubated the median incubation bout length of its population and remained responsible for the nest for at least a period of twice the population bout (population bouts were derived from (Bulla et al. 2016a; Bulla et al. 2016b) and are available here (Bulla & Kempenaers 2016)). This uniparental period did not include 6 hours before start of hatching or 24 hours before the chicks hatched or left the nest. In this way we limited the data to uniparental incubation (a) not confounded by prolonged incubation bout (due to partner's absence) followed by immediate desertion, and (b) not confounded by hatching. Also, by using longer spells of uniparental incubation we could investigate the change in nest attendance within a day and also over the days, i.e. from an attempt to temporarily compensate for delayed return of the partner (Martin Bulla 2016) to finding solutions for being widowed.

This gave us 69 cases of uniparental incubation from 67 nests; two nests had two cases as one parent deserted the nest first temporarily and later for good. We report on the uniparental incubation that occurred after a parent naturally or semi-naturally (e.g. after capture) deserted the nest. We do not know for all cases whether the deserting bird truly deserted, or whether it was predated upon. Some nests were protected against avian predators using one of two enclosure types, both made of mesh wire (Supplementary 1, Picture S1 (Bulla et al. 2015a) and Supplementary Figure 1 (Martin Bulla 2016)). In some nests, the desertion followed after a parent had experienced trouble escaping from the nest through the first type of enclosure (Bulla et al. 2015a) when approached by an avian predator. In the semipalmated sandpiper we also report on 4 nests uniparentally incubated after we experimentally removed a parent (Martin Bulla 2016).

To compare incubation between biparental and uniparental periods, as well as to compare uniparental incubation between biparental and uniparental species, we use nest attendance (constancy of incubation) defined as the proportion of time a bird actually incubated within a given period of time (day or hour). For these analyses, we use only periods (day or hours) where the biparental or uniparental incubation covered at least 75% of the given period. We excluded temperature readings from a dislocated temperature probe (one whole nest and part of the readings in two additional nests). We further excluded two nests where uniparental bird incubated a single egg. This gave us 909 cases of daily nest attendance and 23,613 cases of hourly nest attendance from 88 nests of 10 species (66 nests of 8 biparental species, 22 nests of 2 uniparental species).

Statistical analyses

We tested for the difference in biparental and uniparental nest attendance in two mixed-effect models. The first model contained daily nest attendance (proportion) as a response, day in incubation period (continuous predictor defined as proportion of species' typical incubation bout derive from (del Hoyo et al. 1996; Poole 2005) and available here (Bulla & Kempenaers 2016)) in interaction with type of incubation (three level categorical predictor: biparental or uniparental of biparental species and uniparental of uniparental species), nest and species, both in interaction with type of incubation (biparental or uniparental), as random intercepts and day in incubation period as a random slope. The second model contained hourly nest attendance (proportion) as a response, time of day (continuous predictor; transformed to radians and represented by a sine and cosine) in interaction with type of incubation (three level categorical predictor: biparental or uniparental of biparental species and uniparental of uniparental species), nest and species, both in interaction with type of incubation (biparental or uniparental), as random intercepts, and time of day as a random slope.

In addition, in four biparental species with cases of both female and male uniparental incubation, we tested in two models whether uniparental incubation was sex specific. The first model contained daily uniparental nest attendance as a response, day in incubation

period (continuous predictor) in interaction with sex (categorical predictor: female or male), nest and species as random intercepts and day in incubation period as a random slope. The second model contained hourly uniparental nest attendance as a response, time of day (continuous predictor; transformed to radians and represented by a sine and cosine) in interaction with sex (female or male), nest and species as random intercepts, and time of day as a random slope.

Last, for 54 biparental nests, with uniparental incubation and known nest faith, we tested in a binomial model whether nest success (binary response) was related to when the uniparental incubation started within the incubation period (Start; defined as proportion of species' typical incubation bout) and for how many days it lasted (Duration). Species was specified as a random slope. Correlation between Start and Duration was -0.338 and -0.247 (Pearson's and Spearman's correlation coefficient).

R version 3.3.0 (R-Core-Team 2016) was used for all statistical analyses and the 'lme4' R package (Bates et al. 2015) for fitting the mixed-effect models. We used the 'sim' function from the 'arm' R package and non-informative prior-distribution (Gelman & Hill 2007; Gelman & Su 2015) to create a sample of 5,000 simulated values for each model parameter (i.e. posterior distribution). We report effect sizes and model predictions by the medians, and the uncertainty of the estimates and prediction by the Bayesian 95% credible intervals represented by 2.5 and 97.5 percentiles (95% CI) from the posterior distribution of 5,000 simulated or predicted values. We estimated the variance in the random effects by 'lmer' or 'glmer' function from the 'lme4' R package (Bates et al. 2015) with maximum likelihood.

Results

Abundance of uniparental incubation

We found some uniparental incubation in 8 out of 15 biparental shorebirds species that we studied. Females incubated uniparentally less often than males (in 14 out of 69 cases, and in 4 out of 8 species; Figure 1a).

Uniparental incubation started mostly in the second half of incubation period (median = 71% of incubation period, range: 11 - 155%, $N = 69$ cases of uniparental incubation from 67 nests; Figure 1b). The median remained similar (70%) even after we excluded uniparental incubation that started after the eggs were supposed to hatch (range: 11 - 95%, $N = 62$ uniparental cases from 60 nests).

Uniparental incubation lasted a median of 3 days (range: 1 - 19 days, $N = 69$ cases; Figure 1c). This median is likely underestimated as in 10 nests the monitoring system was taken off the nest before the incubation ended. In two species (American golden plover, *Pluvialis dominica*, and Common redshank, *Tringa totanus*), one nest each, a single parent likely incubated for the whole incubation period (Supplementary Actograms (Bulla & Kempnaers 2016)).

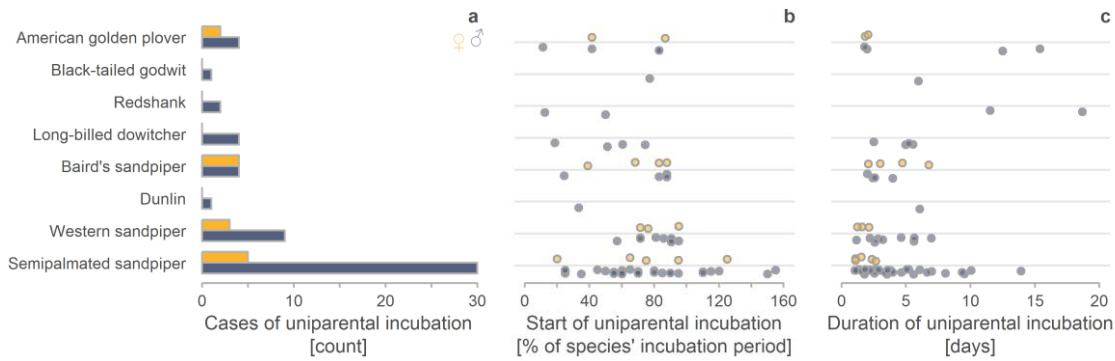


Figure 1 | Uniparental incubation in biparental shorebirds according to sex. **a**, Number of cases where one of the parent incubated uniparentally. **b**, Start of uniparental incubation (distribution) within incubation period of given species defined as % of species' typical incubation period. **c**, Duration of uniparental incubation in days (distribution). **a-c**, Female uniparental incubation (●; yellow), male uniparental incubation (●; blue-grey). $N = 69$ case of uniparental incubation from 67 nests.

Change in nest attendance

After the biparental species switched to uniparental incubation, the daily nest attendance decreased and was overall similar to the daily nest attendance of uniparental species (Figure 2a-b & 3). Whereas daily nest attendance in uniparental species and during biparental incubation is roughly constant over the course of incubation period, the longer the uniparental incubation of biparental species lasted, the higher the nest attendance tended to be (Figure 2b). However, species and individuals varied greatly in this respect (Supplementary Figure 1; random slope explained 34% of the variance – Supplementary Table 1), and the effect seemed absent in females (Supplementary Figure 2a and Supplementary Table 2).

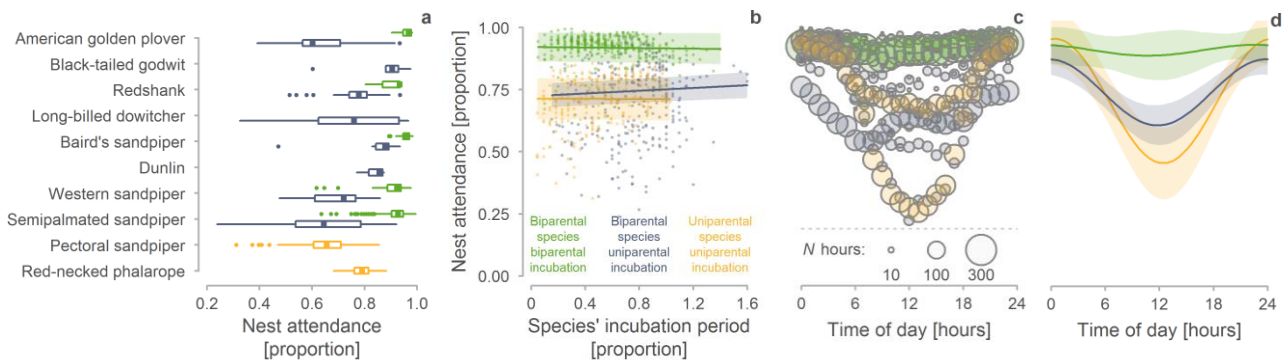


Figure 2 | Daily nest attendance in biparental and uniparental shorebirds. **a**, Distribution of biparental and uniparental daily nest attendance across biparental and uniparental (last two) species ($N = 909$ days from 88 nests of 10 species). **b-d**, Change in daily nest attendance across incubation period (**b**; proportion of species' typical incubation period) and across day (**c-d**) for biparental species incubating biparentally (●; green) and uniparentally (●; blue-grey) and for uniparental species (●; yellow). Dots represent daily nest attendance for each day (**b**) and mean hourly observations for each species (**c**; their size number of hours). Lines with shaded areas indicate model predictions with 95%CI (Supplementary Table 1 & 3) based on the joint posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). $N_b = 909$ days and $N_{c-d} = 23,613$ hours from 88 nests of 10 species. Note that nest attendance of previous hour strongly predicts the nest attendance of current hour (partial temporal-autocorrelation of model residuals in lag one = 0.49) possibly making the 95%CIs (**c**) narrower.

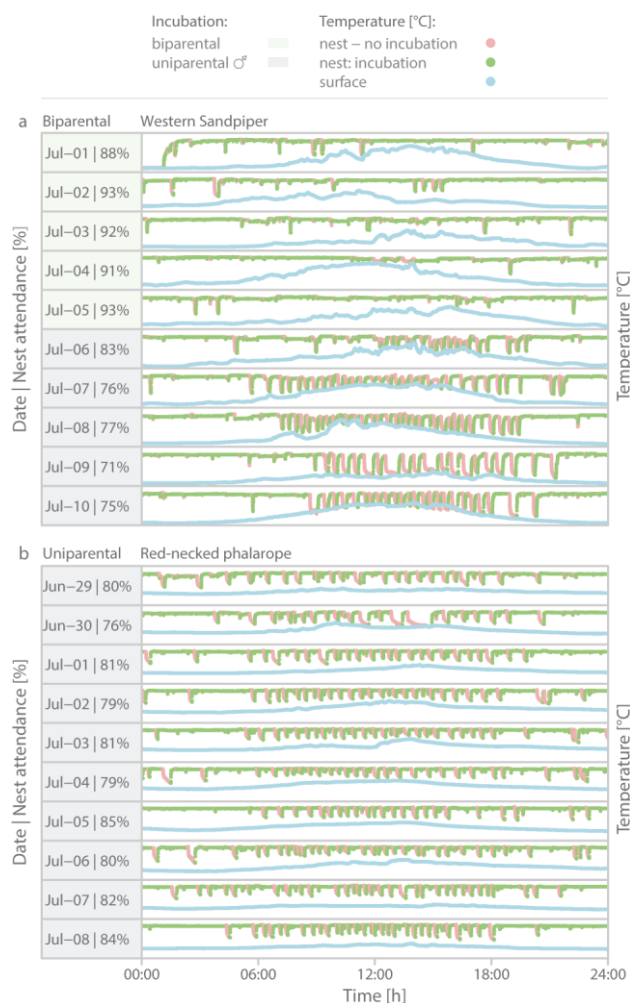


Figure 3 | Example of uniparental incubation rhythm in biparental and uniparental shorebird. a, Switch from biparental incubation (days highlighted by green background) to uniparental incubation (grey background) of biparental Western sandpiper (*Calidris mauri*). **b,** Male uniparental incubation of uniparental Red-necked phalarope. **a-b,** Pink (●) demarcates nest temperatures considered as no incubation, green (●) demarcates nest temperatures considered as incubation and blue (●) indicates surface temperatures of the habitat adjacent to the nest. Daily nest attendance indicates percentage of incubation readings (●) from all 5 s readings for that day (● + ●).

Individuals also varied greatly in how they coped with uniparental incubation over the day: some incubated, at least for some time, only for their incubation bouts and left the nest unattended for the rest of the time (e.g. actograms biparental_33, 38, 42, 44-45, 47 & 51 in Supplementary Actograms (Bulla & Kempnaers 2016)); some incubated, at least for some time, only during the day when it is warm (e.g. biparental_26 & 51 (Bulla & Kempnaers 2016)); some incubated mainly during the night (cold period), but rarely during the day (warm period; e.g. biparental_01 & 06 (Bulla & Kempnaers 2016)); and others developed incubation rhythm similar to the incubation rhythm of uniparental species with continuous nest attendance at night when it is cold, and intermittent incubation with short feeding bouts during the day when it is warm (e.g. biparental_15, 70, 72-3, 76-7 (Bulla & Kempnaers 2016)). However, within individual variation in hourly nest attendance (52% of variance) was far greater than the between individual variation (8% of variance; Supplementary Table 3)

Overall, the uniparental incubation rhythm of biparental species resembled the incubation rhythm of uniparental species (Figure 2c-d & 3). The same as for uniparental species, but in contrast to the biparental incubation, biparental species had the highest uniparental nest attendance during the night when it is cold, and the lowest nest attendance during the day when it is warm (Figure 2c-d; for nest specific relationships see Supplementary Figure 3). However, during the night the uniparental nest attendance tended to be lower and during the day higher than in the uniparental species (Figure 2c-d). The uniparental incubation rhythm of females was similar to the uniparental incubation rhythms of males (Supplementary Figure 2b, Supplementary Table 4).

Nest success

Out of 54 nests, for which we knew the end state, at least one chick hatched in 15 nests of 5 species, 4 nests were depredated and the remaining nests deserted (Figure 4a). The successful nests tended to become uniparental later in the incubation period and tended to be incubated uniparentally longer than the nests that failed (Figure 4b-c and 5).

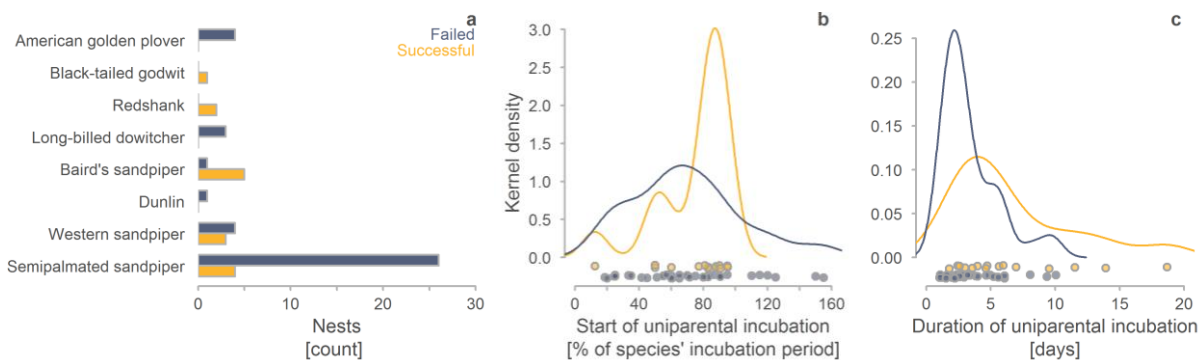


Figure 4 | Distribution of successful and unsuccessful nests incubated uniparentally. a, Across species. b, Across start of uniparental incubation (portrayed as % of species' incubation period). c, Across duration of uniparental incubation. a-c, At least one chick hatched in the successful nests (●; yellow, $N = 15$ nests), unsuccessful nests (●; blue-grey) where either depredated ($N = 4$ nests) or deserted ($N = 35$ nests).

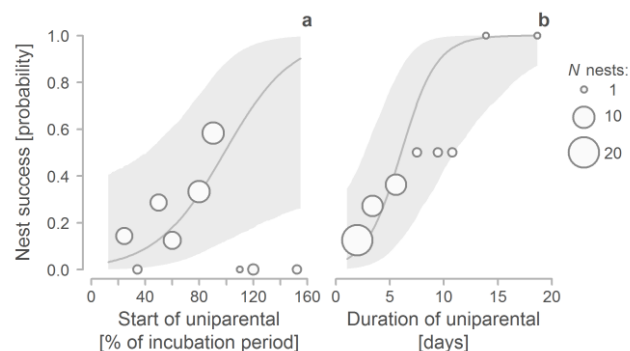


Figure 5 | Predictors of nest success in uniparentally incubated nests. a-b, Nest success as a function of when the uniparental incubation started within the incubation period (a), and as a function of how long the uniparental incubation lasted (b). Circles represent means for intervals spread evenly across the range of the x-values; circle size indicates the number of nests with uniparental incubation. The solid lines depict the model-predicted relationships, the shaded area the 95% credible intervals based on the joint posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman & Su 2015); the predicted relationships stem from a binomial mixed-effect model, where the effect of the other predictor was kept constant (Supplementary Table 5). $N = 54$ nests with uniparental incubation from 8 biparental species.

Discussion

Our findings challenge the belief of unsuccessful uniparental incubation in biparental shorebirds (Poole 2005), because we found uniparental incubation in 8 out of 15 biparentally incubating shorebird species (Figure 1) and evidence of hatching in 5 of these species (Figure 4). Our findings also challenge the belief that females of biparental shorebirds desert their brood after hatching, because we demonstrate that either sex sometimes deserts the nest even prior to hatching.

The uniparental incubation usually started (i.e. the nests where mostly deserted) close to the expected hatching (Figure 1b & 4b) and the uniparental incubation usually lasted only a few days (Figure 1c & 4c). Although this suggests that most desertions might have been relatively safe or that widowed individuals deserted the nest once they have realized that they incubate alone (Martin Bulla 2016), individuals, and especially species, varied greatly in when they deserted the nest and for how long the nests were incubated uniparentally, with some individuals incubating uniparentally for half, or for nearly the whole, incubation period (Figure 1b-c & 4b-c). The drivers of such variation are unclear, but we found some evidence for successful nests to be incubated uniparentally for longer (Figure 5b).

The evidence for hatching, in spite of uniparental incubation, in 5 biparental species reveals a potential for a switch from biparental care to uniparental care. Indeed, the daily and hourly nest attendance of biparental species resembled the nest attendance of uniparental species (Figure 2 & 3). Although overall the hatching success was low (28%, $N = 54$ nests with known fate of 8 species), the species with cases of hatching varied greatly in this respect (13% of 30 Semipalmated sandpiper nests, 43% of 7 Western sandpiper nests, 83% of 6 Baird's sandpiper, *Calidris bairdii*, nests and single Black-tailed godwit, *Limosa limosa*, nest and both Common redshank nests). It would be exciting to investigate whether, based on the conditions at the breeding ground (e.g. a change in sex ratios), these species would realize their potential to switch flexibly from biparental to fully uniparental care.

Open data, codes and materials. All available at <https://osf.io/3rsny> (Bulla & Kempnaers 2016).

Authors' contributions. M.B. and B.K. conceived the study; M.B. with help of B.K., M.V. and H.P. collected the biparental data in Barrow. H.V. and M.B. with help of B.K., M.V., J.A.A. collected the data in Iceland, J.A.A. collected the Iceland godwit data, H.V. and M.B. collected the data in the Czech Republic. W.T. and H.P. collected the redshank data in Holland, M.B. collected the godwit data in Friesland, B.K. and M.V. collected the pectoral sandpiper data, M.S. the phalarope data; M.B. coordinated the study, analysed the data, prepared all supporting information available from OSF and drafted the manuscript. All authors commented on the draft and M.B. with B.K. finalized the paper.

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Supplementary information

Supplementary Table 1 | Effects of incubation type and incubation period on daily nest attendance.

Response	Effect type	Effect	Estimate	95% CI	
				Lower	Upper
Nest attendance (proportion)	Fixed	Intercept (biparental of biparental)	0.92	0.86	0.98
		Incubation period	-0.01	-0.02	0.01
		Type of incubation (uniparental of biparental)	-0.2	-0.27	-0.12
		Type of incubation (uniparental of uniparental)	-0.21	-0.31	-0.11
		Incubation period × Type (uniparental of biparental)	0.03	0.01	0.06
		Incubation period × Type (uniparental of uniparental)	0	-0.02	0.03
	Random (variance*100)	Nest × Type of incubation (intercept)	0.24		
		Incubation period	0.59		
		Species × Type of incubation (intercept)	0.36		
		Incubation period	0		
		Residual	0.54		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015). $N = 909$ days from 88 nests of 10 species. Incubation period represents proportion of species' specific typical incubation period (see Methods). Continuous predictors were z-transformed (mean-centered and divided by SD).

Supplementary Table 2 | Effects of sex and incubation period on daily nest attendance.

Response	Effect type	Effect	Estimate	95% CI	
				Lower	Upper
Nest attendance (proportion)	Fixed	Intercept (♀)	0.75	0.66	0.84
		Incubation period	-0.05	-0.12	0.03
		Sex (♂)	-0.06	-0.13	0.02
		Incubation period × Sex (♂)	0.1	0.02	0.17
	Random (variance*100)	Nest (intercept)	1.1		
		Incubation period	0.23		
		Species (intercept)	0.36		
		Incubation period	1.23		
		Residual	1.29		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015). $N = 218$ days from 57 nests of 4 species. Incubation period represents proportion of species' specific typical incubation period (see Methods). Continuous predictors were z-transformed (mean-centered and divided by SD).

Supplementary Table 3 | Effects of incubation type and time of day on daily nest attendance.

Response	Effect type	Effect	Estimate	95% CI		
				Lower	Upper	
Nest attendance (proportion)	Fixed	Intercept (biparental of biparental)	0.92	0.86	0.98	
		sin (time)	-0.01	-0	0.03	
		cos (time)	0.02	-0.1	0.09	
		Type of incubation (uniparental of biparental)	-0.17	-0.3	-0.1	
		Type of incubation (uniparental of uniparental)	-0.2	-0.3	-0.1	
		sin × Type (uniparental of biparental)	-0	-0	0.04	
		sin × Type (uniparental of uniparental)	0.04	-0	0.09	
		cos × Type (uniparental of biparental)	0.11	0.02	0.2	
		cos × Type (uniparental of uniparental)	0.23	0.11	0.35	
		Random (variance*100)	Nest × Type of incubation (intercept)	0.52		
			sin (time)	1.02		
			cos (time)	0.94		
			Species × Type of incubation (intercept)	0.3		
			sin (time)	0.03		
			cos (time)	0.4		
			Residual	3.58		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015). $N = 23,613$ hours from 88 nests of 10 species.

Supplementary Table 4 | Effects of incubation type and time of day on daily nest attendance.

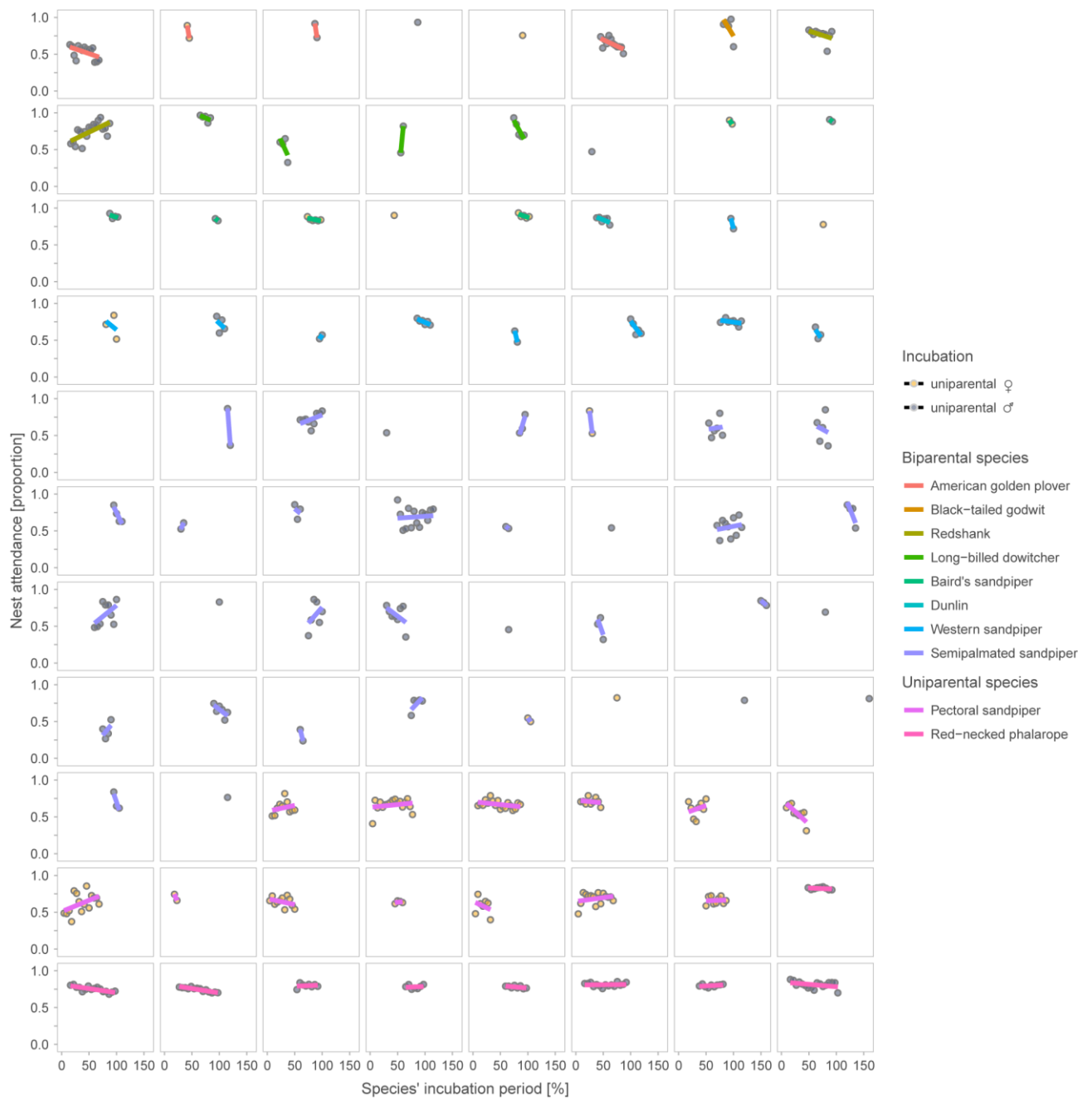
Response	Effect type	Effect	Estimate	95% CI	
				Lower	Upper
Nest attendance (proportion)	Fixed	Intercept (♀)	0.78	0.7	0.86
		sin (time)	-0.02	-0.12	0.07
		cos (time)	0.08	-0.03	0.19
		Sex (♂)	-0.07	-0.14	-0.01
		sin × Sex (♂)	0.02	-0.08	0.12
		cos × Sex (♂)	0.08	-0.02	0.18
	Random (variance*100)	Nest	0.89		
		sin (time)	2.14		
		cos (time)	1.98		
		Species	0.34		
		sin (time)	0.07		
		cos (time)	0.46		
		Residual	7.21		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015). $N = 5,854$ hours from 58 nests of 4 species.

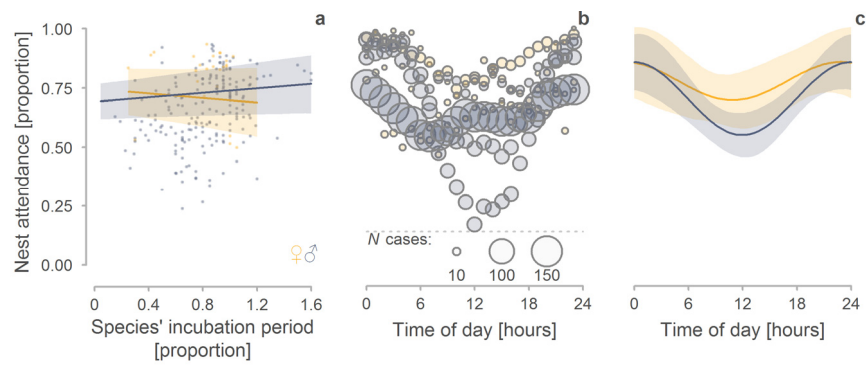
Supplementary Table 5 | Effects of start and duration of uniparental incubation on nest success.

Response	Effect type	Effect	Estimate	95% CI	
				Lower	Upper
Nest success (1,0; on binomial scale)	Fixed	Intercept	-6.47	-11.03	-2.05
		Start (% of incubation period)	0.04	0	0.08
		Duration (days)	0.6	0.2	1
	Random (variance)	Species (intercept)	3.71		

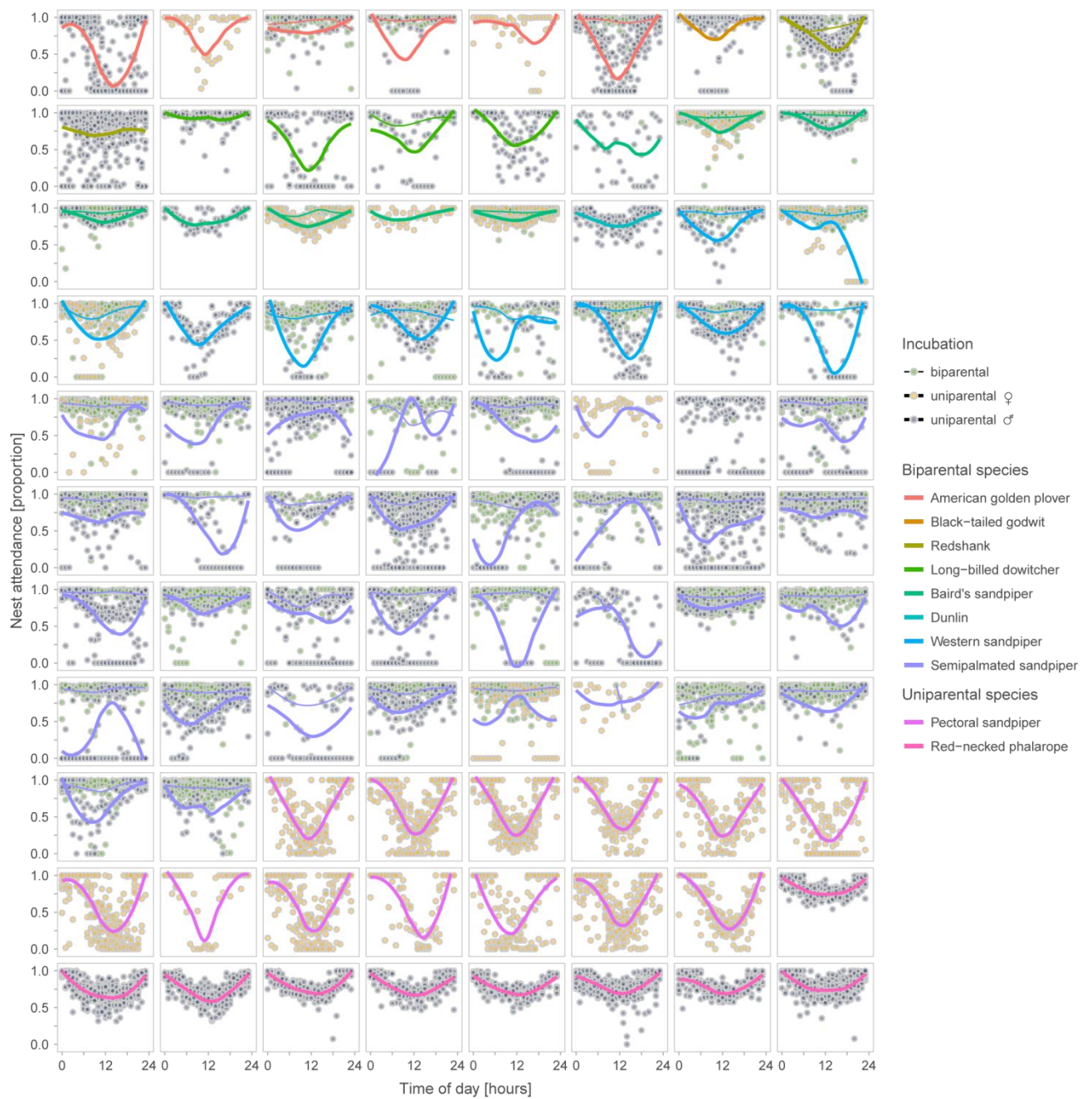
The posterior estimates (medians) of the effect sizes with the 95% credible intervals (95% CI) from a posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). Variance in the random effects is estimated by 'lmer' function in R (Bates et al. 2015). $N = 54$ nests of 8 species. Predictors were z-transformed (mean-centered and divided by SD). The estimates are on a binomial scale. Note that we should control for random slope in Start and Duration, but we lack sufficient sample of nests for each species and thus such model fails to converge.



Supplementary Figure 1 | Diverse change in uniparental nest attendance across incubation period. Each panel represents one of 88 nests. Dots represent daily uniparental nest attendance of female (●; yellow dots) and male (●; blue-grey dots). Where appropriate, lines represent linear regression for each nest (generated by 'ggplot2' R package (Wickham 2009)), their colour indicates species.



Supplementary Figure 2 | Sex specific daily nest attendance. a-c, Change in daily nest attendance across incubation period (a; proportion of species' typical incubation period) and across day (b-c) for four biparental species incubating uniparentally; female uniparental incubation (●; yellow), male uniparental incubation (●; blue-grey). Dots represent daily nest attendance for each day (a) and mean hourly observations for each species (b); their size number of hours). Lines with shaded areas indicate model predictions with 95%CI (Supplementary Table 3 & 5) based on the joint posterior distribution of 5,000 simulated values generated by 'sim' function in R (Gelman & Su 2015). $N_a = 218$ days from 57 nests of 4 species. $N_b = 5,854$ hours from 58 nests of 4 species. Note that nest attendance of previous hour strongly predicts the nest attendance of current hour (partial temporal-autocorrelation of model residuals in lag one = 0.57) possibly making the 95%CIs (c) narrower.



Supplementary Figure 3 | Variation in circadian rhythm of nest attendance. Each panel represents one of 88 nests. Dots represent hourly nest attendance, green dots (●) biparental incubation, yellow dots (●) female uniparental incubation, and blue-grey dots (●) male uniparental incubation. Lines represent loess smoothing for each nest and incubation type (generated by 'ggplot2' R package (Wickham 2009)). Line colour indicates species; thin lines (—) represent biparental incubation, thick lines (—) uniparental incubation.

Chapter 5

Biparental incubation-scheduling: no experimental evidence for major energetic constraints

Martin Bulla, Will Cresswell, Anne L Rutten,
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Incubation is energetically demanding, but it is debated whether these demands constrain incubation-scheduling (i.e., the length, constancy, and timing of incubation bouts) in cases where both parents incubate. Using 2 methods, we experimentally reduced the energetic demands of incubation in the semipalmated sandpiper, a biparental shorebird breeding in the harsh conditions of the high Arctic. First, we decreased the demands of incubation for 1 parent only by exchanging 1 of the 4 eggs for an artificial egg that heated up when the focal bird incubated. Second, we reanalyzed the data from the only published experimental study that has explicitly tested energetic constraints on incubation-scheduling in a biparentally incubating species (Cresswell et al. 2003). In this experiment, the energetic demands of incubation were decreased for both parents by insulating the nest cup. We expected that the treated birds, in both experiments, would change the length of their incubation bouts, if biparental incubation-scheduling is energetically constrained. However, we found no evidence that heating or insulation of the nest affected the length of incubation bouts: the combined effect of both experiments was an increase in bout length of 3.6 min (95% CI: -33 to 40), which is equivalent to a 0.5% increase in the length of the average incubation bout. These results demonstrate that the observed biparental incubation-scheduling in semipalmated sandpipers is not primarily driven by energetic constraints and therefore by the state of the incubating bird, implying that we still do not understand the factors driving biparental incubation-scheduling. These findings reveal a potential for a flexible switch from biparental to uniparental care.

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Original Article

Biparental incubation-scheduling: no experimental evidence for major energetic constraints

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Incubation is energetically demanding, but it is debated whether these demands constrain incubation-scheduling (i.e., the length, constancy, and timing of incubation bouts) in cases where both parents incubate. Using 2 methods, we experimentally reduced the energetic demands of incubation in the semipalmated sandpiper, a biparental shorebird breeding in the harsh conditions of the high Arctic. First, we decreased the demands of incubation for 1 parent only by exchanging 1 of the 4 eggs for an artificial egg that heated up when the focal bird incubated. Second, we reanalyzed the data from the only published experimental study that has explicitly tested energetic constraints on incubation-scheduling in a biparentally incubating species (Cresswell et al. 2003). In this experiment, the energetic demands of incubation were decreased for both parents by insulating the nest cup. We expected that the treated birds, in both experiments, would change the length of their incubation bouts, if biparental incubation-scheduling is energetically constrained. However, we found no evidence that heating or insulation of the nest affected the length of incubation bouts: the combined effect of both experiments was an increase in bout length of 3.6 min (95% CI: –33 to 40), which is equivalent to a 0.5% increase in the length of the average incubation bout. These results demonstrate that the observed biparental incubation-scheduling in semipalmated sandpipers is not primarily driven by energetic constraints and therefore by the state of the incubating bird, implying that we still do not understand the factors driving biparental incubation-scheduling.

Key words: Arctic, biparental incubation, *Calidris pusilla*, constancy, cross-over design, energetic constraints, energetic demands, incubation bout length, replication, scheduling, semipalmated sandpiper, shorebird, statistical power.

INTRODUCTION

Avian incubation is energetically demanding (e.g., Vleck 1981; reviewed by Williams 1996; and by Tinbergen and Williams 2002; Piersma et al. 2003), mainly because incubating parents trade-off their energetic needs with thermal needs of their developing embryos (i.e., trade-off between foraging and incubation; reviewed by Reid et al. 2002; and by Tinbergen and Williams 2002). Thus, energetic demands of incubation should constrain incubation-scheduling, that is, the length of incubation bouts, their constancy (the amount of time birds actually incubate within an incubation bout), and their timing.

Such energetic constraints on incubation-scheduling are expected, reported, and experimentally confirmed for unassisted, uniparental incubation (e.g., Aldrich and Raveling 1983; Bryan and

Bryant 1999; Reid et al. 1999; Cresswell et al. 2004; Ardia et al. 2009) and for extreme events where biparental incubation (temporarily) turns into uniparental incubation, for example, when an off-nest bird delays its return to the nest (Davis 1982; Chaurand and Weimerskirch 1994; Weimerskirch 1995; Gauthier-Clerc et al. 2001). In these cases, there appears to be a body-mass threshold, below which birds interrupt their incubation and leave the nest (Aldrich and Raveling 1983; Chaurand and Weimerskirch 1994; Weimerskirch 1995; Gauthier-Clerc et al. 2001).

In contrast, during (regular) biparental incubation, the energetic constraints on incubation-scheduling are expected to be reduced (Williams 1996; Tinbergen and Williams 2002). Here, parents may always have enough time to replenish their energy reserves, which became depleted during their previous incubation session. The 2 experimental studies addressing this issue in biparentally incubating birds yielded contradictory results (Cresswell et al. 2003; Kosztolanyi et al. 2009). The first study—conducted in the high Arctic on semipalmated sandpipers, *Calidris pusilla*—reported that

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an experimental reduction in the energetic demands of incubation (achieved with a polystyrene insulation of the nest cup) prolonged incubation bouts and concluded that biparental incubation-scheduling is energetically constrained (Cresswell et al. 2003). To date this is the only experiment that explicitly tested the hypothesis that energetic constraints affect biparental incubation-scheduling. However, here we argue that the conclusion of this study needs to be revised because the data and analyses were inconsistent with the experimental design (detailed in [Supplementary 1: Section 1, Reanalysis of the Insulation Experiment](#)). The second study—conducted in a hot, arid environment on Kentish plovers, *Charadrius alexandrinus*—reported that an experimental increase in the energetic demands of incubation (by artificial cooling of the nest during the night) increased constancy of incubation, suggesting that biparental incubation-scheduling is not energetically constrained (Kosztolanyi et al. 2009). However, the night conditions in this arid environment (with ground temperatures around 25 °C) are within the thermo-neutral zone of small shorebird species (Kersten and Piersma 1986), and thus should not be energetically stressful to Kentish plovers. Hence, one could argue that the energetic demands of heating the eggs were negligible under these conditions (Tinbergen and Williams 2002), implying that the cooling treatment might have been ineffective in manipulating the energy reserves of the Kentish plover parents. In sum, it still remains unclear whether energetic demands of incubation constrain incubation-scheduling in biparentally incubating species.

The aim of this study is to resolve whether energetic demands of incubation are a major factor driving incubation-scheduling (i.e., the division of parental care) in biparental semipalmated sandpipers breeding in harsh, energetically stressful conditions in the high Arctic. Using a new experiment and a more rigorous and appropriate analysis of the previous experiment (Cresswell et al. 2003), we tested whether reduced energetic demands of incubation changed incubation-scheduling. Both experiments were carried out at the same site, under similar environmental conditions ([Supplementary 1: Section 2, Seasonal Differences](#)), but were separated by 12 years. Although the previous experiment reduced energetic demands of incubation for both parents, in the new experiment, we reduced energetic demands of incubation for 1 parent only using an artificial egg that provided heat when the focal bird incubated (heating experiment). The expected effect of this manipulation on incubation-scheduling depends on which individual determines incubation bout length. If the level of energy reserves of the incubating parent determines incubation bout length (as implied by Cresswell et al. 2003), then the treated birds should prolong their incubation bouts or increase their incubation constancy because their energetic reserves will last longer when demands are reduced. Alternatively, if the energy reserves of the off-nest parent determine incubation bout length, then the off-nest bout of the treated bird (which is the incubation bout of the untreated bird) should decrease in length. This is because the off-nest bird, which was treated during its previous incubation bout, will have a smaller energy deficit to recover, and thus could return to the nest earlier. Both scenarios could potentially also reduce the number or length of exchange gaps (time period during which eggs are left unattended as part of the exchange process at the nest), but our previous work shows that exchanges are usually immediate (Bulla et al. 2014a). We further investigated in how far the results of the 2 experiments are comparable given potential differences in the strength of the treatment: heating in the new experiment and insulating in the first experiment. To this end, we used artificial nest scrapes, and approximated the amount of energy an artificial brood-patch consumed when a

nest scrape either contained a heating egg (heating experiment) or was insulated (insulation experiment).

MATERIALS AND METHODS

Heating experiment

Study area and species

We studied a population of semipalmated sandpipers near Barrow, Alaska (71.32° N, 156.65° W), between 1 June and 21 July 2012. The study area and species are already described in detail elsewhere (Ashkenazie and Safriel 1979; Bulla et al. 2014a). Barrow has continuous daylight throughout the breeding season, but environmental conditions show consistent and substantial diel fluctuations; ambient temperatures are generally low, below 5 °C, but surface tundra temperatures can reach up to 28 °C ([Supplementary Figure S1 in Bulla et al. 2014a](#)). Previous work on the same study area found that incubation lasted on average for 21 days, with an average bout length of 11.5 h; incubation bout length increased over the incubation period and was ca. 50 min longer in females than in males; females had a slightly higher incubation constancy, and a higher overall probability to incubate during the colder period of the day (Bulla et al. 2014a).

Sampling of individuals and monitoring of incubation behavior

Capture, marking, measuring, and blood sampling of individuals (for sexing), as well as the general procedures to monitor incubation behavior are described in detail elsewhere (Bulla et al. 2014a). Briefly, incubation was determined by a high-resolution MSR® external temperature-probe placed in the middle of a nest between the 4 eggs and connected to a MSR® 145 data logger (MSR® Electronics GmbH, <http://www.msr.ch/en/>); this logger also recorded the tundra surface temperature outside of the nest. Both temperatures were logged every 5 s throughout the incubation period. Constant incubation-temperatures higher than tundra temperatures were interpreted as continuous incubation; the start of incubation was determined from a steep increase, the interruption of incubation from a steep decrease in nest temperatures ([Supplementary Figure S4 in Bulla et al. 2014a](#)).

A radio frequency identification device (RFID)—a thin antennae loop fitted into a nest cup and connected to a data logger—registered every 5 s the identity of an incubating bird (marked with a green flag with embedded passive-integrated transponder; details in Bulla et al. 2014a). Thus, the temperature-based determination of incubation was overlaid with the RFID data, which allowed assigning each incubation bout to a parent ([Supplementary Figure S4 in Bulla et al. 2014a](#)).

The length of each incubation bout was extracted as the total time allocated to a single parent (i.e., the time between the arrival of a parent and its departure from the nest followed by incubation by its partner). The exchange-gap duration (the time between the departure of 1 parent and the return of the other) was excluded from the length of the incubation bout. The constancy of incubation was calculated from the temperature-based incubation data as the percentage of time a bird actually incubated within a given incubation bout (i.e., sat tightly on the eggs as opposed to egg rolling, nest maintenance or being off the nest).

In addition to previously described procedures, in this study, we protected control and treatment nests against avian predators using enclosures made of mesh wire ([Supplementary 1: Section 3 Pictures, Picture S1](#)).

Heating treatment

We reduced the energetic demands of incubation by exchanging 1 egg for an artificial heat-producing egg (29.4 × 21.0 mm; Jan Petrů, <http://www.forestspsy.com>). This egg was made of a heating element (with resistance 13.7–13.9 Ω and heating power of 10.5 W; Jan Petrů, <http://www.forestspsy.com>), a 1-wire digital thermometer (0.5 °C accuracy; model DS18S20, Maxim Integrated Products, <http://www.maximintegrated.com>), and a highly conductive “liquid metal” (70% mixture of powder aluminum—with particles 65 μm in diameter—and high-temperature epoxy), and was painted to resemble a semipalmated sandpiper egg (Supplementary 1: Section 3, Picture S2 and S3). This artificial egg was connected to a 12-V 12-Ah battery (Gel Werker) and the RFID. The RFID contained the “heat-SD-card” with a pre-programmed action—to heat or not—for each incubation bout, depending on the identity of the bird on the nest. If the transponder of the focal bird was read and the given incubation bout was set to “heat,” the RFID automatically turned on the artificial egg and the nest was heated (for further details, see Experimental procedure). If the focal bird was absent for more than 10 min, the egg automatically turned itself off. The temperature sensor inside the egg was set to 42 °C. Whenever the sensor detected a temperature less than 41.5 °C, the thermistor turned on. Due to thermal inertia of the egg material, the temperature on the surface of the egg (where the bird was touching it) was approximately 40 °C (±1 °C), which is at the higher end of incubation temperatures of semipalmated sandpipers. The actual energy provided by the artificial egg to the nest during incubation was measured by a data logger (SH1, Jan Petrů, <http://www.forestspsy.com>) connected between the 12-V battery and the artificial egg. The logger recorded the energy consumption of the artificial egg every 50th of a second.

Experimental procedure

The general aim was to conduct the heating experiment such that it could detect a possible 55-min effect on bout length, that is, the effect reported in Cresswell et al (2003), with sufficient statistical power (0.8; recommended by Cohen 1988).

The exact experimental procedure was based on sets of a priori power analyses (described in Supplementary 1: Section 4, A Priori Power Analyses). Thus, using 50 incubation monitoring systems, the specific aim was to collect incubation data for 4 incubation bouts in each bout category (i.e., before treatment, treated, and after treatment) for both the treated and the untreated parent in at least 22 treated nests (experimentally heated) and 22 control nests (natural nests without any treatment and without artificial egg).

In the field, we assigned the first nest found as treated with the male as the treated parent, the second nest as control with the male as the “treated” parent, the third nest as treated with the female as the treated parent, the fourth nest as a control with the female as “treated,” and so on. If the treated-assigned nest failed before the application of the treatment (e.g., due to predation), we adjusted the assignment of the treatment to the sex in the remaining, not yet treated nests, so that the final sample of female- and male-treated nests remained similar (details in Supplementary 1: Section 5, Sample Sizes). The sex of individuals was known from previous years or estimated from measurements and later confirmed by molecular analyses (Bulla et al. 2014a).

In the treated nests, the chronology of the experiment across the season was as follows. We introduced the artificial egg to the treated nests between the 2nd and 11th day of incubation (median = 6th day of incubation; $N = 21$ nests). During the same nest-visit, we exchanged

the SD-card of the RFID, which allowed the identification of parents transpondered in the previous year and a check of whether birds transpondered in the current year were successfully detected by the system. Three days later, between the 6th and 14th day of incubation (median = 9th day of incubation; $N = 21$ nests), we connected the artificial egg to the 12-V battery and exchanged the SD-card in the RFID for the “heat-SD-card.” If the treated bird incubated when the heat-SD-card was inserted, the treatment started with the third incubation bout after the insertion (Figure 1A); if the untreated bird incubated, the treatment started with the fourth incubation bout after the insertion (Figure 1B). This led to variable number of before-treatment bouts. The artificial egg was heated on 4 consecutive bouts of the treated bird (Figure 1). Before-treatment bouts were defined from the first bout after the insertion of the artificial egg until the first heated bout (as indicated in Figure 1), but maximum 4 before-treatment bouts per individual were used for statistical analyses (Figure 1B); treated bouts were the heated bouts of the treated parent (4, 6, 8, and 10) and the subsequent bouts of the untreated parent (5, 7, 9, and 11; as indicated in Figure 1); later bouts of both birds were classified as after-treatment bouts (as indicated in Figure 1), and the first 4 after-treatment bouts per individual were used for statistical analyses.

In the control nests, before-treatment bouts of the “treated” bird were assigned from day 4 of incubation until day 7, then 4 “treated” (control) bouts were assigned and the remaining bouts were after-treatment. In 6 nests, the before-treatment bouts were assigned to start before day 4 to be able to include at least 1 after-treatment bout (in 2 nests that failed early), or at least 1 before-treatment bout (in 4 late-found nests). As in the treated nests, the bouts of the “untreated” birds were assigned following the assignment for the “treated” bird.

The final data set consisted of 25 control nests (24 in case of comparison of incubation constancy) and 21 treated nests (the distribution of bouts for all treated and control nests is in Supplementary 1: Section 5, Table S2, and the raw data for each nest in Supplementary 2).

Background of the insulation experiment

The insulation experiment was conducted between 10 June and 4 July 2000 in the same study area, on the same species and using a similar, RFID-based, incubation monitoring system as in the heating experiment; details are in Cresswell et al. (2003). Briefly, the insulation quality of nests was improved by a polystyrene drinking cup (cut down to 5 cm and painted dull brown) inserted under the lining of the nest. The experiment used a matched-pairs cross-over design, that is, one nest of a pair was insulated for 48 h, while its paired nest acted as a control (first period of the experiment), then the insulation was swapped within the pair and the previously insulated nest served as a control for 48 h, while its paired nest was insulated (second period of the experiment). The statistical analyses were conducted on the mean bout length per nest and treatment (control or insulated). Nests, not individual birds, were the units of analyses. The reported 55-min effect (95% CI: 11–99 min) is based on the within-nest comparison (paired *t*-test) of mean length of untreated incubation bouts and mean length of insulated incubation bouts (which crucially included some control bouts outside the two 48-h periods to increase the sample size incubation bouts). The analysis did not control statistically for a period effect (i.e., whether control or insulation occurred within the first or second 48-h experimental period). Also, contrary to the requirements of the experimental design, the data set was unbalanced. Hence, we reanalyzed the data, following the procedures outlined in Supplementary 1: Section 1, which also includes full details on the sources of bias and error in the original analysis.

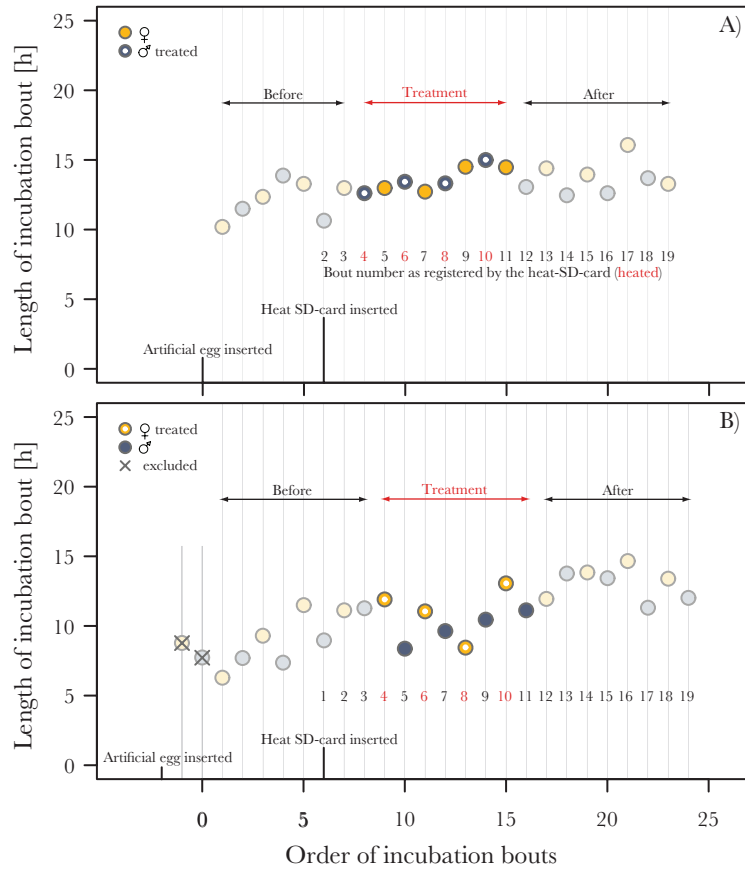


Figure 1

Examples illustrating the experimental procedure. The first bout after introduction of the artificial egg marked the start of the before-treatment period (first circle), which lasted until the first heated bout (first circle emphasized by a white point inside); maximum 4 before-treatment bouts per individual were used in the statistical analyses (i.e., earlier bouts were excluded; indicated by crosses in (B)). Once the incubation monitoring system received a “heat-SD-card” (sixth circle in (A) and sixth uncrossed circle in (B)), it started to count the incubation bouts (black and red numbers). The egg produced heat during bout 4, 6, 8, and 10 (depicted in red and emphasized by white points inside the circles); these bouts together with the subsequent bouts of the untreated parent (5, 7, 9, and 11) were called treatment bouts. The following bouts (maximum 4 per individual) were defined as after-treatment bouts. If the treated bird incubated when the heat-SD-card was inserted, this bout was recorded as number 1 (B). Similar graphs depicting the raw data for all treated and control nests are in [Supplementary 2](#).

Artificial experiment

We tested the difference in the strength of the treatment between the heating and insulation experiment with an artificial experiment. On 3 June 2013, we made 3 artificial nest scrapes and equipped each with an artificial egg (heat-producing egg described in Heating treatment). The experiment consisted of 3 treatments: artificial egg turned on (as in the heating experiment), artificial egg turned off (control), and artificial egg turned off but nest insulated (as in the insulation experiment; see [Supplementary 1: Section 3, Picture S2](#)). We made an artificial brood-patch by embedding a heat-producing egg in polystyrene ([Supplementary 1: Section 3, Picture S3](#)) and placed it over each nest scrape in contact with the artificial egg ([Supplementary 1: Section 3, Picture S4](#)). The heat-producing egg inside the “brood-patch” was connected to a data logger (described in Heating treatment) that registered its energy consumption for 50 min. Hence, this setup allowed measuring how much energy the brood-patch needed to keep the artificial egg warm in each of the 3 treatments. We repeated the experiment on the same day, such that each nest scrape consecutively received each of the 3 treatments. The whole procedure was repeated 10 days later.

Statistical analyses

R version 3.0.3 (R Core Team 2014) was used for all statistical analyses, the “lme4” package (Bates and Maechler 2010) for mixed-effects modeling and the “rmeta” package (Lumley 2012) for the meta-analysis. The results of the linear and mixed models include adjusted approximations of confidence intervals (CIs) and *P* values based on multiple comparisons (simultaneous inference) of predictors using the “glht” function from the “multcomp” package (Hothorn et al. 2008). This function allows immediate test of only specifically defined hypotheses (reported in the Results; the full statistical summaries are reported in the [Supplementary 1: Section 6, Models](#)). Uncertainties are reported as 95% CIs.

Data and R-scripts

Data are available from figshare.com digital repository at http://figshare.com/articles/Data_from_Biparental_incubation_scheduling_no_experimental_evidence_for_major_energetic_constraints_/1035052 (Bulla et al. 2014b). R-script (of the statistical analyses, figures, power analyses, etc.) is available from figshare.com digital repository at http://figshare.com/articles/R_script_from_Biparental_incubation_scheduling_no_experimental_evi-

dence_for_major_energetic_constraints/1035048 (Bulla et al. 2014c).

RESULTS

Energy provided by the heating

The actual energy provided by the heated artificial egg to the nest was measured at 3 nests (during 5 female and 7 male incubation bouts). The artificial egg provided 537 mW (95% CI: 476–597 mW; $N = 12$ incubation bouts; variance of random intercept [nest] = 175, residual variance = 10750). Assuming that a 27-g semipalmated sandpiper invests between 68 and 284 mW to keep 4 eggs at incubation temperature (based on Norton 1973; Biebach 1979; Vleck 1981; described in Supplementary 1: Section 7, Estimating Energetic Demands of Incubation), the artificial egg provided approximately 2–8 times more energy than required to incubate the clutch and provided energy equivalent to approximately 40% of the bird's resting metabolic rate (Norton 1973). Thus, the heating treatment should have led to a substantial reduction in the overall energetic demands of incubation for the treated parent (including a reduction in the costs of thermoregulation).

Heating experiment

To investigate whether the heating treatment changed the length or constancy of incubation, we specified the 3-way interaction of interest, namely whether the nest, parent, and incubation bout were treated (Supplementary 1: Section 6, Tables S3–S6). We used both simple models without covariates and complex models including covariates known to explain variation in the dependent variable (Bulla et al. 2014a). In each model, we controlled for pseudoreplication by adding nest as a random intercept and day of incubation (quadratic) as a random slope. Because the simple and complex models gave qualitatively

similar results (Supplementary 1: Section 6, Tables S3–S6), here we only describe in detail the outcome of the simple models and for the complex model present the estimates of interest in Figure 2A.

There was no major effect of the heating on the length of incubation bouts (Figure 2). During heating, the treated birds in treated nests had 3.9 min (95% CI: –52 to 59.8 min) longer incubation bouts than “treated” birds in control nests ($P = 1$, $N_{\text{total}} = 976$ incubation bouts from 46 nests; see Figure 2A); the statistical power to detect an effect of 55 min was >0.8 (detailed in Supplementary 1: Section 4). In comparison, during the treatment period, the untreated birds in treated nests had 34 min (–24 to 92 min) longer incubation bouts than untreated birds in control nests—an effect in the opposite direction to that expected for the untreated partner ($P = 0.4$; $N_{\text{total}} = 976$ incubation bouts from 46 nests; Figure 2A). The change in the length of incubation bouts from before-treatment to treatment in the treated birds in treated nests was 5 min (–64 to 74 min) larger than in “treated” birds in control nests ($P = 1$; Figure 2A, difference in slopes); here, the statistical power to detect an effect of 55 min was <0.6 (Supplementary 1: Section 4, Figure S2). We did not test for a sex-specific effect of the heating treatment because of low statistical power (<0.2 ; Supplementary 1: Section 4, Figure S2).

The lack of response to the heating in terms of incubation bout length was not compensated by major changes in the constancy of incubation, that is, in the proportion of actual incubation within bouts. During heating, the bouts of treated birds in treated nests had 0.5% (95% CI: –2.0 to 2.9%) larger incubation constancy than “treated” bouts in control nests ($P = 0.95$, $N_{\text{total}} = 952$ incubation bouts from 45 nests). During the treatment period, the bouts of untreated birds in treated nests had 0.3% (–2.3 to 2.9 %) lower incubation constancy than the bouts of “untreated” birds in control nests ($P = 0.98$). The change in the incubation constancy from before-treatment to treatment in the treated birds in treated

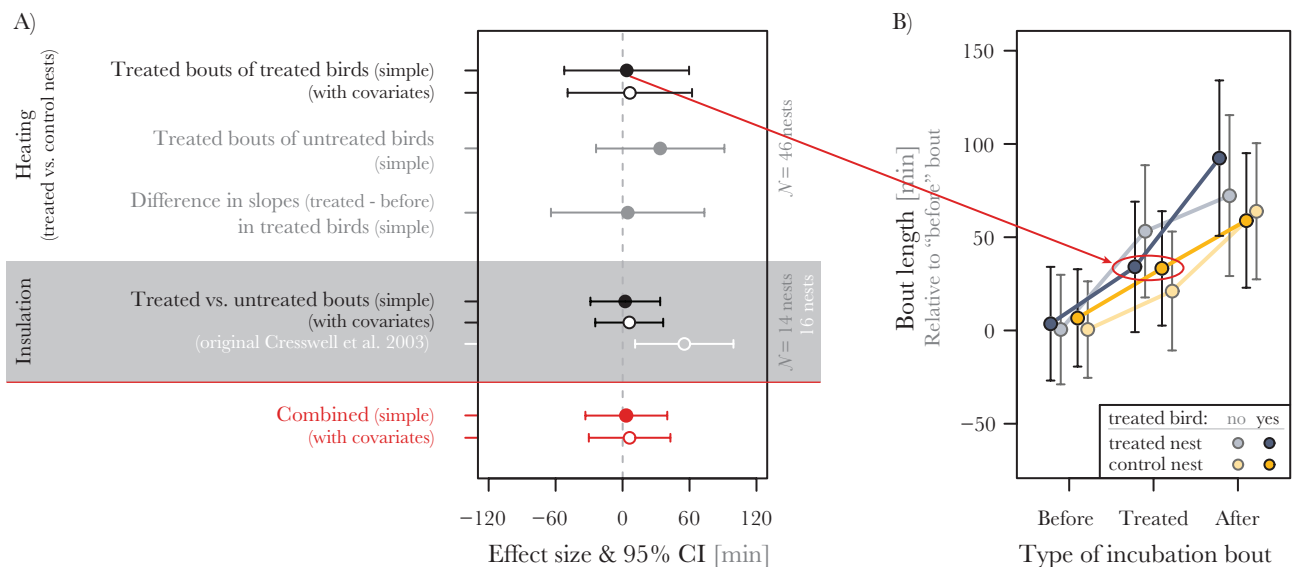


Figure 2

No major effects of heating (A and B) or nest insulation (A, gray area) on the length of incubation bouts. In (A), the red dots show the combined effect size for the heating and insulation experiment; filled circles: simple model estimates (statistical details are in Supplementary 1: Section 6, Tables S3 and S5); open circles: estimates from complex models with covariates (statistical details are in Supplementary 1: Section 6, Tables S4 and S6); in white: the estimate from the original insulation study (Cresswell et al. 2003). In (B), the red ellipse highlights the main comparison of interest, namely the difference between treated bouts in treated nests (heated bouts) and control nests (nonheated bouts). The values depicted in (B) are derived from the simple model using the “allEffects” function of the R package “effects” (Fox 2003); shown are bout lengths relative to the before-treatment bout length (i.e., for each individual, the mean before-bout length was calculated and subtracted from all incubation bouts). This allowed direct comparison of the treatment effects among nests, and controlled for changes in bout length with date and with day of incubation.

nests was 0.4% (−2.8 to 3.7%) larger than in “treated” birds in control nests ($P = 0.98$).

Moreover, the presence and duration of exchange gaps was unaffected by the heating (Supplementary 1: Section 6: Tables S7 and S8).

In sum, we found no evidence that reduced energetic demands of incubation (through egg heating) changed the length or constancy of incubation bouts in biparentally incubating semipalmated sandpipers.

Insulation experiment: reanalysis of Cresswell et al. (2003)

To verify whether the different outcomes of the heating experiment and the insulation experiment (as originally reported) hold, after taking into account the matched-pair cross-over experimental design (Hills and Armitage 1979; Jones and Kenward 1989; Díaz-Uriarte 2002), we reanalyzed the data from the insulation experiment. A detailed description of the original analysis and the reanalysis is in Supplementary 1 (Section 1, Reanalysis of the Insulation Experiment).

Once the analysis controlled for the period within which the control or treatment was applied (first or second 48 h), in all models (3 using nest-mean bout length, 2 mixed models on individual bout lengths) the originally reported effect (an increase in bout length of 55 min after insulation) disappeared (Figure 2A; Supplementary 1: Section 1, Table S1). Here, we only describe in detail the outcome of the 2 mixed models.

The treated bouts were 2.7 min (95% CI: −28.6 to 33.9 min) longer than untreated bouts ($P = 0.87$, $N = 45$ treated and 42 untreated bouts from 14 nests and 7 pairs; Figure 2A; statistical details are in Supplementary 1: Section 6, Table S9, the raw data for each nest are in Supplementary 3). Even after controlling the model for the confounding variables (sex and day of incubation; Bulla et al. 2014a), the estimated difference remained small; treated bouts were 6.2 min (95% CI: −24.3 to 36.6 min) longer than untreated bouts ($P = 0.69$; Figure 2A; statistical details are in Supplementary 1: Section 6, Table S10).

In sum, contrary to the original finding (Figure 2A), we found no evidence that reduced energetic demands of incubation by nest insulation increased the length of incubation bouts.

Artificial experiment: comparing the treatments

To find out in how far the results of the 2 experiments are comparable, we investigated whether the heating and insulation experiment differed in the strength of their treatment. The approximate amount of energy needed to “incubate” nests was measured with 3 artificial nest scrapes (heated, control, and insulated).

The artificial brood-patch consumed the least energy when the nest was heated: on average, 233 mW (95% CI: 111–354, $P < 0.0001$) less than in control nests and 158 mW (95% CI: 36–279, $P = 0.0079$) less than in insulated nests (mixed model with “nest” and “day of the experiment” as random intercepts; $N = 15$, 50-min measurements acquired during 2 days with 3 repeats per day from each of 3 nest scrapes; 3 missing values are due to system failure at one nest scrape during day 1; statistical details are in Supplementary 1: Section 6, Table S11).

These results indicate that—at least under the described experimental conditions—the heating treatment was stronger than the insulation treatment, and that both potentially saved energy for the incubating birds.

Combined effect of the 2 experiments

To estimate the overall effect of reduced energetic demands of incubation on the length of incubation bouts, we performed a

meta-analysis that combined the effects from the heating and insulation experiment and weighted them by the number of nests. The combined effect of heating and insulation on the length of incubation bouts was a prolongation of 3.6 min (95% CI: −33 to 40; red dot in Figure 2A) for the estimates from the simple models and 6.5 min (95% CI: −30 to 43; red circle in Figure 2A) for the estimates from models that controlled for the confounding variables. Both combined effects demonstrate no major energetic constraint on the length of incubation bouts.

DISCUSSION

We found no evidence for major energetic constraints on biparental incubation-scheduling in this system. Both the new experimental heating and the previous experimental insulation (here reanalyzed) had little influence on the length of incubation bouts (Figure 2). The experimental heating also left the incubation constancy unaffected (Supplementary 1: Section 6, Tables S5 and S6) and did not influence the presence or duration of exchange gaps (Supplementary 1: Section 6, Tables S7 and S8). Further, neither the parent that received heat nor the untreated parent changed their incubation bout length (Figure 2) or constancy (Supplementary 1: Section 6, Tables S5 and S6). These results indicate that it is unlikely that the energetic reserves either of the incubating parent or of the off-nest parent determine incubation-scheduling in semipalmated sandpipers. Below, we discuss potential limitations of our approach, the benefit of replicating a previously published study, and the main biological implications of our results.

Limitations

The absence of major energetic constraints on the length and constancy of incubation bouts under the current experimental setup does not exclude the possibility of minor energetic constraints on incubation-scheduling or the possibility that such constraints become relevant when the demands of incubation are more extreme.

First, although the heating treatment was severe (providing energy equivalent of up to 40% of the parent’s resting metabolic rate), the setup had sufficient statistical power only to detect a change in the length of treated incubation bouts higher than 52 min (Supplementary 1: Section 4, Figures S1–S4). Thus, smaller changes in bout length were likely to be undetected. However, the effect of heating was only in the order of a few minutes (Figure 2A), equivalent to a 0.2% change in the average incubation bout of semipalmated sandpipers (Bulla et al. 2014a).

Second, regardless of the strength of the treatment, we only manipulated the birds in one direction (decreasing energetic demands) and we did not measure the energy expenditure or weight loss of the incubating birds. Thus, we do not know how the treatments influenced the birds’ condition. We cannot exclude the possibility that an increase in the energetic demands of incubation (e.g., due to severe weather or through experimental cooling of the nest) would influence the length of incubation bouts. Contrary to this prediction and in line with our findings, experimental cooling of Kentish plovers’ nests increased (not decreased) incubation constancy (Kosztolanyi et al. 2009). However, this experiment was conducted under conditions that were less stressful to the birds (temperatures within their thermo-neutral zone) and effects on incubation bout length were not measured.

In sum, our results cannot fully exclude the existence of some energetic constraints on incubation-scheduling, but suggest that such constraints—if they exist—will only appear under severe

conditions. Future studies would benefit from measuring changes in the condition of manipulated birds.

Replication

Our finding revises previously published work (Cresswell et al. 2003), which suggested (using experimental nest insulation) that incubation-scheduling in semipalmated sandpipers was energetically constrained and driven by the energy reserves of the incubating parent. We failed to replicate this finding using a nest-heating experiment that targeted a single parent and was carried out in the same study area, on the same species and using a similar incubation monitoring system. This then prompted a reanalysis of the data from the earlier insulation experiment that targeted both parents. Using a rigorous statistical control of the matched-pair cross-over experimental design, the originally reported 55-min effect disappeared. Our results further demonstrate that both experiments should have had large effects on the energetic demands of incubation, whereby the heating procedure saved more energy than the insulation procedure. Furthermore, both experiments were carried out in relatively similar environmental conditions (apart from rain; Supplementary 1: Section 2, Figure S1). In sum, our findings amend the previously published results and interpretations, and demonstrate the benefit of replicating published experiments and the advantage of making data freely available for reanalysis.

Biological implications

The lack of major energetic constraints on biparental incubation-scheduling has 3 biological implications. First, the absence of such constraints in relatively severe high Arctic conditions is perhaps surprising, but suggests either that food is abundant, and hence parents less constrained by foraging time, or that the incubating parents of Arctic breeding species are adapted to buffer fluctuations in energetic demands of incubation (e.g., due to a spell of colder weather), just as their eggs (developing embryos) are adapted to survive prolonged conditions below the optimal for embryonic development (reviewed by Hicklin and Gratto-Trevor 2010).

Second, our findings suggest that biparental incubation-scheduling is less energetically constrained than uniparental incubation (e.g., Aldrich and Raveling 1983; Bryan and Bryant 1999; Reid et al. 1999; Cresswell et al. 2004; Ardia et al. 2009). This implies that individual semipalmated sandpipers—and perhaps most biparentally incubating species—might be able to incubate continuously for much longer than they actually do (see also Kosztolanyi et al. 2009). Therefore, other factors, such as predation risk, circadian fluctuations in prey availability, or synchronization of the daily rhythms of the 2 parents (discussed in Bulla et al. 2014a), may play a more important role in determining the length of incubation bouts.

Third, our findings also revise Cresswell et al.'s (2003) conclusion that the incubating parent may play an important role in driving incubation-scheduling. The fact that our heating experiment, which manipulated energy demands of only one of the 2 pair members, did not cause a change in bout length in either the treated or the untreated parent implies that we still do not understand which parent drives the length of incubation bouts. Knowledge about how parents behave while off-nest or near the nest during the exchange (e.g., whether the returning bird waits for a signal from its incubating partner, or whether the incubating parent waits for its off-nest partner to return) may help understand the factors determining biparental incubation-scheduling.

CONCLUSIONS

Our study illustrates the merit of replicating previously published experiments, as well as the usefulness of making data of published work freely available. Most importantly, our results reveal that it is unlikely that biparental incubation-scheduling in the semipalmated sandpiper is driven by major energetic constraints and that we still do not understand what drives variation in biparental incubation patterns, both in this and in other species.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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Supplementary

1. REANALYSIS OF THE INSULATION EXPERIMENT

There are four potential sources of bias and error in the original analysis of Cresswell et al. (2003) that we addressed with the reanalysis: unbalanced number of incubation bouts, lack of control for the period effects, unbalanced nest-pairs, and the use of means instead of the initial unit of measurement. Here we describe each issue separately and demonstrate how it contributed to the overestimation of the originally reported 55 minutes effect (95%CI: 11-99 minutes, $t_{15} = 2.67$, $P = 0.017$; Table S1).

Unbalanced number of incubation bouts

The matched-pair cross-over experimental design requires that each nest contains only control incubation bouts from within one of the 48 h experimental periods, but control bouts outside of these periods were included. Thus, in nests that first served as control and then were treated, bouts from before the 48 h control-period and from after the 48 h treatment period were included as control, whereas in nests that first were treated and then served as control, bouts from before the treatment period and from after the control period were included (see Supplementary 3).

We recalculated the mean bout lengths per nest and experimental period, excluding bouts that ended outside the first or started outside the second 48 h experimental period. Applying the same test (paired t -test) as in the original analysis to the new dataset reduced the treatment effect to 32.7 minutes (-9.7-75.1 minutes; paired t -test: $t_{15} = 1.6$, $P = 0.12$; Table S1 – model 1).

Lack of control for the period effects

The data were collected using a matched-pair cross-over experimental design, but analyzed as a typical matched-pair design (paired t -test). Such analysis did not explicitly account for period effects (i.e., whether control or treatment was applied in the first or second 48 h experimental period; an issue emphasized by Hills and Armitage 1979; Jones and Kenward 1989; Díaz-Uriarte 2002). The period effect might have been substantial because the bout lengths of semipalmated sandpipers increase over the incubation period (Ashkenazie and Safriel 1979; Cresswell et al. 2003; Bulla et al. 2014). Carryover effects (i.e., whether the after-treatment control periods were influenced by the treatment) might also bias the results, but the experimental design prohibits controlling for those.

Using the same dataset as above, but controlling for the period effect (by including it in the linear model; a method described by, e.g., Jones and Kenward 1989; Díaz-Uriarte 2002), further reduced the effect of treatment: 30.3 minutes (95% CI: -20.6-81.2 minutes, $P = 0.32$, $N = 32$ period nest-means from 16 nests; Table S1 – model 2; an alternative method to control for the period effect is described in Hills and Armitage 1979).

Unbalanced nest-pairs

The matched-pair cross-over experimental design also requires that each nest-pair contains one nest that first serves as control and then is treated (CT) and one nest that is first treated and then serves as control (TC), but Cresswell et al. (2003) included one nest-pair where both nests were CT. Because the incubation bouts prolong

over the incubation period (Ashkenazie and Safriel 1979; Cresswell et al. 2003; Bulla et al. 2014), this nest-pair likely led to an overestimate of the final treatment effect on the length of incubation bouts. Indeed, excluding this nest-pair from the analysis (presented above) decreased the treatment effect to 19.4 minutes (-20.7-59.4 minutes, $P = 0.47$, $N = 28$ period nest-means from 14 nests; Table S1 – model 3).

Table S1

Period and treatment estimates (in minutes) from models on nest-mean bout lengths for control and treatment.

Model	Type	<i>N</i>	48 h period (95% CI)	Treatment (95% CI)
Original study	Paired <i>t</i> -test	32 period nest-means; 16 nests		55.2 (11.2-99.3), $t = 2.7$, $P = 0.02$
1	Paired <i>t</i> -test	32 period nest-means ^a ; 16 nests		32.7 (-9.7-75.1), $t = 1.6$, $P = 0.12$
2	Linear model	32 period nest-means ^a ; 16 nests	19.4 (-31.6-70.3), $t = 0.93$, $P = 0.63$	30.3 (-20.6-81.2), $t = 1.5$, $P = 0.32$
3	Linear model	28 period nest-means ^a ; 14 nests	8.4 (-31.7-48.5), $t = 0.51$, $P = 0.88$	19.4 (-20.7-59.4), $t = 1.2$, $P = 0.47$

^a Period nest-means (recalculated) included only bouts that ended within the 1st or started within the 2nd 48 h experimental period.

Use of means instead of original measurements

Semipalmated sandpipers show large within-nest variation in the length of incubation bouts (SD is about 17% of median incubation bout length; Bulla et al. 2014). Because of this variation, the precision of the nest means depends on the number of incubation bouts used for their calculation. Because the original mean-based analysis did not control for the number of bouts used to calculate the nest means, the precision of the final result depends on how balanced the number of bouts between nests and treatment sessions was (see Supplementary 3; e.g., in 5 nests one of the period means was derived from only one incubation bout). Furthermore, the use of nest-means made controlling the models for some confounding variables of bout length (e.g., sex) impossible.

Thus, we used mixed-effect models with individual bout lengths (instead of nest means) as dependent variable. We controlled for period effects (by including the period in the model) and for other confounding effects by centering bout lengths within the nest, by including day of incubation (quadratic) as a random slope and nest ID as random intercept, and by including confounding variables that act on the level of the bout in the analysis. These are the results reported in the main text and Supplementary Table S8 and S9.

2. SEASONAL DIFFERENCES

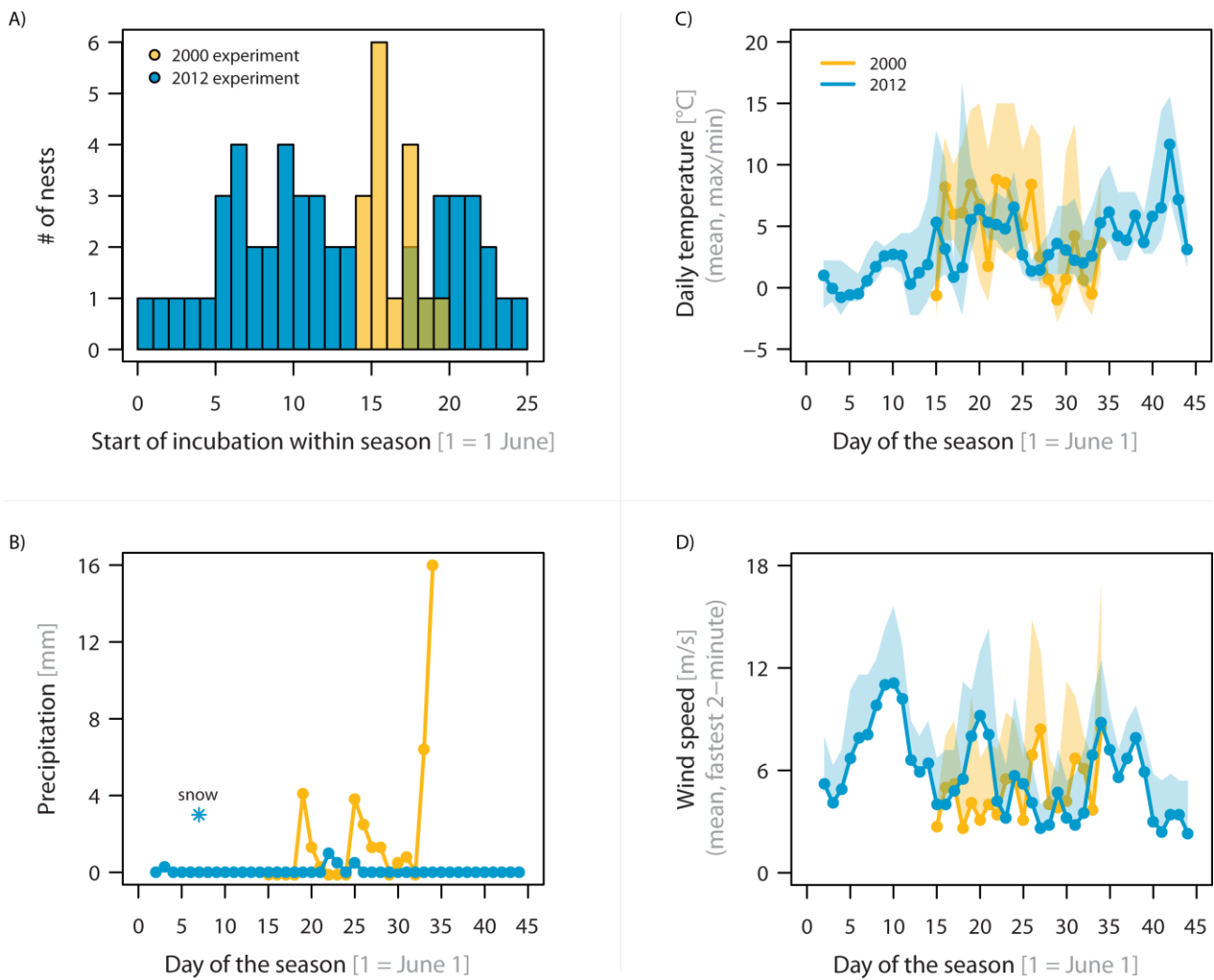


Figure S1

Between-year differences in the distribution of the start-date of incubation **A**, daily precipitation **B**, daily mean, minimum and maximum temperatures **C**, and daily mean and fastest 2 minutes wind speed **D**. The data for each year are limited to the period experienced by the nests prior or during the experiment (i.e., the period between the earliest start-date of incubation and the latest day of the experiment). The environmental data are freely available from NOAA:

<http://www.ncdc.noaa.gov/cdo-web/>

and <http://cdo.ncdc.noaa.gov/pls/plclimprod/poemain.accessrouter?datasetabbv=DS3505>.

3. PICTURES



Picture S1

Exclosure that protected the nest against avian predators (approximate size $0.8 \times 0.7 \times 0.5$ m; mesh size 5×5 cm and 5×10 cm where the cage touched the ground; wire \varnothing 1.9 mm).



Picture S2

Artificial nest scrape with artificial egg and polystyrene insulation. The white cable connects the temperature probe with the data-logger.



Picture S3

Artificial brood patch – heated egg embedded in polystyrene of approximately $9 \times 8 \times 2.5$ cm.



Picture S4

Artificial brood patches (white) covering the artificial nest scrapes.

4. A PRIORI POWER ANALYSES

In all power analyses the bout lengths were sampled from a normal distribution with mean bout length of 687 minutes (based on Bulla et al. 2014). The results of the power analyses are summarized in Figures S2-5. The statistical power for each comparison (each point in the graph) represents the proportion of correct findings ($P < 0.05$) from 1000 tests of 1000 randomly generated datasets.

In the first set of power analyses (Figure S2), each dataset was tested in two types of linear mixed-effect models, with bout length as dependent variable and nest as random intercept. In the first model, nest (control or treated) was entered in interaction with type of incubation bout (before, treated, or after); we only tested the difference of the “treated” bouts between control and treated nests, and the difference in slopes (treated bouts minus before bouts) in control and treated nests. In the second model, sex was entered in interaction with nest (control or treated) and type of incubation bout (before, treated, or after); we only tested the difference between male treated-bouts and female treated-bouts in treated nests.

Only the difference of the “treated” bouts between control and treated nests had sufficient statistical power with attainable sample sizes (Figure S2). Hence, the remaining three sets of power-analyses (Figure S3-S5) concerned only the treatment-assigned bouts (“treated”) in control nests and treated (heated) bouts in treated nests. The analyses explored the effect of the number of repeats per period, ranging from 1 to 5 bouts of before, during and after treatment, as well as a scenario with 3 before, 4 treated and 3 after-treatment incubation bouts. Although 5 or more repeats would increase statistical power, their use would not be feasible because it would be difficult to fit the experiment within the 21-day incubation period, given that nests are found at various stages of incubation and that usually one or both birds have to be caught before the experiment can start.

Each dataset was tested in the linear mixed-effect model with bout length as dependent variable, nest (control or treated) in interaction with type of incubation bout (before, treated, or after) as a predictor, and nest as a random intercept. We only tested the difference in treated bouts in control and treated nests, and the difference in slopes (treated bouts minus before bouts) in control and treated nests; the figures display only the first comparison.

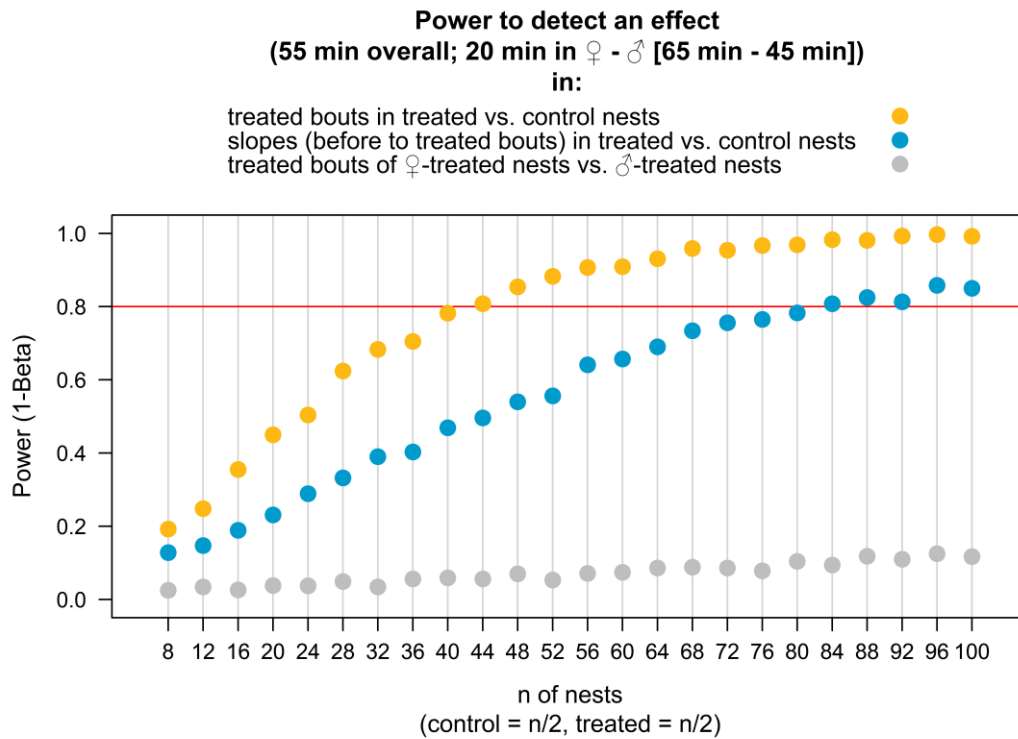


Figure S2 - Statistical power for the experiment in relation to sample size.

Depicted are the relationships between sample size and statistical power when “treated” bouts in control nests are compared with treated bouts in treated nests (yellow dots), when slopes (e.g., from before to treated bouts) in control nests are compared with slopes in treated nests (blue dots) or when treated bouts in female-treated nests are compared with treated bouts in male-treated nests (grey dots). Effect size was 65 minutes for females and 45 minutes for males (averaging 55 minutes – the effect reported in Cresswell et al. 2003), standard deviation (SD) in bout length was 118 minutes (based on the within-nest SD in bout length from Bulla et al. 2014), each bout type had 4 repeats within each nest (i.e., 4 before, 4 treated, 4 after bouts). The samples contained equal numbers of female-treated and male-treated nests. The red horizontal line indicates the acceptable recommended power of 0.8 (Cohen 1988).

Power to detect 55 min effect in control vs. treated nests (in treated bouts)

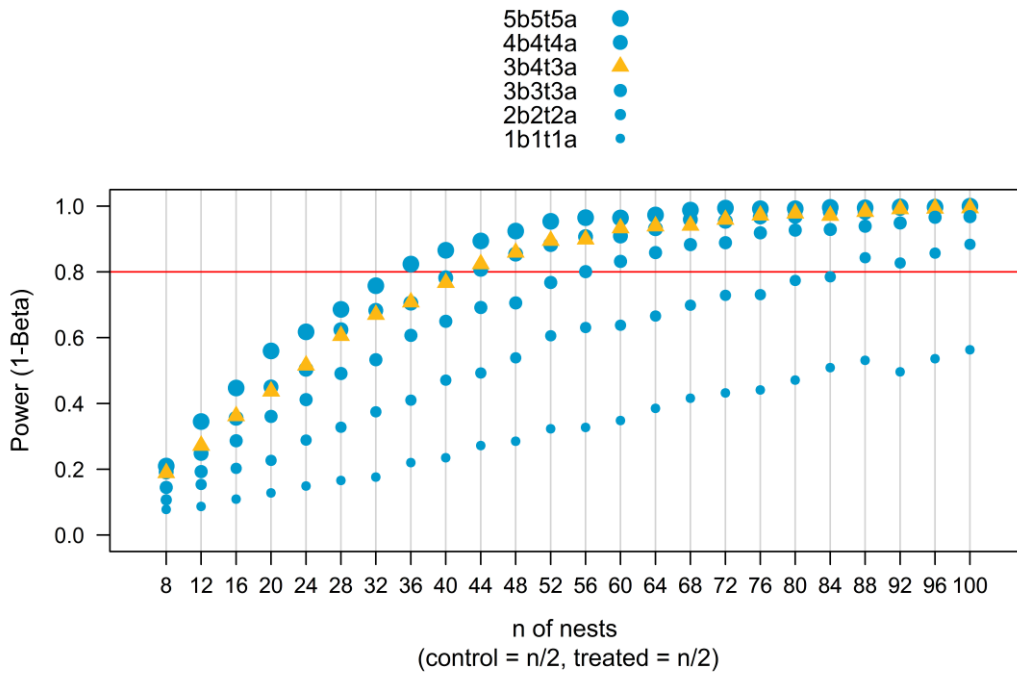


Figure S3 - Statistical power for the experiment in relation to sample size

Depicted are the relationships between sample size and statistical power for different experimental protocols (different symbols), differing in the number of before-treatment bouts (b), treated bouts (t) and after-treatment bouts (a). Effect sizes and bout length SD are similar as in Figure S2. The red horizontal line indicates the acceptable recommended power of 0.8 (Cohen 1988).

**Power to detect given effect in
control vs. treated nests (in treated bouts)
with n = 44 nests (22 control, 22 treated)**

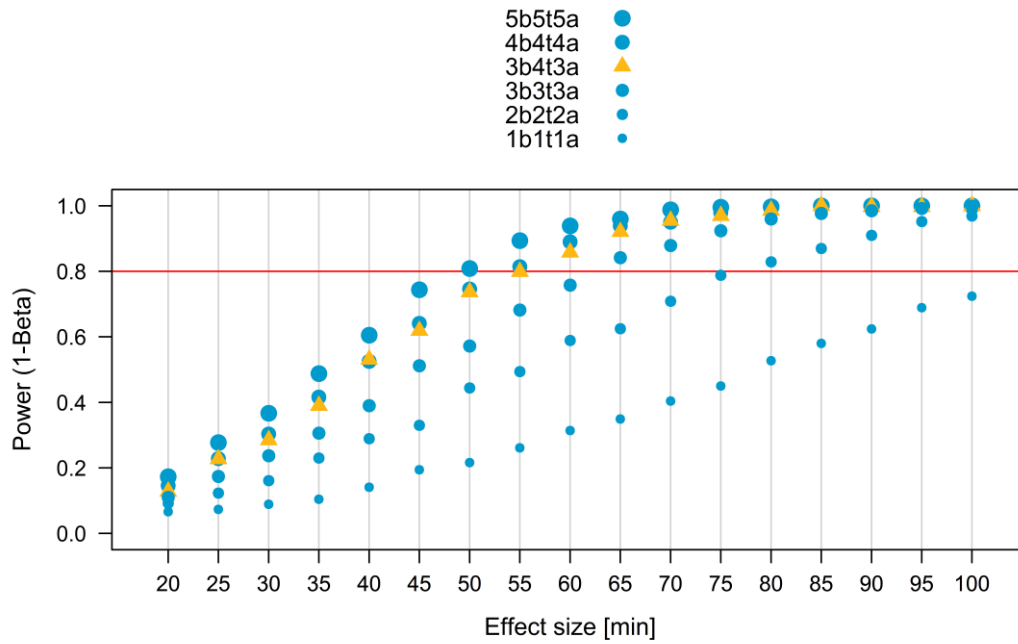


Figure S4 - Statistical power for the experiment in relation to effect size

Depicted are the relationships between effect size and statistical power for different experimental protocols (different symbols), differing in the number of before-treatment bouts (b), treated bouts (t) and after-treatment bouts (a). The results are based on a sample size of 22 control and 22 treated nests (based on Figure S2), and a SD in bout length of 118 minutes (based on the within-nest SD in bout length from Bulla et al. 2014). The red horizontal line indicates the acceptable recommended power of 0.8 (Cohen 1988).

Power to detect 55 min effect in control vs. treated nests (in treated bouts) with n = 44 nests (22 control, 22 treated)

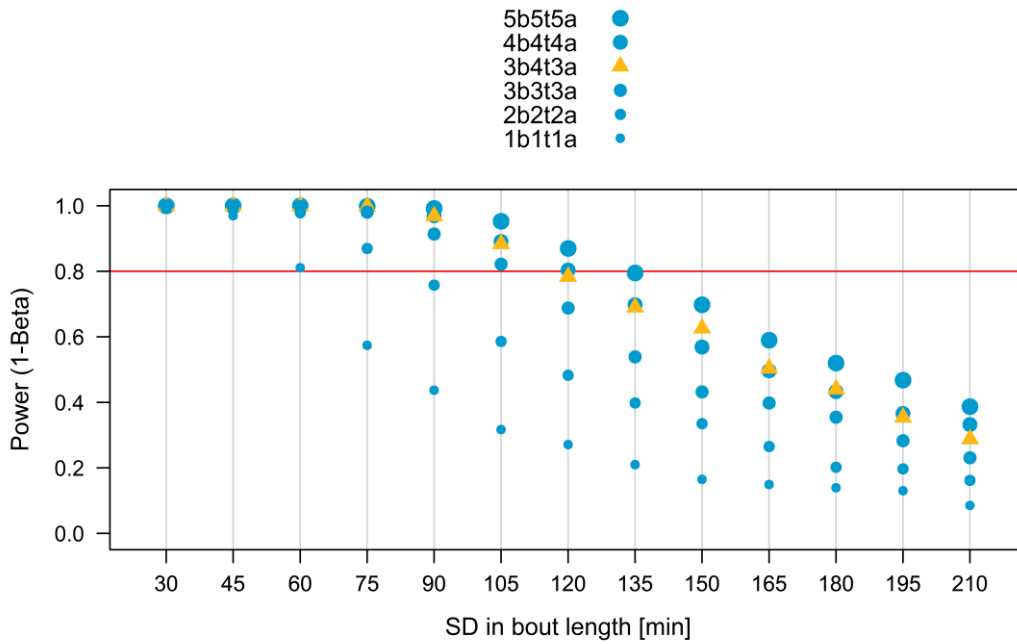


Figure S5 - Statistical power for the experiment in relation to the standard deviation (SD) in bout length.

Depicted are the relationships between SD in bout length and statistical power for different experimental protocols (different symbols), differing in the number of before-treatment bouts (b), treated bouts (t) and after-treatment bouts (a). The results are based on a sample size of 22 control and 22 treated nests (based on Figure S2), and an overall effect size of 55 minutes (based on Cresswell et al. 2003). The red horizontal line indicates the acceptable recommended power of 0.8 (Cohen 1988).

5. SAMPLE SIZES

Out of 99 nests equipped (at least for some time) with the incubation monitoring system, the following nests were excluded: nests with less than 4 recorded incubation bouts, nests where the monitoring system failed or nests used to test other experimental procedures ($N = 30$); control nests with less than 9 days of recorded incubation data ($N = 12$); treated nests where the treatment failed because a heated egg never turned on ($N = 2$), or because the nest was deserted by at least one parent or depredated ($N = 9$). This left 25 control nests (13 coded as female “treated”, 12 as male “treated”) and 21 treated nests (11 female-treated, 10 male-treated).

For the 46 nests used in the study, the following bouts were excluded: bouts during which eggs were laid; bouts when the nest was deserted or depredated; bouts that ended within 6 h before the start of hatching; bouts that started 2 days after the estimated hatch date; bouts during which the incubation-monitoring system was installed at the nest (if at the same time catching took place and the off-nest bird, instead of the incubating [caught] bird, returned after catching, this “after catching” bout was also excluded); bouts during which the artificial egg was inserted in the nest. Additional bouts were excluded in 2 nests with only one tagged parent. In these nests, the heated egg was heating whenever the battery was connected and the focal bird sat on the nest. As a result, when connecting and disconnecting the battery, the heating might have started or ended in the middle of the incubation bout. These bouts together with the next bout (bout of the untreated partner) were also excluded. Finally, given the experimental set up, a maximum of 4 before-treatment bouts and 4 after-treatment bouts per individual were used.

The final dataset contained 976 incubation bouts from 46 nests (median [range] = 22 [10 - 24] incubation bouts per nest; 100 “treated” incubation bouts in control nests, 81 treated incubation bouts in treated nests). The distribution of the incubation bouts (Table S2) deviated from the ideal one (4 before, 4 treated and 4 after bouts), for following reasons. First, the treatment-assigned birds in all 25 control nests had always 4 “treated” bouts, but in 9 nests were assigned less than 4 before bouts because these nests were found later in the incubation period, and in 4 nests were assigned less than 4 after bouts because later only a single bird incubated (3 nests), or the nest was depredated (1 nest). Second, the treated birds in all 21 treated nests had always 3 or 4 before-treatment bouts, depending on whether the nest was found early or late in the incubation period, and whether the treated bird incubated when the artificial egg or heat-SD-card was inserted. The treated birds had less than 4 treated bouts, if the nest was depredated during treatment (2 nests) or if the system was accidentally turned off before the end of the treatment (1 nest). Similarly, the treated birds had less than 4 after-treatment bouts, if the nest was depredated (3 nests), deserted (1 nest), later only a single bird incubated (3 nests), or was found later in the incubation period and thus started hatching (3 nests).

The final dataset for incubation-constancy contained 952 incubation bouts from 45 nests (median [range] = 22 [10 - 24] incubation bouts per nest; 96 “treated” incubation bouts in control nests, 81 treated incubation bouts in treated nests; the distribution of incubation bouts is in Table S2). One control nest was excluded because it lacked incubation temperatures and thus constancy could not be calculated.

The final dataset for probability of detectable exchange gap contained 928 exchanges from 46 nests (median [range] = 21 [9 - 23] exchanges per nest; 100 exchanges following “treated” incubation bouts [of

treatment-assigned birds] in control nests, 80 exchanges following treated incubation bouts [of treated birds] in treated nests).

The final dataset for duration of detectable exchange gaps (≥ 5 s) contained 655 detectable exchange gaps from 44 nests (median [range] = 15 [3 - 23] detectable exchange gaps per nest; 71 detectable exchange gaps following “treated” incubation bouts [of treatment-assigned birds] in control nests, 55 exchanges following treated incubation bouts [of treated birds] in treated nests).

Table S2

Distribution (number of nest with given number) of incubation bouts.

Bout type Number of bouts	Before			Treated				After				
	2	3	4	1	3	4	5	0	1	2	3	4
Control nest, “treated” assigned bird	3	6	16 ^a	25 ^a				2			2	21 ^a
Control nest, untreated bird	3	6	16 ^a	25 ^a				1	1	1	3	19 ^a
Treated nest, treated bird	1	12	8	1	2	16	2 ^b	3	3	1	3	11
Treated nest, untreated bird		6	15	1	3	15	2 ^b	4	2	4	1	10

^aThe dataset for incubation-constancy contained one nest less.

^bAt two nests with only one tagged parent the heating ran until the battery was disconnected.

6. MODELS

Table S3

Mixed model estimates of incubation bout length (transformed^a) in relation to whether the nest, parent, and incubation bout were treated (heated).

Fixed effects on bout length (minutes)	Relative to	Estimate	95% CI	z	P
(Intercept)		-4.1	(-39.3, 31.1)		
Nest (treated)	control	1.9	(-51.8, 55.5)	0.1	1
Parent (treated)	untreated	6.2	(-43, 55.5)	0.35	1
Incubation bout (treated)	before	22.4	(-32.7, 77.6)	1.12	0.88
Incubation bout (after)	before	68.8	(7.2, 130.4)	3.08	0.02
Nest (treated) × Parent (treated)		-2.8	(-75.5, 69.9)	-0.11	1
Nest (treated) × Incubation bout (treated)		32.1	(-47.5, 111.7)	1.11	0.88
Nest (treated) × Incubation bout (after)		10.4	(-85.5, 106.2)	0.3	1
Parent (treated) × Incubation bout (treated)		5.5	(-61.7, 72.7)	0.23	1
Parent (treated) × Incubation bout (after)		-11.6	(-80.8, 57.7)	-0.46	1
Nest (treated) × Parent (treated) × Incubation bout (treated)		-27.3	(-127.3, 72.7)	-0.75	0.99
Nest (treated) × Parent (treated) × Incubation bout (after)		25.4	(-82, 132.9)	0.65	1
Random effects		Variance			
Nest (intercept)		3301			
Day of incubation (1 st polynomial)		845782			
Day of incubation (2 nd polynomial)		1475503			
Residual		13857			

N = 976 incubation bouts from 46 nests (25 control, 21 treated); 100 “treated” incubation bouts (of treatment-assigned birds) in control nests, 81 treated incubation bouts (of treated birds) in treated nests. The model lacked major spatial and temporal auto-correlation, thus, unlike in Bulla et al. (2014), was not controlled for the length of the previous (partner’s) incubation bout.

^a By subtracting for each individual the mean before-treatment bout length from all other incubation bout lengths.

Table S4

Mixed model estimates of incubation bout length (transformed^a) in relation to whether the nest, parent, and incubation bout were treated (heated); model was controlled for disturbance^b, sex, and day of incubation (quadratic).

Fixed effects on bout length (minutes)	Relative to	Estimate	95% CI	z	P
(Intercept)		-1.8	(-59.5, 55.8)		
Disturbance		41.8	(16.4, 67.3)	4.75	<0.0001
Sex (male)	female	-14	(-35.6, 7.6)	-1.87	0.50
Day of incubation (1 st polynomial)		139.9	(-804.7, 1084.4)	0.43	1
Day of incubation (2 nd polynomial)		-800.2	(-1518.6, -81.9)	-3.21	0.02
Nest (treated)	control	-7.4	(-63.2, 48.4)	-0.38	1
Parent (treated)	untreated	8.1	(-42.8, 59)	0.46	1
Incubation bout (treated)	before	4.1	(-57.9, 66)	0.19	1
Incubation bout (after)	before	53.8	(-27.1, 134.7)	1.92	0.47
Nest (treated) × Parent (treated)		-3.6	(-78.5, 71.4)	-0.14	1
Nest (treated) × Incubation bout (treated)		45.3	(-37.3, 127.8)	1.58	0.72
Nest (treated) × Incubation bout (after)		35.8	(-65.8, 137.3)	1.02	0.98
Parent (treated) × Incubation bout (treated)		6.8	(-62.5, 76.1)	0.28	1
Parent (treated) × Incubation bout (after)		-11.2	(-82.9, 60.5)	-0.45	1
Nest (treated) × Parent (treated) × Incubation bout (treated)		-27.7	(-130.7, 75.3)	-0.78	1
Nest (treated) × Parent (treated) × Incubation bout (after)		27	(-83.8, 137.7)	0.7	1
Random effects		Variance			
Nest (intercept)		3111			
Day of incubation (1 st polynomial)		852144			
Day of incubation (2 nd polynomial)		1358075			
Residual		13418			

N = 976 incubation bouts from 46 nests (25 control, 21 treated); 100 “treated” incubation bouts (of treatment-assigned birds) in control nests, 81 treated incubation bouts (of treated birds) in treated nests. The model lacked major spatial and temporal auto-correlation, thus, unlike in Bulla et al. (2014), was not controlled for the length of the previous (partner’s) incubation bout.

^a By subtracting for each individual the mean before-treatment bout length from all other incubation bout lengths.

^b Disturbance (no = 0, yes = 1; continuous) was defined as in Bulla et al. (2014).

Table S5

Mixed model estimates of incubation-constancy within incubation bout (transformed^a) in relation to whether the nest, parent, and incubation bout were treated (heated).

Fixed effects on constancy of incubation (%)	Relative to	Estimate	95% CI	z	P
(Intercept)		0.1	(-1.6, 1.8)		
Nest (treated)	control	0.1	(-2.4, 2.6)	0.08	1
Parent (treated)	untreated	0.1	(-2.4, 2.5)	0.06	1
Incubation bout (treated)	before	0.4	(-2.2, 3)	0.43	1
Incubation bout (after)	before	2.4	(-1.6, 6.4)	1.63	0.53
Nest (treated) × Parent (treated)		0	(-3.6, 3.5)	-0.04	1
Nest (treated) × Incubation bout (treated)		-0.4	(-4.2, 3.4)	-0.29	1
Nest (treated) × Incubation bout (after)		-2	(-8.3, 4.3)	-0.87	0.97
Parent (treated) × Incubation bout (treated)		-0.4	(-3.8, 2.9)	-0.37	1
Parent (treated) × Incubation bout (after)		0.7	(-2.7, 4.2)	0.59	1
Nest (treated) × Parent (treated) × Incubation bout (treated)		0.8	(-4, 5.7)	0.47	1
Nest (treated) × Parent (treated) × Incubation bout (after)		-1.3	(-6.6, 4)	-0.68	0.99
Random effects		Variance			
	Nest (intercept)	47			
	Day of incubation (1 st polynomial)	58091			
	Day of incubation (2 nd polynomial)	9862			
	Residual	32			

N = 952 incubation bouts from 45 nests (24 control, 21 treated); 96 “treated” incubation bouts (of treatment-assigned birds) in natural nests, 81 treated incubation bouts (of treated birds) in treated nests. The model lacked spatial and temporal auto-correlation.

^a By subtracting for each individual the mean before-treatment incubation constancy from all other incubation constancies.

Table S6

Mixed model estimates of incubation-constancy within incubation bout (transformed^a) in relation to whether the nest, parent, and incubation bout were treated (heated); model was controlled for disturbance^b, sex, and length of incubation bout.

Fixed effects on constancy of incubation (%)	Relative to	Estimate	95% CI	<i>z</i>	<i>P</i>
(Intercept)		-6.5	(-9.6, -3.5)		
Disturbance		-0.6	(-1.8, 0.7)	-1.31	0.87
Sex (male)	female	0.1	(-0.9, 1.1)	0.28	1
Length of incubation bout		0.01	(0.007, 0.01)	8.11	<0.0001
Nest (treated)	control	-0.2	(-2.8, 2.3)	-0.26	1
Parent (treated)	untreated	0.3	(-2.1, 2.7)	0.35	1
Incubation bout (treated)	before	-0.2	(-2.7, 2.4)	-0.2	1
Incubation bout (after)	before	1.4	(-2.7, 5.4)	0.95	0.98
Nest (treated) × Parent (treated)		-0.1	(-3.6, 3.5)	-0.06	1
Nest (treated) × Incubation bout (treated)		-0.4	(-4.2, 3.4)	-0.31	1
Nest (treated) × Incubation bout (after)		-1.5	(-7.8, 4.8)	-0.68	1
Parent (treated) × Incubation bout (treated)		-0.5	(-3.8, 2.8)	-0.46	1
Parent (treated) × Incubation bout (after)		0.8	(-2.7, 4.2)	0.64	1
Nest (treated) × Parent (treated) × Incubation bout (treated)		1.1	(-3.8, 6)	0.63	1
Nest (treated) × Parent (treated) × Incubation bout (after)		-1.6	(-6.9, 3.6)	-0.89	0.99
Random effects		Variance			
Nest (intercept)		52			
Day of incubation (1 st polynomial)		66460			
Day of incubation (2 nd polynomial)		12366			
Residual		30			

N = 952 incubation bouts from 45 nests (24 control, 21 treated); 96 ‘treated’ incubation bouts (of treatment-assigned birds) in natural nests, 81 treated incubation bouts (of treated birds) in treated nests. The model lacked spatial and temporal auto-correlation.

^a By subtracting for each individual the mean before-treatment incubation constancy from all other incubation constancies.

^b Disturbance (no = 0, yes = 1; continuous) was defined as in Bulla et al. (2014).

Table S7

Binomial mixed model estimates^a of the presence of an exchange gap^b (≥ 5 s) in relation to whether the nest and parent in the preceding incubation bout were treated (heated); model was controlled for disturbance^c, and day of incubation^d.

Fixed effects on presence of detectable exchange gap	Relative to	Estimate ^a	95% CI	z	P
(Intercept)		0.2	(-1, 1.5)		
Disturbance		-0.2	(-0.7, 0.4)	-0.8	0.99
Day of incubation		-0.6	(-1.2, 0.1)	-2.55	0.11
Nest (treated)	control	1	(-0.5, 2.6)	1.93	0.40
Parent (treated)	untreated	0.6	(-0.4, 1.7)	1.68	0.58
Incubation bout (treated)	before	0.9	(-0.3, 2.1)	2.14	0.27
Incubation bout (after)	before	1.3	(-0.3, 3)	2.26	0.21
Nest (treated) × Parent (treated)		-0.3	(-2, 1.4)	-0.48	1
Nest (treated) × Incubation bout (treated)		-0.2	(-1.8, 1.4)	-0.3	1
Nest (treated) × Incubation bout (after)		-0.4	(-2.4, 1.5)	-0.61	1
Parent (treated) × Incubation bout (treated)		-0.7	(-2.1, 0.8)	-1.33	0.84
Parent (treated) × Incubation bout (after)		-1.2	(-2.7, 0.3)	-2.25	0.22
Nest (treated) × Parent (treated) × Incubation bout (treated)		-0.2	(-2.5, 2.1)	-0.27	1
Nest (treated) × Parent (treated) × Incubation bout (after)		0.8	(-1.7, 3.3)	0.9	0.98
Random effects		Variance			
Nest (intercept)		1.43			
Day of incubation		0.13			

$N = 928$ exchanges from 46 nests (25 control, 21 treated); 100 exchanges following “treated” incubation bouts (of treatment-assigned birds) in control nests, 80 exchanges following treated incubation bouts (of treated birds) in treated nests. Results for only specifically defined (simultaneously tested) hypotheses demonstrate no major effect of the heating on the occurrence of the exchange gap: the detectability of exchange gaps following the treated bouts in treated nests was higher than after the “treated” bouts in control nests (0.4, 95%CI: -0.9–1.6, $z = 0.71$, $P = 0.82$) – an effect in the opposite direction to that expected for exchange gaps following treated bouts; during treatment period, the occurrence of exchange gaps following the untreated bouts in treated nests (i.e., off-nest bouts of the treated bird) was higher than after the untreated bouts in control nests (0.9 [-0.4–2.2], $z = 1.59$, $P = 0.26$) – an effect in the opposite direction to that expected for exchange gaps following off-nest bouts of treated birds during treatment period; for comparison, during before-treatment period the occurrence of exchange gaps following the untreated bouts in treated nests was also higher than after the untreated bouts in control nests (1 [-0.2–2.3], $z = 1.42$, $P = 0.14$) – a similar effect to the (above described) effect during treatment period.

^a On logit scale.

^b Exchange gap (undetected = 0, detected = 1)

^c Disturbance (no = 0, yes = 1; continuous) was defined as in Bulla et al. (2014).

^d Day of incubation was mean centered.

Table S8

Mixed model estimates^a of exchange gap duration (in minutes, ln transformed^b) in relation to whether the nest and parent in preceding incubation bout were treated (heated); model was controlled for disturbance^c, and day of incubation^d.

Fixed effects on duration of detectable exchange gap	Relative to	Estimate ^a	95% CI	z	P
(Intercept)		-0.1	(-0.7, 0.6)		
Disturbance		0.1	(-0.2, 0.4)	0.99	0.96
Day of incubation		0	(-0.3, 0.4)	0.24	1
Nest (treated)	control	0	(-0.6, 0.7)	0.09	1
Parent (treated)	untreated	-0	(-0.6, 0.6)	-0.04	1
Incubation bout (treated)	before	-0.1	(-0.8, 0.6)	-0.24	1
Incubation bout (after)	before	-0.5	(-1.5, 0.4)	-1.55	0.67
Nest (treated) × Parent (treated)		0	(-0.8, 0.9)	0.04	1
Nest (treated) × Incubation bout (treated)		0	(-0.9, 0.9)	0.09	1
Nest (treated) × Incubation bout (after)		0.5	(-0.7, 1.7)	1.2	0.89
Parent (treated) × Incubation bout (treated)		0.2	(-0.7, 1)	0.53	1
Parent (treated) × Incubation bout (after)		0.4	(-0.5, 1.3)	1.22	0.88
Nest (treated) × Parent (treated) × Incubation bout (treated)		-0.4	(-1.6, 0.8)	-1.03	0.95
Nest (treated) × Parent (treated) × Incubation bout (after)		-0.5	(-1.8, 0.9)	-0.94	0.97
Random effects		Variance			
Nest (intercept)		0.26			
Day of incubation		0.15			
Residual		1.36			

N = 655 detectable exchange gaps (≥ 5 s) from 44 nests (24 control, 20 treated); 71 detectable exchange gaps following “treated” incubation bouts (of treatment-assigned birds) in control nests, 55 detectable exchange gaps following treated incubation bouts (of treated birds) in treated nests. Results for only specifically defined (simultaneously tested) hypotheses demonstrate no major effect of the heating on the duration of detectable exchange gaps: the detectable exchange gaps following the treated bouts in treated nests were shorter than the exchange gaps following the “treated” bouts in control nests (-0.4, 95%CI: -1–0.2, $z = -1.47$, $P = 0.36$) – a tendency for an effect in the direction to that expected for exchange gaps following treated bouts; during treatment period, the detectable exchange gaps following the untreated bouts in treated nests (i.e., following the off-nest bouts of the treated bird) were similar to the exchange gaps following the untreated bouts in control nests (0 [-0.6–0.7], $z = 0.19$, $P = 1$); for comparison, during before-treatment period the detectable exchange gaps following the untreated bouts in treated nests were similar to the exchange gaps following the untreated bouts in control nests (0 [-0.5–0.6], $z = 0.09$, $P = 1$).

^a On ln-scale.

^b By subtracting for each individual the mean before-treatment exchange gap from all other exchange gaps.

^c Disturbance (no = 0, yes = 1; continuous) was defined as in Bulla et al. (2014).

^d Day of incubation was mean centered.

Table S9

Mixed model estimates of incubation bout length (mean-centered within individual) in relation to period (first or second 48 h of the experiment) and whether the incubation bout was treated (insulated).

Fixed effects on bout length (minutes)	Relative to	Estimate	95% CI	<i>z</i>	<i>P</i>
(Intercept)		-5.2	(-39.3, 29)		
Period (2 nd)	1 st	16.8	(-20.6, 54.2)	1.05	0.57
Incubation bout (treated)	untreated	2.7	(-34.7, 40.1)	0.17	1
Random effects		Variance			
Nest (Intercept)		8			
Day of incubation (1 st polynomial)		1922			
Day of incubation (2 nd polynomial)		26248			
Residual		4842			

N = 87 incubation bouts from 14 nests from 7 nest-pairs; 42 treated bouts, 45 untreated bouts. The model lacked major temporal auto-correlation, thus, unlike in Bulla et al. (2014), was not controlled for the length of previous (partner's) incubation bout. Model with random intercept of nest ID nested within pair ID did not converge.

Table S10

Mixed model estimates of incubation bout length (mean-centered within individual) in relation to period (first or second 48 h of the experiment) and whether the incubation bout was treated (insulated); model was controlled for sex, and quadratic day of incubation.

Fixed effects on bout length (minutes)	Relative to	Estimate	95% CI	<i>z</i>	<i>P</i>
(Intercept)		-14.2	(-55.3, 26.8)		
Sex (male)	female	1.6	(-38.9, 42)	0.1	1
Day of incubation (1 st polynomial)		-26.9	(-238.7, 184.9)	-0.33	1
Day of incubation (2 nd polynomial)		-118.3	(-312.4, 75.7)	-1.59	0.47
Period (2 nd)	1 st	21.9	(-23.1, 66.9)	1.27	0.70
Incubation bout (treated)	untreated	6.2	(-34.3, 46.7)	0.4	1
Random effects		Variance			
Nest (Intercept)		0			
Day of incubation (1 st polynomial)		109			
Day of incubation (2 nd polynomial)		2313			
Residual		5142			

N = 87 incubation bouts from 14 nests from 7 nest-pairs; 42 treated bouts, 45 untreated bouts. The model lacked major temporal auto-correlation, thus, unlike in Bulla et al. (2014), was not controlled for the length of the previous (partner's) incubation bout. Model with random intercept of nest ID nested within pair ID did not converge.

Table S11

Mixed model estimates of energy provided to the nest-scrape (transformed^a) with treatment (heated egg, polystyrene insulation, or control).

Fixed effects on provided energy (mW)	Relative to	Estimate	95% CI	<i>z</i>	<i>P</i>
(Intercept)		-241	(-384, -97)		
Treatment (control)	heated egg	233	(104, 361)	4.25	<0.0001
Treatment (insulation))	heated egg	158	(29, 287)	2.89	0.011
Random effects		Variance			
Nest (Intercept)		0			
Day of experiment (Intercept)		4415			
Residual		7482			

N = 15 fifty-minute measurements acquired during 2 days with 3 repeated measurement from 3 nest scrapes (i.e., treatment was rotated among the nest-scrapes); 3 missing measurements due to system failure at one nest scrape during day one

^a Provided energy was transformed within nest scrape and day of experiment by subtracting, for each nest scrape and day of the experiment, the control value from all other values.

7. ESTIMATING ENERGETIC DEMANDS OF INCUBATION

Precise estimates of energetic demands of incubation (i.e., costs of keeping eggs at incubation temperature) are scarce. Probably the most precise estimates for average demands of incubation were derived from the difference in oxygen consumption of incubating and non-incubating birds: for 11.6 g zebra finches, *Taenopygia guttata*, this was about 84 mW at 10°C (i.e., 7.3 mW/g or 305 W/h; estimated from equations in Vleck 1981); for 75 g starlings, *Sturnus vulgaris*, about 188 mW at 10°C (2.5 mW/g or 675 W/h; estimated from equations in Biebach 1979). Both estimates are about 20% of the resting metabolic rate. Although similar measurements are absent for semipalmated sandpipers, its energetic demands of incubation can be estimated either from Vleck’s zebra finch and Biebach’s starling equations or as 20% of semipalmated sandpiper’s resting metabolic rate. In either case the estimate is body mass and temperature dependent.

Our estimates (Table S12) are based on the average body mass of semipalmated sandpipers in Barrow, which is about 27 g (associated data in Dryad: Bulla et al. 2013; Bulla et al. 2014), and temperatures of 10°C (as in zebra finch and starling study) and 6.2°C (median tundra temperature in Barrow).

Table S12

Estimated energetic demands of keeping eggs at incubation temperature for a 27 g semipalmated sandpiper.

Temperature [°C]	Cost [mW]	Cost [mW/g]	Assumption	From
10.0	197	7.31	cost for zebra finch	(Vleck 1981)
6.2	215	7.95	cost for zebra finch	(Vleck 1981)
10.0	68	2.50	cost for starling	(Biebach 1979)
6.2	90	3.34	cost for starling	(Biebach 1979)
10.0	261	9.67	resting metabolic rate of 1305 mW*	(Norton 1973)
6.2	284	10.50	resting metabolic rate of 1422 mW*	(Norton 1973)

*Assuming that 1 liter of O₂ = 20.1 kJ

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Unexpected diversity in socially synchronized rhythms of shorebirds

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The behavioural rhythms of organisms are thought to be under strong selection, influenced by the rhythmicity of the environment¹⁻⁴. Behavioural rhythms are well studied in isolated individuals under laboratory conditions^{1,5}, but in free-living populations, individuals have to temporally synchronize their activities with those of others, including potential mates, competitors, prey and predators⁶⁻¹⁰. Individuals can temporally segregate their daily activities (e.g. prey avoiding predators, subordinates avoiding dominants) or synchronize their activities (e.g. group foraging, communal defence, pairs reproducing or caring for offspring)^{6-9,11}. The behavioural rhythms that emerge from such social synchronization and the underlying evolutionary and ecological drivers that shape them remain poorly understood^{5-7,9}. Here, we address this in the context of biparental care, a particularly sensitive phase of social synchronization¹² where pair members potentially compromise their individual rhythms. Using data from 729 nests of 91 populations of 32 biparentally-incubating shorebird species, where parents synchronize to achieve continuous coverage of developing eggs, we report remarkable within- and between-species diversity in incubation rhythms. Between species, the median length of one parent's incubation bout varied from one to 19 hours, while period length – the cycle of female and male probability to incubate – varied from six to 43 hours. The length of incubation bouts was unrelated to variables reflecting energetic demands, but species relying on crypsis had longer incubation bouts than those that are readily visible or actively protect their nest against predators. Rhythms entrainable to the 24-h light-dark cycle were less likely at high latitudes and absent in 18 species. Our results indicate that even under similar environmental conditions and despite 24-h environmental cues, social synchronization can generate far more diverse behavioural rhythms than expected from studies of individuals in captivity^{5-7,9}. The risk of predation, not the risk of starvation, may be a key factor underlying the diversity in these rhythms.

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Unexpected diversity in socially synchronized rhythms of shorebirds

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Incubation by both parents prevails in almost 80% of non-passerine families¹³ and is the most common form of care in shorebirds¹⁴. Biparental shorebirds are typically monogamous¹⁵, mostly lay three or four eggs in an open nest on the ground¹⁵, and cover their eggs almost continuously¹³. Pairs achieve this through synchronization of their activities such that one of them is responsible for the nest at a given time (i.e. an incubation bout). Alternating female and male bouts generate an incubation rhythm with a specific period length (cycle of high and low probability for a parent to incubate).

We used diverse monitoring systems (Methods & Extended Data Table 1) to collect data on incubation rhythms from 91 populations of 32 shorebird species belonging to 10 genera (Fig. 1a), extracted the length of 34,225 incubation bouts from 729 nests, and determined the period length for pairs in 584 nests (see Methods, Extended Data Fig. 1 & 2).

We found vast between- and within- species variation in incubation bout length and in period length (Fig. 1-3 & Extended Data Fig. 3). Different species, but also different pairs of the same species, adopted strikingly different incubation rhythms, even when breeding in the same area (see, e.g. incubation rhythms in Barrow, Alaska, represented by ① in Fig. 1b-c; incubation rhythms for each nest are in Supplementary Actograms¹⁶). Whereas in some pairs parents exchanged incubation duties about 20 times a day (Fig. 2a; e.g. *Charadrius semipalmatus*, Fig. 1b), in others a single parent regularly incubated for 24 hours (Fig. 2a; e.g. *Limnodromus scolopaceus*, Fig. 1b), with exceptional bouts of up to 50 hours (Supplementary Actograms¹⁶). Similarly, whereas incubation rhythms of pairs in 22% of nests followed a strict 24-h period (Fig. 2b; e.g. *Tringa flavipes*, Fig. 1b), the rhythms of others dramatically deviated from a 24-h period (Fig. 2b) resulting in ultradian (<20-h in 12% of nests; e.g. *Numenius phaeopus*; Fig. 1b), free-running like (e.g. *Calidris alpina*; Fig. 1b) and infradian rhythms (>28-h in 8% of nests), some with period lengths up to 48-h (e.g. *Limnodromus scolopaceus*; Fig. 1b). This variation in period length partly related to the variation in bout length (Fig. 3): in the suborder Scolopaci period length correlated positively with median bout length, but in the suborder Charadrii species with 24-h periods had various bout lengths, and species with similar bout lengths had different period lengths.

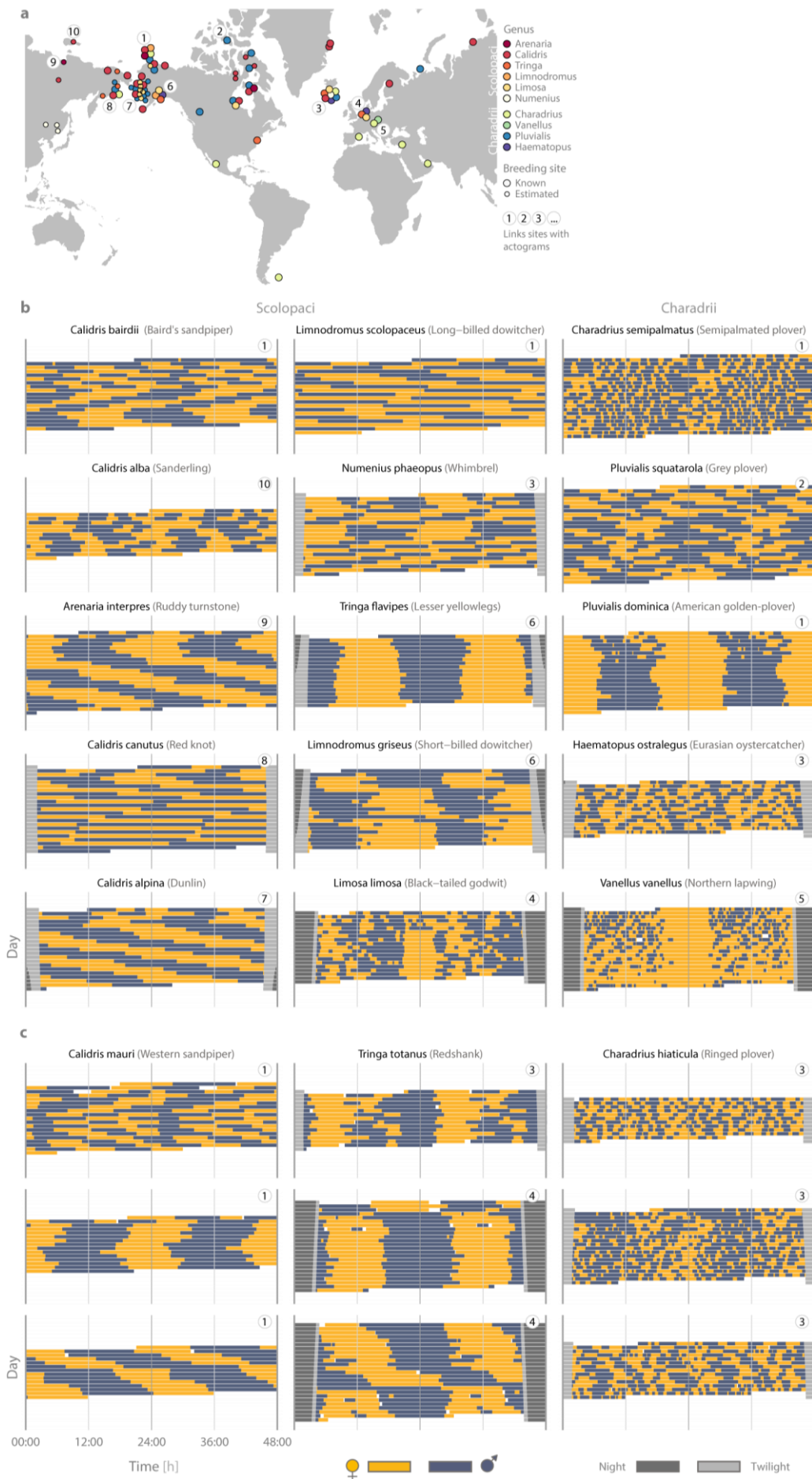


Figure 1 | Map of studied breeding sites and the diversity of shorebird incubation rhythms. **a**, Map of breeding sites with data on incubation rhythms. The colour of the dots indicates the genus (data from multiple species per genus may be available), the size of the dots refers to data quality (○, large: exact breeding site known; ○, small: breeding site estimated, see Methods). For nearby or overlapping locations, the dots are scattered to increase visibility. Contours of the map made with Natural Earth, <http://www.naturalearthdata.com>. **b-c**, Illustrations of between-species diversity (**b**) and within-species diversity (**c**; note that the three rhythms for Western sandpiper and Ringed plover come from the same breeding location.). Each actogram depicts the bouts of female (yellow; ♀) and male (blue-grey; ♂) incubation at a single nest over a 24-h period, plotted twice, such that each row represents two consecutive days. If present, twilight is indicated by light grey bars (▨) and corresponds to the time when the sun is between 6° and 0° below the horizon, night is indicated by dark grey bars (■) and corresponds to the time when the sun is < 6° below the horizon. Twilight and night are omitted in the centre of the actogram (24:00) to make the incubation rhythm visible. **a-c**, The circled numbers (① ② ③ ...) indicate the breeding site of each pair and correspond to the numbers on the map.

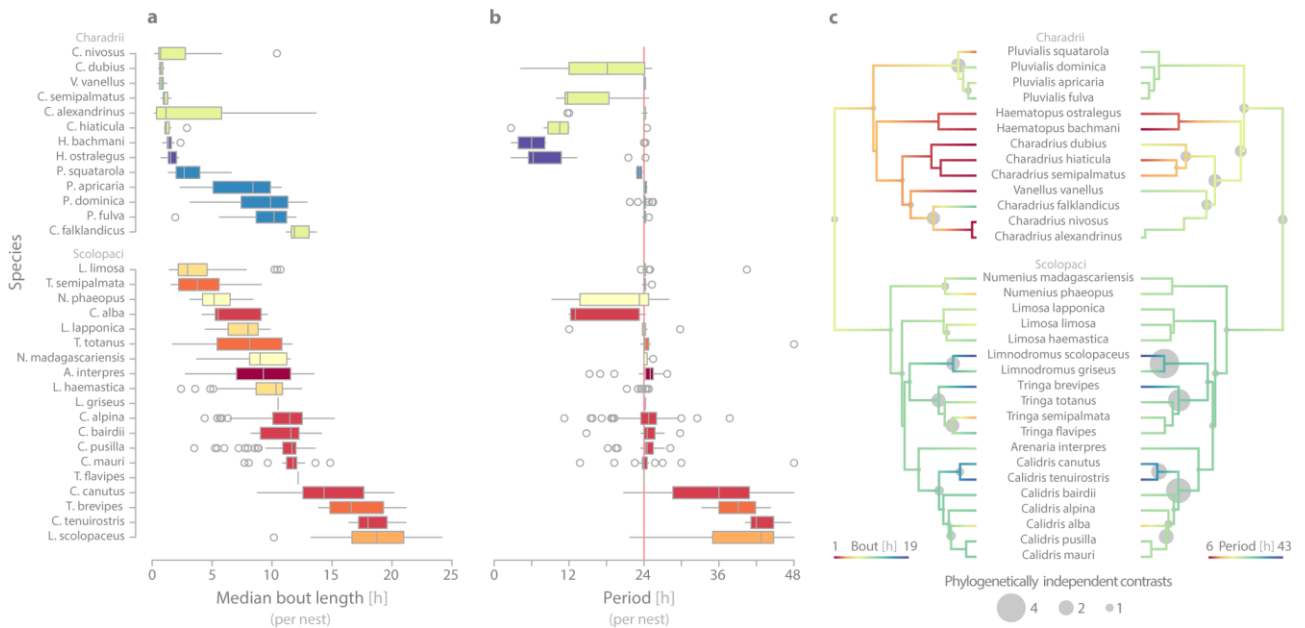


Figure 2 | Between- and within-species variation in incubation rhythms and their estimated evolution. **a-b**, Box plots are ordered by species (within suborder) from the shortest to the longest median bout length, and depict the genus (colour as in Fig. 1a), median (vertical line inside the box), the 25th and 75th percentiles (box), 25th percentiles minus 1.5 times interquartile range and 75th percentile plus 1.5 times interquartile range or minimum/maximum value, whichever is smaller (bars), and the outliers (circles). $N_{\text{median bout length}} = 729$ and $N_{\text{period}} = 584$ nests. **b**, The red vertical line indicates a 24-h period. **c**, Observed and reconstructed incubation bout and period length visualised (by colour) on the phylogenetic tree²⁹ using species' medians (based on population medians) and one of 100 sampled trees (see Methods). The grey circles represent phylogenetically independent contrasts³⁰ and hence emphasize the differences at each tree node.

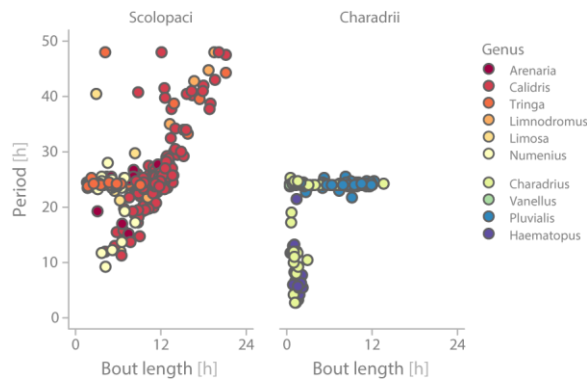


Figure 3 | Relationship between bout and period length. Each dot represents a single nest ($N = 584$ nests), colours depict the genus. In the suborder Scolopaci the median bout length and period length correlate positively ($r_{\text{Spearman}} = 0.56$, $N = 424$ nests); in the suborder Charadrii periods longer than ~ 24 h are absent, and there is no simple relationship between bout and period length ($N = 160$ nests). For species-specific relationships see Extended Data Fig. 3.

Despite substantial within-species variation, we found a strong evolutionary signal for both bout and period length with a coefficient of phylogenetic signal λ close to 1 (Extended Data Table 2). This is consistent with the notion that biological rhythms are largely genetically determined and conserved among related species⁸⁻¹⁰. However, the phylogenetic effect seems unevenly distributed over taxonomic level. Suborder explained 33% of the phenotypic variance in both bout and period length, with the Scolopaci having longer incubation bouts and periods than the Charadrii (Extended Data Table 3; Fig. 2 & 3). Species explained 41% of the phenotypic variation in bout length and 46% in period length, but genus explained little (<1% in both; Extended Data Table 3), suggesting that despite a strong phylogenetic signal, these traits can rapidly diverge (Fig. 2c).

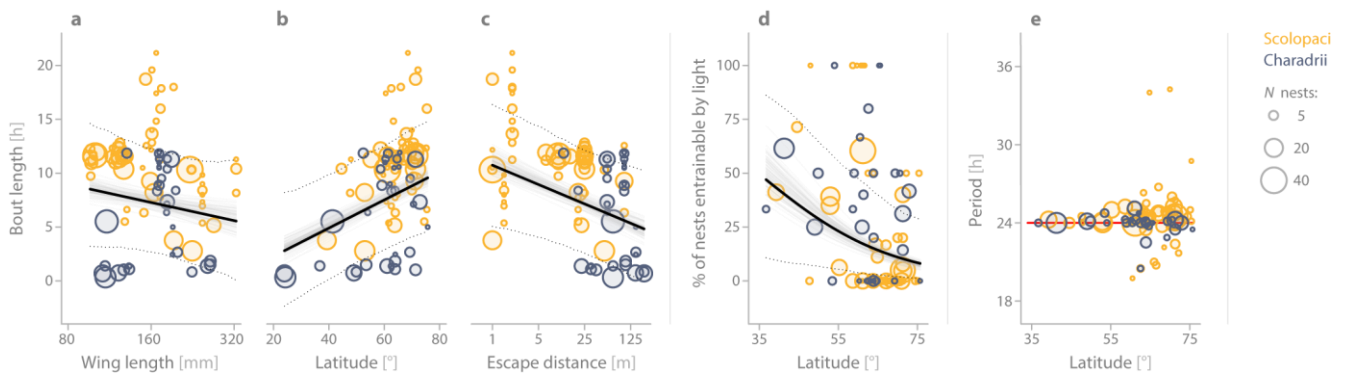


Figure 4 | Predictors of variation in incubation rhythms. **a-c**, Relationships between bout length and body size, measured as female wing length (**a**), breeding latitude (**b**) and anti-predation strategy, quantified as escape distance (**c**) for $N = 729$ nest from 91 populations belonging to 32 species. **d**, The relationship between the proportion of nests with a period length that is entrainable by the 24-h light-dark cycle (i.e. period lengths: 3, 6, 12, 24, or 48h) and breeding latitude ($N = 584$ nests from 88 populations belonging to 30 species). **e**, The distribution of period length over latitude. The period was standardized to 24h so that all 24-h harmonics are depicted as 24h (red line) and respective deviations from each harmonic as deviations from 24h (e.g. period of 12.5h is depicted as 25h). **a-e**, Each circle represents the population median; circle size indicates the number of nests. **a-c**, The solid lines depict the model-predicted relationships, the dotted lines the 95% credible intervals based on the joint posterior distribution of 100 separate MCMCglmm runs each with one of the 100 phylogenetic trees with $\sim 1,100$ independent samples per tree. The grey areas depict the predicted relationships for each of 100 runs (i.e. the full range of regression line estimates across 100 models) and illustrate the uncertainty due to the phylogenetic tree. The predicted relationships stem from a Gaussian phylogenetic mixed-effect models, where the effects of other predictors were kept constant (**a-c**, Extended Data Table 4), or from a binomial phylogenetic mixed-effect model (**d**, Extended Data Table 4).

Two ecological factors may explain the observed variation in bout length. First, the ‘energetic demands hypothesis’ stipulates that the length of an incubation bout depends on a bird’s energetic state^{13,17}. This predicts that (1) large species will have longer incubation bouts than smaller species, because they radiate less body heat per unit of mass and (2) incubation bouts will shorten with increasing breeding latitude, because – everything else being equal – energy stores will deplete faster in colder environments (Extended Data Fig. 4a-b shows latitudinal cline in summer temperatures). However, bout length was unrelated to body size (Fig. 4a) and correlated positively (instead of negatively) with latitude (Fig. 4b). These correlational results across populations and species support recent experimental findings within species¹⁸ and suggest that in biparentally-incubating shorebirds energetic demands are not an important ecological driver underlying variation in bout length.

An alternative explanation for variation in the length of incubation bouts relates to anti-predation strategies. Those species that rely primarily on parental crypsis (Extended Data Fig. 5a) benefit from reduced activity near the nest, because such activity can reveal the nest’s location to potential predators^{19,20}. Thus, in these species, selection will favour fewer change-overs at the nest, and hence longer incubation bouts. In contrast, species that are clearly visible when sitting on the nest or that rely on active anti-predation behaviour (Extended Data Fig. 5b), including having a partner on the watch for predators, leaving the nest long before the predator is nearby and mobbing the predator¹⁵, obtain no advantage from minimizing activity. For these species, bout length can shorten, which may be advantageous for other reasons (e.g. reduced need to store fat). We quantified anti-predation strategy as the distance at which the incubating parent left the nest when approached by a human (escape distance), because cryptic species stay on the nest longer (often until nearly stepped upon)¹⁵. Despite the large geographical distribution of the studied species, with related variability in the suite of predators and predation pressure²¹, and even when controlling for phylogeny (which captures much of the variation in anti-predation strategy, Extended data Fig. 6), escape distance negatively correlated with the length of incubation bouts (Fig. 4c). This result suggests that bout length co-evolved with the anti-predation strategy.

Under natural conditions, most organisms exhibit 24-h rhythmicity, but during summer, when most shorebirds breed, the 24-h variation in light decreases with latitude leading to continuous polar daylight²² (Extended Data Fig. 5c-d). Such reduced variation in 24-h light intensity may cause a loss of 24-h rhythmicity²³⁻²⁵. As a consequence, circadian behavioural rhythms should exhibit a latitudinal cline²². As predicted, incubation rhythms with periods that do not follow the 24-h light-dark cycle, such as ‘free running-like patterns’ (left column in Fig. 1b), occurred more often in shorebirds breeding at higher latitudes (Fig. 4d). The absolute deviations of periods from 24-h and 24-h harmonics also increased with latitude (Fig. 4e; Extended Data Table 4). Although this supports the existence of a latitudinal cline in socially emerged behavioural rhythms²², we found a substantial number of rhythms that defy the 24-h day even at low and mid latitudes (Fig 4d-e).

Many shorebirds predominantly use tidal habitats, at least away from their breeding ground¹⁵. To anticipate tidal foraging opportunities, these species may have activity patterns with a period length resembling the tidal period. As changing to a different rhythm is costly²⁶, these tidal activity patterns might carry over to incubation. Although half of our species are tidal away from their breeding grounds, and some forage in tidal areas also during breeding (~12% of populations), in only 5% of nests did pairs display a period length that can be entrained by the tide. Moreover, tidal species had similar (not longer) periods than non-tidal ones (Extended Data Table 4). Hence, unlike the 24-h light-dark cycle, tidal life-history seems to play at best a negligible role in determining incubation rhythms.

Three main questions arise from our results. First, is variation in incubation bout length in cryptic species related to the actual predation pressure? This can be tested by comparing bout length between populations of a particular species that are exposed to different predator densities, or between years that differ in predation pressure. Second, it remains unclear how the diverse social rhythms emerge. Are these rhythms a consequence of behavioural flexibility, or a ‘fixed’ outcome of synchronization between the circadian clocks of the two individuals involved? An experimental study on ring doves (*Streptopelia risoria*) suggests that parents may even use two timers - circadian oscillation and interval timing - to determine when to incubate²⁷. Parents rapidly adjusted their schedules to phase-shifted photoperiods and their incubation rhythm ‘free-ran’ in constant dim illumination (implying a circadian mechanism), whereas an experimental delay in the onset of an incubation bout did not change the length of the bout because the incubating parent refused to leave the nest until its incubation bout reached the ‘typical’ duration (implying interval timing). Third, what – if any – are the fitness consequences for the parents of having a certain incubation rhythm? For example, the costs of having a particular incubation rhythm may be unevenly distributed between the two parents (e.g. because one parent is on incubation duty when food is more readily available, or because one parent ‘enforces’ its own rhythm at a cost to the other parent).

In conclusion, our results reveal that under natural conditions social synchronization can generate much more diverse rhythms than expected from previous work^{5-7,9,28}, and that these rhythms often defy the assumptions of entrainment to the 24-h day-night cycle. Not risk of starvation, but risk of predation seems to play a key role in determining some of the variation in incubation rhythms. We describe this diversity in the context of biparental incubation, but diverse behavioural rhythms may also arise in many other social settings (e.g. in the context of mating interactions²⁵, vigilance behaviour during group foraging). Essentially, the reported diversity suggests that the expectation that individuals within a pair (or group) should optimize their behavioural rhythms relative to the 24-h day may be too simplistic, opening up a wide field to study the evolutionary ecology of plasticity in circadian clocks.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is freely available at open science framework <https://osf.io/wxufm/>¹⁶

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Author Contributions M.B. and B.K. conceived the study. All authors except B.H. collected the primary data. MB coordinated the study and managed the data. MB and M.V. developed the methods to extract incubation. M.B. extracted bout lengths and with help from A.R. and M.V. created actograms. M.B. with help from M.V. analysed the data. M.B. prepared the Supporting Information. M.B. and B.K. wrote the paper with input from the other authors. Except for the first, second, and last author, the authors are listed alphabetically by their first name.

Author Information All information, primary and extracted data, computer code and software necessary to replicate our results, as well as the Supplementary Actograms are open access and archived at Open Science Framework <https://osf.io/wxufm/>¹⁶. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to M.B. (bulla.mar@gmail.com) and B.K. (b.kempenaers@orn.mpg.de).

METHODS (on-line only)

Recording incubation. Incubation data were obtained between 1994 and 2015, for as many shorebird species ($N = 32$) and populations ($N = 91$) as possible, using six methods (for specifications of the equipment see Extended Data Table 1). (1) In 261 nests, a radio frequency identification reader ('RFID') registered presence of tagged parents at the nest. The passive-integrated tag was either embedded in a plastic flag^{31,32}, with which the parents were banded, or glued to the tail feathers³³. In 200 nests the RFID was combined with a temperature probe placed between the eggs. The temperature recordings allowed us to identify whether a bird was incubating even in the absence of RFID readings; an abrupt change in temperature demarcated the start or end of incubation³¹. (2) For 396 nests, light loggers were mounted to the plastic flag or a band that was attached to the bird's leg^{34,35}. The logger recorded maximum light intensity (absolute or relative) for a fixed sampling interval (2-10 min). An abrupt change in light intensity (as opposed to a gradual change caused, e.g. by civil twilight) followed by a period of low or high light intensity demarcated the start or end of the incubation period (Extended Data Fig. 2). (3) For nine nests a GPS tag, mounted on the back of the bird, recorded the position of the bird³⁶. The precision of the position depends on cloud cover and sampling interval³⁶. Hence, to account for the imprecision in GPS positions, we assumed incubation whenever the bird was within 25 m of the nest (Extended Data Fig. 2b). (4) At three nests automated receivers recorded signal strength of a radio-tag attached to the rump of a bird; whenever a bird incubated, the strength of the signal remained constant²⁴ (Supplementary Actograms p. 257-9¹⁶). (5) At 53 nests video cameras and (6) for 8 nests continuous observations were used to identify the incubating parents; parent identification was based on plumage, colour rings or radio-tag. In one of the populations, three different methods were used, in seven populations representing seven species two methods. In one nest, two methods were used simultaneously (Extended Data Fig. 2b).

Extraction of incubation bouts. An incubation bout was defined as the total time allocated to a single parent (i.e. the time between the arrival of a parent at and its departure from the nest followed by incubation of its partner). Bout lengths were only extracted if at least 24h of continuous recording was available for a nest; in such cases, all bout lengths were extracted. For each nest, we transformed the incubation records to local time as $(\text{UTC time} + \frac{\text{nest's longitude}}{15})$. Incubation bouts from RFIDs, videos and continuous observations were mostly extracted by an R-script and the results verified by visualizing the extracted and the raw data^{16,31,37,38}; otherwise, MB extracted the bouts manually from plots of raw data^{39,40} (plots of raw data and extracted bouts for all nests are in the Supplementary Actograms¹⁶; the actograms were generated by 'ggplot' and 'xyplot' functions from the 'ggplot2' and 'lattice' R package⁴¹⁻⁴³). Whenever the start or end of a bout was unclear, we classified these bouts as uncertain (see next paragraph for treatment of unsure bouts). In case of light logger data, the light recordings before and after the breeding period, when the birds were definitely not incubating, helped to distinguish incubation from non-incubation. Whenever an individual tagged with a light logger nested in an environment where the sun was more than 6° below the horizon for part of a day (i.e. night), we assumed an incubation bout when the individual started incubating before the night started and ended incubating after the night ended. When different individuals incubated at the beginning vs. at the end of the night, we either did not quantify these bouts or we indicated the possible time of exchange (based on trend in previous exchanges), but classified these bouts as uncertain (see Supplementary Actograms¹⁶). In total, we extracted 34,225 incubation bouts.

The proportion of uncertain bouts within nests had a distribution skewed towards zero (median = 0%, range: 0-100%, $N = 729$ nests), and so did the median proportion of uncertain bouts within populations (median = 2%, range: 0-74%, $N = 91$ populations). Excluding the uncertain bouts did not change our estimates of median bout length (Pearson's correlation coefficient for median bout length based on all bouts and without uncertain

bouts: $r = 0.96$, $N = 335$ nests with both certain and uncertain bouts). Hence, in further analyses all bouts were used to estimate median bout length.

Note that in some species sexes consistently differ in bout length (Figure 1b, e.g. Northern lapwing). As these differences are small compared to the between-species differences and because in 27 nests (of 8 species) the sex of the parents was unknown, we here use median bout length independent of sex.

Extraction of period length. The method used for extracting the period length of incubation rhythm for each nest is described in the Extended Data Fig. 1.

Extraction of entrainable periods. We classified 24-h periods and periods with 24-h harmonics (i.e. 3, 6, 12, 48h) as strictly entrainable by 24-h light fluctuations ($N = 142$ nests out of 584). Including also nearest adjacent periods (± 0.25 h) increased the number of nests with entrainable periods ($N = 277$), but results of statistical analyses remained quantitatively similar. We consider periods and harmonics of 12.42h (i.e. 3.1, 6.21, 12.42, 24.84h) as strictly entrainable by tide. However, because the periods in our data were extracted in 0.25-h intervals (Extended Data Fig. 1), we classified periods of 3, 6.25, 12.5, 24.75h (i.e. those closest to the strict tide harmonics) as entrainable by tide ($N = 32$ nests out of 584). Including also the second nearest periods (i.e. 3.25, 6, 12.25, 25) increased the number of nests entrainable by tide to $N = 55$.

Population or species life-history traits. For 643 nests, the exact breeding location was known (nests or individuals were monitored at the breeding ground). For the remaining 86 nests (from 27 populations representing 8 species, where individuals were tagged with light loggers on the wintering ground), the breeding location was roughly estimated from the recorded 24-h variation in daylight, estimated migration tracks, and the species' known breeding range⁴⁴⁻⁵¹. One exact breeding location was in the Southern Hemisphere, so we used absolute latitude in analyses. Analyses without populations with estimated breeding location or without the Southern Hemisphere population generated quantitatively similar estimates as the analyses on full data.

For each population, body size was defined as mean female wing length⁵², either for individuals measured at the breeding area or at the wintering area. In case no individuals were measured, we used the mean value from the literature (see open access data for specific values and references⁵³).

Anti-predation strategy was assessed by estimating escape distance of the incubating bird when a human approached the nest, because species that are cryptic typically stay on the nest much longer than non-cryptic species, sometimes until nearly stepped upon^{48,54}. Escape distance was obtained for all species. Forty-four authors of this paper estimated the distance (in m) for one or more species based on their own data or experience. For 10 species, we also obtained estimates from the literature⁴⁸. We then used the median 'estimated escape distance' for each species. In addition, for 13 species we obtained 'true escape distance'. Here, the researcher approached a nest (of known position) and either estimated his distance to the nest or marked his position with GPS when the incubating individual left the nest. For each GPS position, we calculated the Euclidian distance from the nest. In this way we obtained multiple observations per nest and species, and we used the median value per species (weighted by the number of estimates per nest) as the 'true escape distance'. The species' median 'estimated escape distance' was a good predictor of the 'true escape distance' (Pearson's correlation coefficient: $r = 0.89$, $N = 13$ species). For analysis, we defined the escape distance of a species as the median of all available estimates.

For each species, we determined whether it predominantly uses a tidal environment outside its breeding ground, i.e. has tidal vs. non-tidal life history (based on^{48,50,51}). For each population with exact breeding location, we scored whether tidal foraging habitats were used by breeding birds for foraging (for three

populations this information was unknown)⁵³. For all populations with estimated breeding location we assumed, based on the estimated location and known behaviour at the breeding grounds, no use of tidal habitat.

Statistical analyses. Unless specified otherwise, all analyses were performed on the nest level using median bout length and extracted period length.

We used phylogenetically informed comparative analyses to assess how evolutionary history constrains the incubation rhythms (estimated by Pagel's λ coefficient of phylogenetic signal^{55,56}) and to control for potential non-independence among species due to common ancestry. This method explicitly models how the covariance between species declines as they become more distantly related^{55,57,58}. We used the Hackett⁵⁹ backbone phylogenetic trees available at <http://birdtree.org>⁶⁰, which included all but one species (*Charadrius nivosus*) from our dataset. Following a subsequent taxonomic split⁶¹, we added *Charadrius nivosus* to these trees as a sister taxon of *Charadrius alexandrinus*. Phylogenetic uncertainty was accounted for by fitting each model with 100 phylogenetic trees randomly sampled from 10,000 phylogenies at <http://birdtree.org>⁶⁰.

The analyses were performed with Bayesian phylogenetic mixed-effect models (Fig. 4 and Extended Data Table 2 and 4) and the models were run with the 'MCMCglmm' function from the R package 'MCMCglmm'⁶². In all models, we also accounted for multiple sampling within species and breeding site (included as random effects). In models with a Gaussian response variable, an inverse-gamma prior with shape and scale equal to 0.001 was used for the residual variance (i.e. variance set to one and the degree of belief parameter to 0.002). In models with binary response variables, the residual variance was fixed to one. For all other variance components the parameter-expanded priors were used to give scaled F-distributions with numerator and denominator degrees of freedom set to one and a scale parameter of 1,000. Model outcomes were insensitive to prior parameterization. The MCMC chains ran for 2,753,000 iterations with a burn-in of 3,000 and a thinning interval of 2,500. Each model generated ~1,100 independent samples of model parameters (Extended Data Table 2 and 4). Independence of samples in the Markov chain was assessed by tests for autocorrelation between samples and by using graphic diagnostics.

First, we used MCMCglmm to estimate Pagel's λ (phylogenetic signal) for bout and period length (Gaussian), and to show that our estimates of these two incubation variables were independent of how often the incubation behaviour was sampled ('sampling' in min, ln-transformed; Extended Data Table 2). Hence, in subsequent models, sampling was not included.

Then, we used MCMCglmm to model variation in bout length and period length. Bout length was modelled as a continuous response variable and latitude ($^{\circ}$, absolute), female wing length (mm, ln-transformed) and approach distance (m, ln-transformed) as continuous predictors. Predictors had low collinearity (at nest, population and species level; all Pearson or Spearman correlation coefficients $|r| < 0.28$). To test for potential entrainment to 24-h, period length was modelled as a binary response variable (1 = rhythms with period of 3, 6, 12, 24, or 48 h; 0 = rhythms with other periods) and latitude as a continuous predictor. To test how circadian period varies with latitude or life history, period was transformed to deviations from 24-h and 24-h harmonics and scaled by the time span between the closest harmonic and the closest midpoint between two harmonics. For example, a 42h period deviates by -6h from 48h (the closest 24-h harmonic) and hence -6h was divided by 12h (the time between 36h – the midpoint of two harmonics - and 48h -the closest harmonic). This way the deviations spanned from -1 to 1 with 0 representing 24-h and its harmonics. The absolute deviations were then modelled as a continuous response variable and latitude as continuous predictor. The deviations were also modelled as a continuous response and species life history (tidal or not) as categorical predictor.

In all models the continuous predictor variables were centred and standardized to a mean of zero and a standard deviation of one.

We report model estimates for fixed and random effects, as well as for Pagel's λ , by the modes and the uncertainty of the estimates by the highest posterior density intervals (referred to as 95% CI) from the joint posterior distributions of all samples from the 100 separate runs, each with one of the 100 separate phylogenetic trees from <http://birdtree.org>.

To help interpret the investigated relationships we assessed whether incubation rhythms evolved within diverged groups of species by plotting the evolutionary tree of the incubation rhythm variables (Fig. 2c), as well as of the predictors (Extended Data Fig. 6).

The source of phylogenetic constraint in bout and period length was investigated by estimating the proportion of phenotypic variance explained by suborder, genus and species (Extended Data Table 3). The respective mixed models were also specified with 'MCMCglmm'⁶² using the same specifications as in the phylogenetic models. Because suborder contained only two levels, we first fitted an intercept mixed model with genus, species, and breeding site as random factors, and used it to estimate the overall phenotypic variance. We then entered suborder as a fixed factor and estimated the variance explained by suborder as the difference between the total variance from the first and the second model. To evaluate the proportion of the variance explained by species, genus and breeding site, we used the estimates from the model that included suborder.

R version 3.1.1⁶³ was used for all statistical analyses.

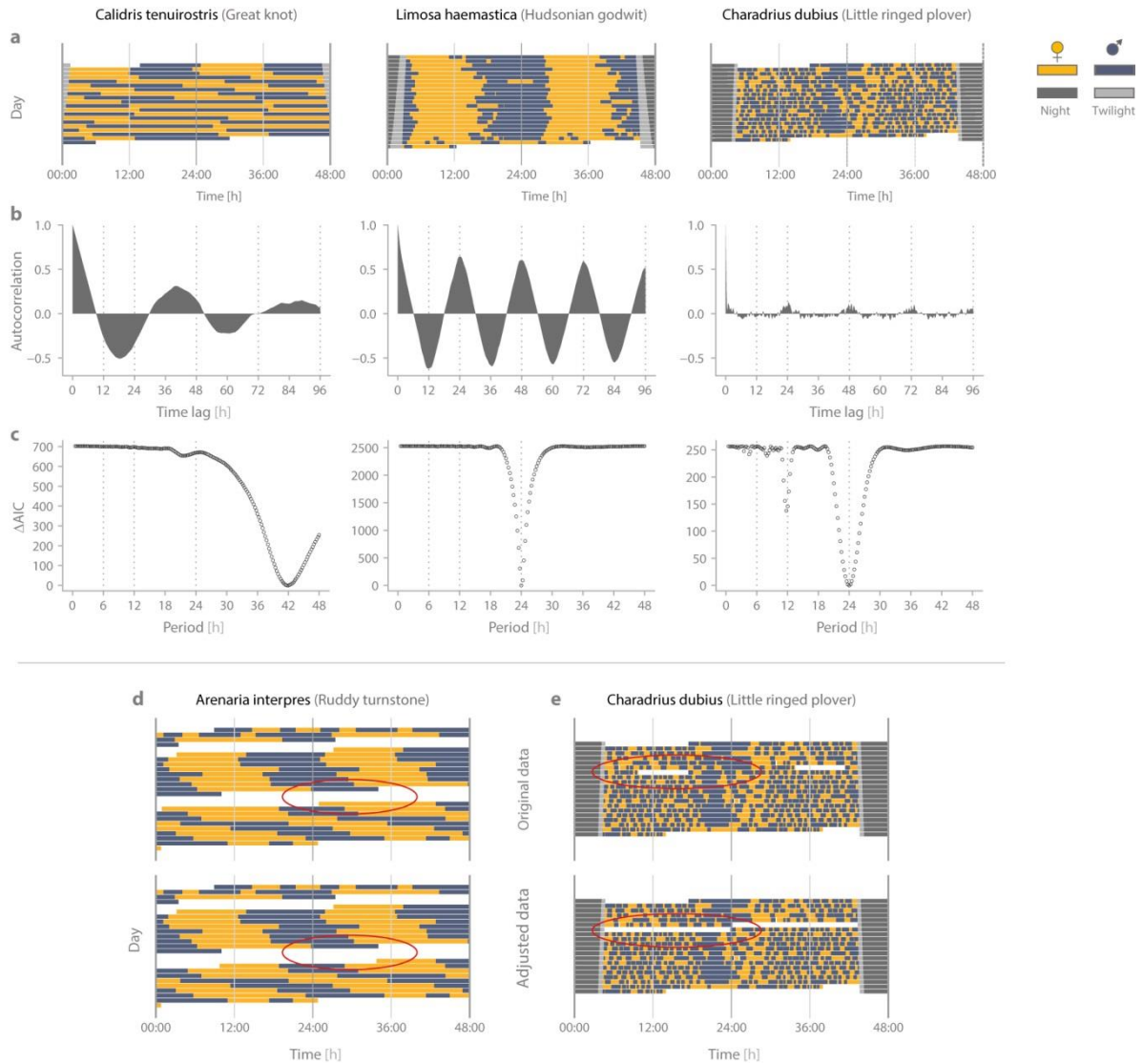
Code availability. All statistical analyses are replicable with the open access data and r-code available from <https://osf.io/wxufm/>¹⁶.

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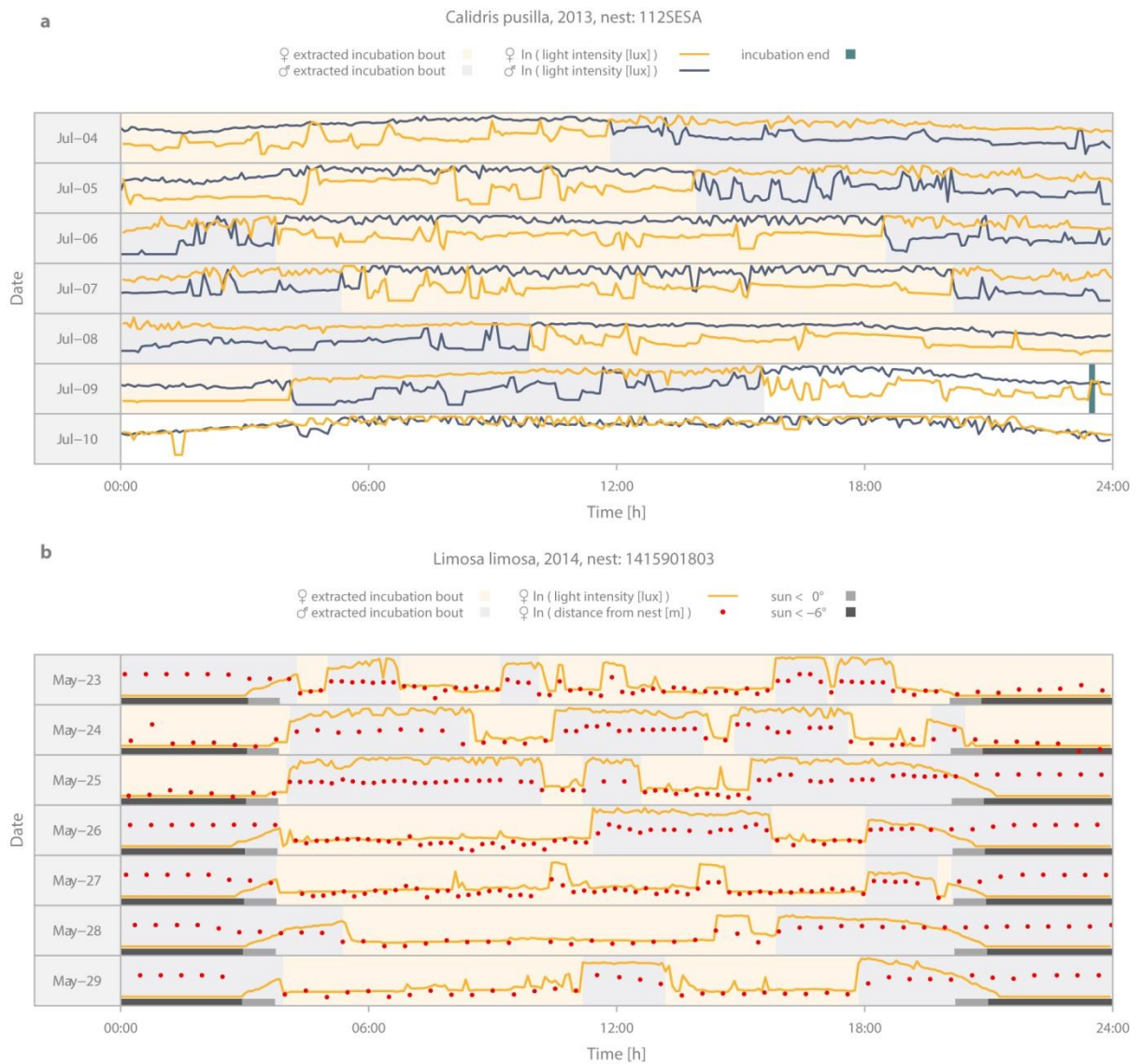
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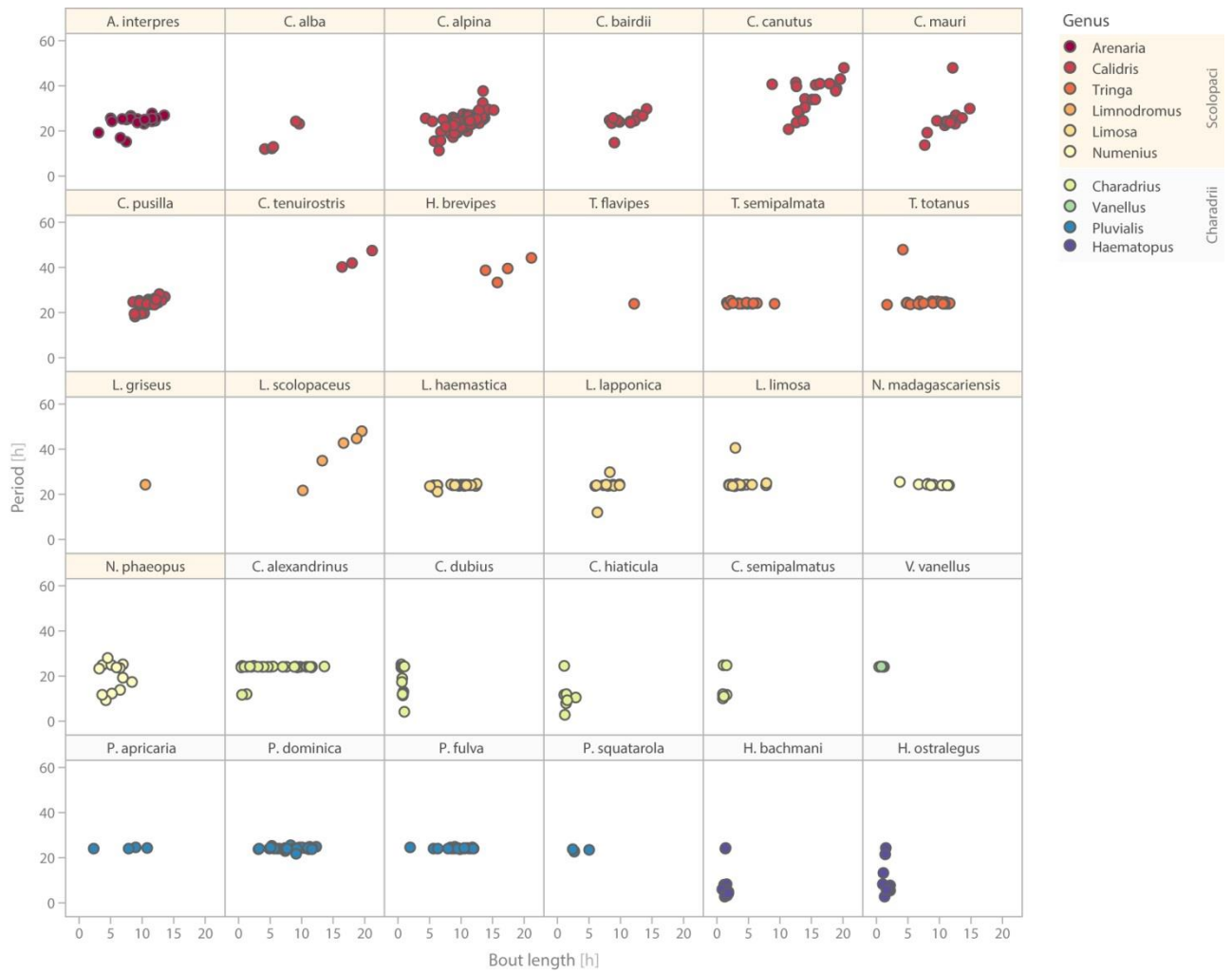
EXTENDED DATA



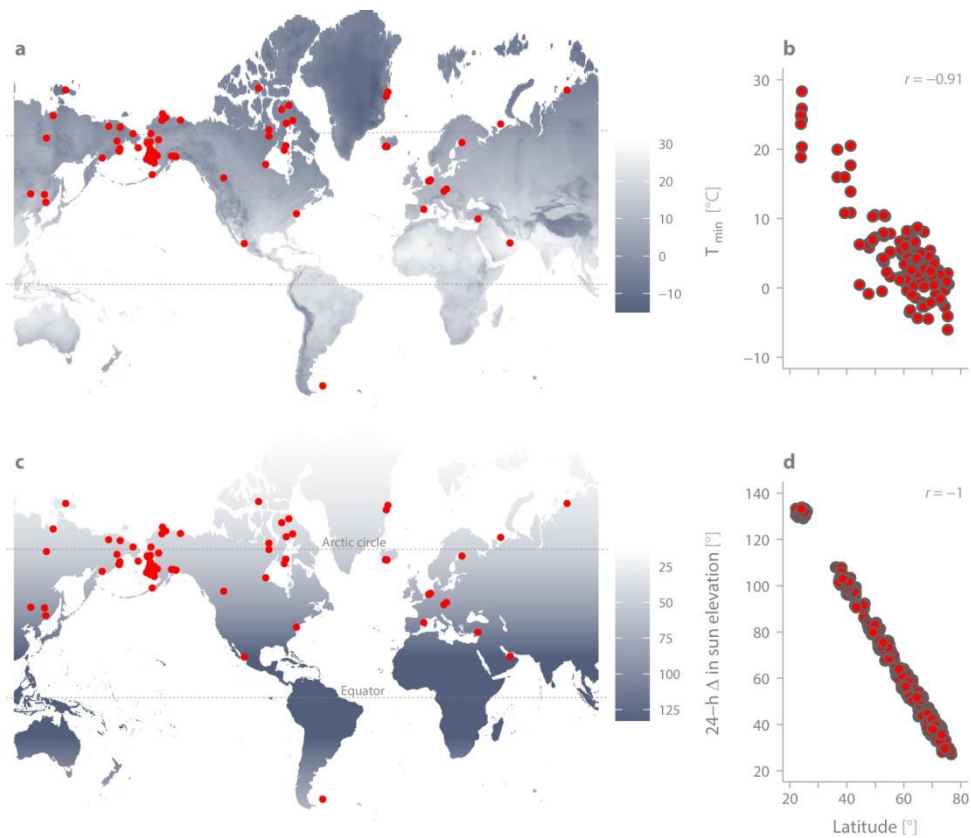
Extended Data Figure 1 | Extracting period length of incubation rhythms. **a-c**, Each column represents an example for a specific nest with long, intermediate and short incubation bouts. **a**, From the extracted bout lengths we created a time series that indicated for each nest, and every 10 min, whether a specific parent (female, if sex was known) incubated or not. Exchange gaps (no parent on the nest) had to be < 6 h to be included (for treatment of exchange gaps > 6 h see **d, e**). **b**, We then estimated the autocorrelation for each 10 min time-lag up to 4 days (R ‘acf’ function⁶³). Positive values indicate a high probability that the female was incubating, negative values indicate that it was more likely that the male was incubating. We used only nests that had enough data to estimate the autocorrelation pattern ($N = 584$ nests from 88 populations of 30 species). The visualized autocorrelation time series never resembled white or random noise indicative of an arrhythmic incubation pattern. To determine the period (i.e. cycle of high and low probability for a parent to incubate) that dominated the incubation rhythm, we fitted to the autocorrelation estimates a series of periodic logistic regressions. In each regression, the time lag (in hours) transformed to radians was represented by a sine and cosine function $f(t) = a_0 + b \cdot \left(\cos \frac{2 \cdot \pi \cdot t}{T}\right) + c \cdot \left(\sin \frac{2 \cdot \pi \cdot t}{T}\right) + e$, where $f(t)$ is the autocorrelation at time-lag t , a_0 is the intercept, b is the slope for sine and c the slope for cosine, T represents the length of the fitted period (in hours), and e is an error term. We allowed the period length to vary from 0.5 h to 48 h (in 15 min intervals, giving 191 regressions). **c**, By comparing the Akaike’s Information Criterion⁶⁴ (AIC) of all regressions, we estimated, for each nest, the length of the dominant period in the actual incubation data (best fit). Regressions with ΔAIC ($AIC_{\text{model}} - AIC_{\text{min}}$) close to 0 are considered as having strong empirical support, while models with ΔAIC values ranging from 4-7 have less support⁶⁴. In 73% of all nests, we determined a single best model with $\Delta AIC \leq 3$ (**c**, middle ΔAIC graph), in 20% of nests two best models emerged and in 6% of nests 3 or 4 models had $\Delta AIC \leq 3$ (**c**, left and right ΔAIC graphs). However, in all but three nests, the models with the second, third, etc. best ΔAIC were those with period lengths closest to the period length of the best model (**c**, left and right ΔAIC graphs). This suggests that multiple periodicities are uncommon. **d-e**, The extraction of the period length (described in **a-c**) requires continuous datasets, but some nests had long (> 6 h) gaps between two consecutive incubation bouts, for example because of equipment failure or because of unusual parental behaviour. In such cases, we excluded the data from the end of the last bout until the same time the following day, if data were then available again (**d**), or we excluded the entire day (**e**).



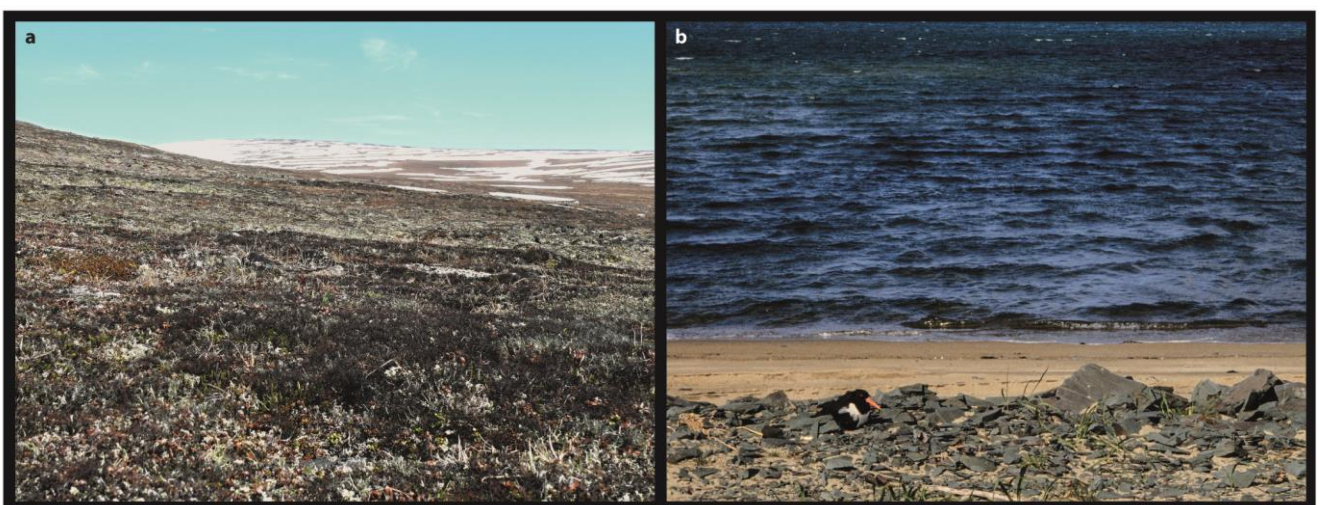
Extended Data Figure 2 | Extracting incubation bouts from light logger data. **a**, An example of a nest with a light intensity signal from both parents (yellow line — and blue-grey line —). The incubation bouts for a given parent reflect periods dominated by lower light values compared to those of the partner. Note the sharp drop in the light levels at the beginning of each incubation bout and the sharp increase in the light levels at the end. Change-overs between partners occur when the light signal lines cross. Such pronounced changes in light intensity detected by the logger were used to assign incubation even when only a single parent was tagged. Note that after the chicks hatch and leave the nest (July 9, vertical bar), the light intensity signal from both parents remains similar. **b**, An example of a nest where one incubating parent was simultaneously equipped with a light logger and with a GPS tag. The yellow line (—) indicates light levels, red dots (•) indicate the distance of the bird to the nest. As expected, low light levels co-occur with close proximity to the nest, and hence reflect periods of incubation. Although light levels decrease during twilight (light grey horizontal bar; ■), the recordings were still sensitive enough to reflect periods of incubation, i.e. the light signal matches the distance (e.g. May-25: female incubated during dawn, but was off the nest during dusk). **a-b**, Rectangles in the background indicate extracted female (light yellow polygon, ■) and male (light blue-grey polygon, ■) incubation bouts.



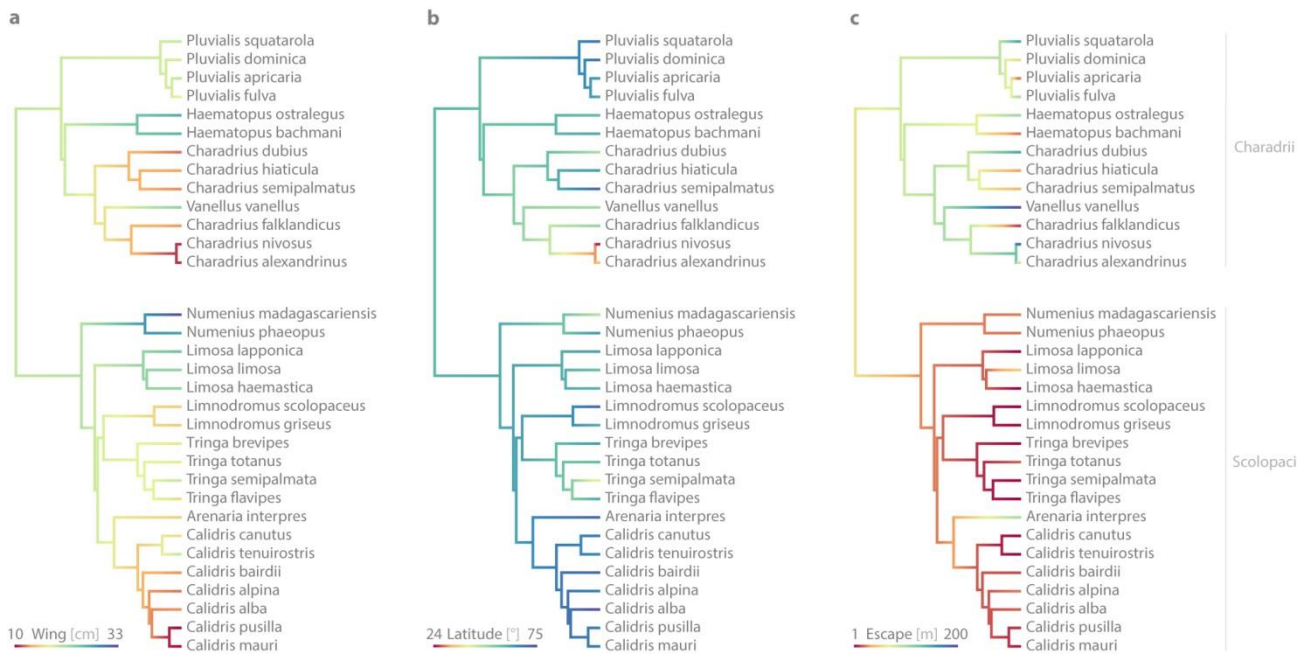
Extended Data Figure 3 | Relationship between bout and period length for 30 shorebird species. Each dot represents one nest ($N = 584$ nests), colours indicate the genus.



Extended Data Figure 4 | Ecological correlates of latitude. **a**, Variation in minimum temperature across the globe represented by mean minimum June temperature for the Northern Hemisphere and mean minimum December temperature for the Southern Hemisphere. **b**, Correlation between absolute latitude and the mean minimum temperature based on the month represented by mid-day of incubation data for each nest ($N = 729$). For maximum temperature the correlation was similar ($r = -0.91$, $N = 729$ nests). **c**, Daily variation in sun elevation (i.e. in light conditions) represented as the difference between the noon and midnight sun-elevation for the summer solstice in the Northern Hemisphere and the winter solstice in the Southern Hemisphere. **d**, Correlation between absolute latitude and daily variation in sun elevation for mid-day of incubation data for each nest ($N = 729$ nests). The points are jittered, as else they form a straight line. **a, c**, Red points indicate the breeding sites ($N = 91$). **a-b**, The minimum and maximum monthly temperature data were obtained from www.worldclim.org using the 'raster' R-package⁶⁵. **c-d**, Sun-elevation was obtained by the 'solarpos' function from the 'mapproj' R-package⁶⁶.



Extended Data Figure 5 | Between-species variation in parental crypsis during incubation. **a-b**, Shorebirds vary in how visible they are on the nest while incubating. The nearly invisible Great knot (*Calidris tenuirostris*; **a**; central and facing right) sits tight on the nest when approached by a human until nearly stepped upon. In contrast, the conspicuous Eurasian oystercatcher (*Haematopus ostralegus*; **b**) is visible on the nest from afar and when approached by a human leaves the nest about 100 m in advance (Credits: **a**, M. Šálek; **b**, Jan van de Kam).



Extended Data Figure 6 | Phylogenetic relationships for predictors. **a**, Body size, estimated as female wing length. **b**, Latitude (absolute), **c**, Escape distance. **a-c**, We visualised the evolution of these traits^{29,67} using species' medians (**a-b**; based on population medians), species' estimates of escape distance (**c**) and one of the 100 sampled trees (see Methods).

Extended Data Table 1 | Incubation monitoring methods and systems.

Method	Model	Company	www	Year	Sampling interval (min)	N populations	N nests	N both parents tagged
RFID + tag embedded in the flag ^{31,32}	tag: 9.0 × 2.1 mm, 0.087 g, 134.2 kHz	Biomark	http://www.biomark.com/	2011-2014	0.08	19	200	157
	RFID: custom made	Calima Engineering, & Max Planck Institute for Ornithology	http://www.calima.de http://www.orn.mpg.de/en					
	temperature probe: TinyTag Talk PB-5005-0M6 (ø 2.5 mm) with Talk 2 logger TK-4023 or MSR® (12 × 6 mm) with MSR® 145 logger	Gemini Data Loggers Ltd	www.tinytag.info				197	
	tag: 11.5 × 2.12 mm, 0.1 g, 125 kHz	Trovan®	http://www.trovan.com	2007	5	1	3	3
RFID + tag glued to the tail ³³	RFID: custom made	EID Aalten BV	http://www.dorset.nu/en/					
	temperature probe: TinyTag Talk PB-5005-0M6 (ø 2.5 mm) with Talk 2 logger TK-4023	Gemini Data Loggers Ltd	www.tinytag.info					
	tag: 11.5 × 2.12 mm, 0.09g, 128 kHz	Trovan®	http://www.trovan.com	2005-2008	1.7-5.5	1	34	34
	RFID: UID650 with extended memory, driver TM613, Antenna ANT614							
Light logger ^{34,35,69}	tag: TIRIS 12 × 6 × 3 mm, 0.4 g, 134.2 kHz	Texas Instruments	http://www.ti.com	1997	1/3	1	6	6
	RFID: TIRIS Micro-reader							
	TIRIS tag: 12 × 6 × 3 mm, 0.4 g, 134.2 kHz	Texas Instruments	http://www.ti.com	2006	1/3	1	18	18
	RFID: custom made	Francis Scientific Instruments Limited	https://www.duedil.com/company/01964877/francis-scientific-instruments-limited					
GPS-tracker ³⁶	MK10, 12, 14 18, 20: 0.7-1.4g, light scale 0-64 (64 ≥ 100 lux)	British Antarctic Survey, currently Biotrack	http://www.biomark.com/	2008-2013	2-10	48	261*	55
	Intigeo W65A9RK: 0.7g, absolute light levels (lux)	Migrate Technology Ltd	http://www.migratetech.co.uk	2012-2014	5-10	23	136*	11
Radio-transmitter ²⁵	UvA-BiTS 4C: 62 × 30 × 12, 14 g	University of Amsterdam	http://www.uva-bits.nl/	2010	10-30	1	8	8
	UvA-BITS 2CDse: 52 × 22 × 9, 7.5 g			2014	20	1	1**	0
Video ⁷⁰⁻⁷³	iTag: 26 × 15 × 9 mm, 4 g	e-obs GmbH	http://www.e-obs.de/	2009	0.07	2	3	3
				2005-2006	1/3	1	28	-
Observations				2005-2011	constant	3	25	-
				1994	30	1	5	-
				2011	constant	1	3	-

For details about methods used in each populations, see Supplementary Data⁵³.

*At one nest a bird with MK logger was recaptured and the logger exchanged for Intigeo logger. This nest appears in *N* for both logger types.

**Simultaneously equipped with light logger (Intigeo). This nest appears in *N* for both GPS-tracer and Intigeo.

Extended Data Table 2 | Effects of phylogeny and sampling on bout length and period length.

Response	Effect type	Effect	Posterior mode	95% CI		N (range)
				Lower	Upper	
Median bout [h]	Fixed	Intercept	7.2	1.04	12	1100 (924-2079)
		Sampling	0.16	-0.2	0.61	1100 (809-1644)
	Random (variance)	Phylogeny	25.33	4.6	59.6	1100 (753-1383)
		Species	0.01	0	12.1	1100 (779-1636)
		Breeding site	2.13	0.96	4.28	1100 (808-2242)
	Pagel's λ	Residual	5.04	4.51	5.61	1100 (838-1444)
		1	0.5	1	1100 (814-1316)	
Period [h]	Fixed	Intercept	21.94	12.8	30.67	1100 (765-1392)
		Sampling	0.13	-0.41	0.65	1100 (741-1468)
	Random (variance)	Phylogeny	66.22	14.3	153	1100 (729-1638)
		Species	0.06	0	29.36	1100 (729-1435)
		Breeding site	0.01	0	0.88	1100 (814-1378)
	Pagel's λ	Residual	14.87	13.3	16.84	1100 (884-1460)
			1	0.54	1	1100 (740-1523)

The posterior estimates (modes) of the effect sizes with the highest posterior density intervals (95% CI) and the median and range of the effective sample sizes (N (range)) come from the joint posterior distribution of 100 separate runs each with one of 100 separate phylogenetic trees from <http://birdtree.org>. $N_{\text{bout}} = 729$ nests from 91 populations belonging to 32 species. $N_{\text{period}} = 584$ nests from 88 populations belonging to 30 species. Sampling (how often the incubation behaviour was sampled) was ln-transformed and then mean-centred and scaled (divided by SD). For procedures and specifications related to phylogenetic Bayesian mixed models see Methods. Estimating Pagel's λ on the species level ($N_{\text{bout}} = 32$ species, $N_{\text{period}} = 30$ species) with phylogenetic generalized least-squares using the function 'pgls' from the R-package 'caper'⁷³ gave similar results (median (range) $\lambda_{\text{bout}} = 0.73$ (0.63-1) and $\lambda_{\text{period}} = 0.95$ (0.64-1), based on 100 estimates each for one of the 100 trees).

Extended Data Table 3 | Source of phylogenetic signal

Suborder included	Response	Effect type	Fixed effects	Posterior mode	95% CI		N
					Lower	Upper	
No	Bout [h]	Fixed	Intercept	7.69	4.11	10.76	1100
			Random (variance)	Genus	9.54	0.02	46.6
		Species		11	4.84	25.77	1100
		Breeding site		2.25	1.06	4.5	1100
		Residual		5.03	4.55	5.61	1100
		Yes	Bout [h]	Fixed	Intercept (Charadrii)	4.48	1.05
Suborder (Scolopaci)	6.07				1.52	10.44	1100
Random (variance)	Genus			0.09	0	21.35	1100
	Species			11.29	5.53	23.99	1275
	Breeding site			2.31	0.98	4.28	1100
	Residual			5.04	4.52	5.58	1100
No	Period [h]	Fixed	Intercept	23.46	18.22	27.39	1100
			Random (variance)	Genus	19.05	0	97.79
		Species		41.02	17.04	72.66	1100
		Breeding site		0.01	0	0.9	1100
		Residual		14.94	13.35	16.76	1100
		Yes	Period [h]	Fixed	Intercept (Charadrii)	18.61	13.12
Suborder (Scolopaci)	8.92				0.6	15.4	990
Random (variance)	Genus			0.33	0	59.09	769
	Species			34.41	16.91	68.14	1142
	Breeding site			0.01	0	0.84	1100
	Residual			15.01	13.34	16.86	891

The posterior estimates (modes) of the effect sizes with the highest posterior density intervals (95% CI) and the effective sample sizes (N) come from a posterior distribution of 1,100 simulated values generated by 'MCMCglmm' in R⁶². $N_{\text{bout}} = 729$ nests from 91 populations belonging to 32 species. $N_{\text{period}} = 584$ nest from 88 populations belonging to 30 species.

Extended Data Table 4 | Effect of latitude, body size, escape distance and life history on biparental incubation rhythms in shorebirds

Response	Effect type	Fixed effects	Posterior mode	95% CI		N (range)
				Lower	Upper	
Bout [h]	Fixed	Intercept	7.45	2.65	12	1100 (804-1496)
		Wing length	-0.78	-2.5	1.05	1100 (839-1638)
		Latitude	1.72	0.63	2.65	1100 (850-1642)
	Random (variance)	Escape distance	-1.68	-3.3	-0.25	1100 (634-2046)
		Phylogeny	0.19	0	45	1100 (803-1875)
		Species	0.07	0	14.4	1100 (695-1580)
		Breeding site	1.4	0.59	3.02	1100 (833-1480)
		Residual	5.02	4.53	5.64	1100 (516-1916)
		Page's λ	0.72	0.13	1	1100 (731-1407)
Light entrainable rhythm [1,0] on binomial scale	Fixed	Intercept	-1.62	-3.19	-0.13	1100 (731-1633)
		Latitude	-0.56	-1.15	-0.07	1100 (765-1575)
	Random (variance)	Phylogeny	0.05	0	5.54	1100 (883-1371)
		Species	0.02	0	2.68	1100 (965-2246)
		Breeding site	0	0	0.63	1100 (605-1304)
	Page's λ	0.74	0.02	1	1100 (932-1498)	
Absolute deviations from 24-h	Fixed	Intercept	0.17	-0	0.35	1100 (459-1501)
		Latitude	0.03	-0	0.07	1100 (777-1488)
	Random (variance)	Phylogeny	0	0	0.07	1100 (786-1393)
		Species	0	0	0.03	1100 (861-1412)
		Breeding site	0	0	0	1100 (826-1860)
	Page's λ	Residual	0.03	0.03	0.04	1100 (948-2039)
		0.74	0.02	1	1100 (843-1471)	
Deviations from 24-h	Fixed	Intercept (non-tidal)	0.02	-0.04	0.09	1100 (851-1742)
		Life history (tidal)	-0.02	-0.1	0.04	1100 (702-2257)
	Random (variance)	Phylogeny	0	0	0.01	1100 (806-1692)
		Species	0	0	0	1100 (692-1601)
		Breeding site	0	0	0.01	1100 (656-1490)
	Page's λ	Residual	0.07	0.06	0.08	1100 (760-1563)
		0.77	0.01	1	1100 (864-1451)	

The posterior estimates (modes) of the effect sizes with the highest posterior density intervals (95% CI) and the median and range of the effective sample sizes (N (range)) come from the joint posterior distribution of 100 separate runs each with one of the 100 separate phylogenetic trees from <http://birdtree.org>. $N_{\text{bout}} = 729$ nests from 91 populations belonging to 32 species. For models on light entrainable rhythm, absolute deviations and deviations from 24-h: $N = 584$ nests from 88 populations belonging to 30 species. Latitude (in bout model: absolute value), wing length (ln-transformed), and escape distance (ln-transformed) were mean-centred and scaled (divided by SD). The estimates for the light- entrainable rhythm are on a binomial scale. For procedures and specifications related to phylogenetic Bayesian mixed models see Methods.

General discussion

Socially synchronized rhythms

When, in 2010, we embarked on the journey with an aim to reveal socially synchronized rhythms in the wild, little was known about such rhythms in general, and in the context of biparental care in particular. Specifically, there were five major knowledge-gaps regarding the biparental incubation rhythms. (1) The detailed description of within- and between-pair diversity in biparental incubation rhythms over the day, season and many pairs was missing. Thus, which parent – the incubating one or the off-duty one – drives the incubation rhythm was unclear. (2) Whether incubating parents compensate for temporary absence of their partner's care, and, if so, how they compensate was unknown. (3) Whether biparental species flexibly switch from biparental to uniparental care was uncertain. (4) The incubation rhythm was believed to be energetically constrained (Cresswell et al. 2003). (5) Finally, within- and between-species diversity of socially synchronized incubation rhythms, as well as drivers of such diversity were unexplored.

Major findings

We have been addressing the above described gaps by reporting on a complex social behaviour (incubation rhythms) of non-model organisms (shorebirds) recorded in the wild. In our quest, we combined a within-species approach (**Chapter 1, 2, 3, & 5**) with a between-species approach (**Chapter 4**), and with phylogenetically informed comparative analyses (**Chapter 6**).

First, we used unique data from the entire incubation period and 48 pairs of semipalmated sandpipers to reveal significant within- and between-pair diversity in the socially synchronized incubation-rhythm (Figure 3 & 7 and Supplementary Actograms in Bulla et al. 2014a – **Chapter 1**; Figure 2 & 4 in Bulla et al. 2015a – **Chapter 2**), to hypothesise about the potential drivers of this diversity, as well as to reveal that the off-duty parent plays a key role in determining the length of incubation bouts, i.e. in determining the incubation rhythm.

Then, using 25 pairs we demonstrated that parents of semipalmated sandpipers partially compensate for the absence of their partner's care, albeit that these responses varied greatly between individuals, ranging from no to full response (Figure 2 & 3 in **Chapter 3**). We further used data from 15 biparentally incubating shorebird species to uncover, in 5 of those, the potential for switching from biparental to uniparental care (Figure 1 & 4 in **Chapter 4**).

Next, we ruled out the energy as a key factor determining the length of incubation bouts of semipalmated sandpipers (descriptively in **Chapter 2**, Table 4; and experimentally in Bulla et al. 2015b – **Chapter 5**, Figure 2) and also of other shorebirds (comparatively in Bulla et al. 2016a – **Chapter 6**, Figure 4a-b).

Finally, we used unique, large-scale, primary data from 729 nests of 91 populations of 32 shorebird species to reveal unprecedented within- and between-species diversity in the socially-synchronized incubation rhythms (Figure 1 & 2 in Bulla et al. 2016a and Supplementary Actograms in Bulla et al. 2016b; **Chapter 6**), as well as to demonstrate that these diverse rhythms relate strongly to phylogeny (Figure 2), predation risk (Figure 4c), and daily environmental rhythms (Figure 4d-e), but not to energetics (Figure 4a-b) and tidal environmental rhythms (see results in **Chapter 6**). Strikingly, we showed that social synchronization generates rhythms that defy the 24-h day, even in day-night environments (Figure 4d-e in **Chapter 6**).

Key biological implications

Diverse incubation rhythm of semipalmated sandpiper

Although biparental incubation prevails in birds (Deeming 2002), accessing the generality of our findings about properties and within- and between-pair diversity of incubation rhythms (**Chapter 1**), is difficult. Continuous data throughout the incubation period are scarce, and the little that is available comes from species – such as albatrosses, penguins and petrels – with incubation bouts lasting >24h, i.e. those without a need to time incubation over a day (e.g. Davis 1982; Weimerskirch et al. 1986; Weimerskirch et al. 1992; Chaurand & Weimerskirch 1994; Weimerskirch 1995; Gauthier-Clerc et al. 2001). We can thus generalize only from our own data regarding 32 other shorebird species (**Chapter 6**); within- and between-pair diversity of incubation rhythms prevails in most of these shorebirds and the between-species diversity is immense (**Chapter 6**, Figure 1-3). Yet, the detailed investigation of the species specific incubation rhythms, such as how the amount, timing and quality of incubation change over the day and season, and whether their distribution is sex-specific (as described for semipalmated sandpipers in **Chapter 1**), awaits exploration.

Similarly, although the parent's off-duty behaviour is an integral part of biparental incubation rhythm (e.g. Chaurand & Weimerskirch 1994; Dearborn 2001), such behaviour, again with exception of seabirds, has rarely been described in detail (e.g. Jouventin & Weimerskirch 1990; Weimerskirch 1995; González-Solís et al. 2000; Weimerskirch et al. 2007; Pinet et al. 2012).

There are three main implications of our descriptive results. (1) We reveal variation in the incubation rhythms, with possible different consequences for sex-specific costs of care. For example, only in the “running” pattern (Figure 7 in **Chapter 1**, Figure 1 in **Chapter 6**), throughout the incubation period, can both parents forage during the warmer parts of the

day or be exposed to similar risk of predation, at least on some days. Similar variation is also present in other shorebirds, but whether similar variation is also present in incubation rhythms or other socially synchronized rhythms of other taxa remains unknown.

Nevertheless, with the diverse rhythms we have highlighted the need to investigate not only the central tendency, but also the variation in costs of parental care over time. This is crucial because our observation that parents spent more time feeding during the day (when food is available) and during windy conditions at night suggests that there might be a conflict over who is off-duty at the most favourable foraging times. This together with female propensity for night nest attendance further highlight the need to consider the fluctuating environment when addressing individual costs of parental care. However, such considerations make quantification of parental care a formidable task, and hence the investigation of cooperation and conflict during parental care necessarily difficult.

Perhaps, due to this difficulty, the quantification of parental care in descriptive and experimental studies has been mostly simplistic (i.e. only one aspect of care), or has examined only a short snapshot of time (e.g. based on visits of parents to the nest box from 10 to 12 o'clock when chicks were 10 days old). That is, the quantification of care has ignored variation in care and in its costs over the day or season (e.g. Wright & Cuthill 1990; De Ridder et al. 2000; Sanz et al. 2000; Alonso-Alvarez 2001; Harrison et al. 2009; Mutzel et al. 2013; Paul et al. 2014; Wetzel et al. 2015). Thus, the validity of existing findings about the share of parental care, and about parental cooperation in general, are unclear (Royle et al. 2012).

In sum, although our study may miss other forms of care (e.g. brood care), it does demonstrate the value of investigating several aspects of care over long time (e.g. whole incubation or chick-feeding period) and in many individuals. Focusing on only one aspect of care, or on a short snapshot of care in time, is likely to bias our perception of the costs of parental care; it is also likely to hinder the discovery of diverse rhythms, and to yield an insufficient understanding of parental cooperation and of the resulting behaviour rhythms.

(2) The findings that off-duty parents spent their off-nest time far from the nest (Figure 2 in **Chapter 2**) and usually returned to the nest only prior to the exchange, imply that the off-duty parent's decision to return to the nest and to relieve its incubating partner must generally drive the length of incubation bouts. This is also supported by the finding that the off-duty parent is too far away to hear or to be heard by its incubating partner, as well as by the finding that the incubating bird does not search for its off-duty partner (not even 30 min prior to exchange on the nest).

These findings further imply that parental communication is limited to brief moments during the exchange on the nest, which is also typical among seabirds where the off-duty parents forage far out on the sea for several days (Davis 1982; Chaurand & Weimerskirch 1994; Weimerskirch 1995; Gauthier-Clerc et al. 2001). However, we still do not understand the key factors that influence the decision to return to the nest; it is unlikely that such decision is

primarily driven by energy stores (see below). We can only speculate about the other possible factors. In the next point we discuss two of them: assessing parent's and brood's state and interval timing.

(3) The lack of instantaneous communication also suggests that, in contrast to biparental offspring feeding (e.g. Wright & Cuthill 1990; Hinde 2006; Hinde & Kilner 2007; Harrison et al. 2009), optimization of incubation rhythms cannot work via direct and immediate communication between the parents. Information about the state of both partners, or of the brood, can only be obtained during the change-over on the nest. Thus, parents cannot adjust their behaviour immediately to accommodate the needs of the partner or the brood.

Consequently, the species likely evolved mechanisms to enhance the optimization of incubation rhythm, such as improved cognitive skills to assess partner's condition or partner's willingness to invest. This would enable parents to better predict the state of their mate even when not physically present. We would then expect that such predictive ability will improve the longer parents stay together. The evidence for higher hatching success of reunited pairs (e.g. as a consequence of improved synchronization on the nest) is lacking in semipalmated sandpiper (Gratto-Trevor 1991), but is reported from other biparentally incubating species (e.g. Coulson 1966; Davis 1976; Ens et al. 1993; Nisbet & Dann 2009; but see Naves et al. 2007).

Alternatively, if no useful information can be acquired during the exchange on the nest, individuals might be selected to use simple rules, such as coming back after a more or less fixed amount of time. This hypothesis is not unlikely because the incubation of semipalmated sandpipers is continuous, with smooth exchanges on the nest (**Chapter 1**, Figure 1b & 5) and is not energetically constrained (i.e. it is unlikely that the state of the incubating bird drives the length of an incubation bout; **Chapter 5**). Moreover, in ringed doves, *Streptopelia risoria*, experimental evidence confirms the role of interval timing in determining the incubation rhythm (Silver & Bittman 1984). However, whether other species also use such interval timing remains unclear and requires experimental testing.

Diverse response to reduced care of a partner

Our finding, that parents of biparentally incubating semipalmated sandpiper partially compensate for the temporal absence their partner's care (Figure 2 in **Chapter 3**), seems in line with the predictions of established models and results (Houston & Davies 1985; McNamara et al. 1999; McNamara et al. 2003; Harrison et al. 2009). However, we also found, to date unreported, uniform-distribution of individual responses spanning from no to full compensation (Figure 2 & 3 in **Chapter 3**). Such findings suggest the lack of a dominant compensation response within our population. Thus, our results actually defy the predictions of the very same models. How then do the diverse individual responses come to be?

We hypothesise that all individuals attempt full compensation, but some fail because their energy stores get depleted, or because they are less responsive to the temporary absence of

their partner. We provide some correlational evidence for both (Figure 3 & 4 in **Chapter 3**), but the next step is to verify these hypotheses experimentally.

To test whether energy stores of incubating parent truly drive the level of compensation, the saving of energy (e.g. by supplemental feeding) during temporal removal of the partner should reduce the diversity in compensation responses, with all individuals compensating nearly fully. Although technologically difficult, an alternative would be to repeat the very same experiment presented here, but with scales under the nest cup to continuously measure body mass of the incubating bird. This will reveal whether parents leave the nest once their body mass reaches a threshold.

To verify whether responsiveness of the parents drives the compensation, the experiment should be repeated ideally with the same individuals, and with the same, as well as with other taxa. However, if both energy stores and responsiveness of the individuals drive the compensation response, disentangling the two with field experiment might get too complex and difficult and might require an inevitable switch to laboratory settings.

Flexible parental care

Our findings of uniparental incubation in 8 out of 15 biparentally incubating shorebird species (Figure 1 in **Chapter 4**), and of evidence for hatching despite of uniparental incubation in 5 of these species (Figure 4 in **Chapter 4**), challenge the belief of unsuccessful uniparental incubation in biparental shorebirds (Poole 2005). Since reports of flexible switch from biparental to uniparental care are rare (Reneerkens et al. 2014), our findings open up three main questions. (1) Is such a potential for flexible switch from biparental to uniparental care also present in other taxa and in other parental care contexts? (2) What drives such switch from biparental to uniparental care? (3) Do species realize their potential to switch flexibly from biparental to uniparental care based on the conditions at the breeding ground (e.g. based on change in sex ratios)?

Lack of evidence for energetic constraints of incubation rhythm

We collected multiple evidence (descriptive – **Chapter 2**, Table 4; experimental – **Chapter 5**, Figure 2; and comparative – **Chapter 6**, Figure 5a-b) against the belief that incubation rhythms of biparental shorebirds are primarily driven by energetic constraints and therefore by the state of the incubating bird. Our findings suggest that biparental incubation rhythms are less energetically constrained than uniparental incubation rhythms (e.g., Aldrich & Raveling 1983; Bryan & Bryant 1999; Reid et al. 1999; Cresswell et al. 2004; Ardia et al. 2009), and also imply that biparental shorebirds – and perhaps most biparentally incubating species – might be able to incubate continuously for much longer than they actually do, which we partly confirm (**Chapter 3 & 4**; see also Kosztolanyi et al. 2003). Therefore, other factors, such as predation risk, circadian fluctuations in prey availability, or synchronization of the daily rhythms of the two parents (discussed in **Chapter 1**), play a more important role in determining the length of incubation bouts, i.e. drive the variation in biparental incubation patterns. Some of these factors we later confirmed (**Chapter 6**).

Within- and between-species diversity and drivers of incubation rhythms

Our comparative results have three main implications. (1) We found that under natural conditions social synchronization can generate much more diverse rhythms than previously expected (Davidson & Menaker 2003; Castillo-Ruiz et al. 2012; Bloch et al. 2013; Kronfeld-Schor et al. 2013; Paul et al. 2015). We describe this diversity in the context of biparental incubation, but diverse behavioural rhythms may also arise in many other social settings, for example in the context of mating interactions (Lesku et al. 2012) or of vigilance behaviour during group foraging – something worth future investigations. Essentially, these results further emphasize the recognized need to study biological rhythms in the wild (Kronfeld-Schor et al. 2013).

(2) The results further imply a key role of predation, but not of starvation risk, in determining some of the variation in incubation rhythms.

(3) Also, although our findings suggest that tidal life-history seems to play a negligible role in determining incubation rhythms, the findings support the existence of a latitudinal cline²² in socially emerged behavioural rhythms; that is, the findings support the role of 24-h light-dark cycle in shaping the incubation rhythms (Figure 5d-e in **Chapter 6**). Still, the reported rhythms often defy the assumptions of entrainment to the 24-h day-night, which implies that the expectation that individuals within a pair (or group) should optimize their behavioural rhythms relative to the 24-h day may be too simplistic. This opens up a wide field to study the evolutionary ecology of plasticity in circadian clocks.

Concluding remarks on drivers of diverse rhythms

In sum, we used our descriptive findings from semipalmated sandpiper (**Chapter 1-2 & 4**) to highlight the lack of knowledge regarding causes of the diverse incubation rhythms, as well as to summarise and propose hypotheses to explain such diversity (Table 1). We then used descriptive, experimental and comparative methods to reject and confirm some of these hypotheses.

Table 1 | Hypotheses attempting to explain diverse incubation rhythms (derived from **Chapter 1-2 & 3**)

Hypothesis	Diversity in rhythms arises via
Energetics	variation in energetic states of the parents
Predation	variation in anti-predation strategies
Behavioural rules	variation in behavioural rules or responsiveness (e.g. if the rhythms arise from the rule ‘when the foraging partner comes back to the nest, the incubating bird decides when to leave, then the variation in the rhythms may reflect individual differences in the decision to leave the nest when the partner returns)
Life history	variation in life histories (e.g. day-night vs tidal foraging) potentially linked to variation in internal clock
Environmental cues	variation in response to external environmental cues

We found little evidence for rhythms being driven by energetic constraints (**Chapter 2 & 5-6**), but found evidence for anti-predation strategy instead (**Chapter 6**). Whereas instantaneous communication between incubating parents is unlikely in some of the studied species (**Chapter 2 & 6**), and hence room for active negotiation of parental care between parent is limited, the interval timing (**Chapter 1 & 2**) or the responsiveness of the parents (**Chapter 3**) to the state of the brood and the state or absence of the partner might be shaping the incubation rhythm. Whereas we found no evidence for a link between incubation rhythms and tidal life history of the species, day-night environmental cycle is related to variation in incubation rhythms (**Chapter 6**).

Key non-biological implications

Apart from the key biological implications, our results have two implications for the way socially synchronized rhythms can be studied in the wild and two implications for the scientific method in general.

Method to study socially synchronized rhythms in the wild

(1) Given the lack of detailed descriptive studies, our study of incubation rhythms in semipalmated sandpipers (**Chapter 1 & 2**) provides a quantitative framework for future work on the rhythms of biparental care. Such a framework allows quantification of both general trends and of within-population variation. We have partly utilized the very same framework in the large-scale comparative study (**Chapter 6**). Also, this framework has been adopted by others (Huffeldt & Merkel 2016).

(2) Also, within the comparative study (**Chapter 6**), we demonstrate how to decompose complex social behaviour into simple variables that not only describe the socially synchronized rhythms, but also allow for comparison of the rhythms across pairs and species.

Scientific method

(1) Our study about how energetic constraints shape the incubation rhythms illustrates the merit of using diverse approaches to test a single hypothesis, as well as the merit – extensively discussed, but often underappreciated – of replicating previously published experiments (Ioannidis 2005a, b; Nosek et al. 2012; Begley & Ioannidis 2015; Open Science 2015; Baker 2016; Ebersole et al. 2016).

(2) Such replication experience further highlights the usefulness of making the data and computing codes that were used to derive our published work, freely available – a practice that is rarer than believed (Roche et al. 2014; Markowitz 2015), but which we subsequently used throughout the rest of our studies (Bulla 2014; Bulla et al. 2014d; Bulla et al. 2014b; Bulla et al. 2014c; Bulla 2015, 2016a, c; Bulla 2016b; Bulla & Kempnaers 2016; Bulla et al. 2016b).

Outlook

Our results open up five main questions. (1) What drives the switch from biparental to uniparental care? Specifically, is such a switch a response to the conditions at the breeding ground (e.g. based on change in sex ratios)?

(2) Is the variation in incubation bout length in cryptic species related to the actual predation pressure? This can be tested by comparing bout length between populations of a particular species that are exposed to different predator densities, or between years that differ in predation pressure.

(3) Are diverse behavioural rhythms also present in other species and contexts?

(4) How do diverse social rhythms emerge? That is, are the rhythms a consequence of behavioural flexibility, or a 'fixed' outcome of synchronization between the circadian clocks of the two individuals involved? An experimental study on ring doves, *Streptopelia risoria*, suggests that parents may even use two timers - circadian oscillation and interval timing - to determine when to incubate (Silver & Bittman 1984). Such a suggestion is not unlikely because other organisms have also been shown to have various timing mechanisms, e.g. circadian and tidal clock (e.g. Takekata et al. 2012; Zhang et al. 2013).

(5) What – if any – are the fitness consequences for the parents of having a certain incubation rhythm? For example, the costs of having a particular incubation rhythm are likely unevenly distributed between the two parents (e.g. because one parent is on incubation duty when food is more readily available, or because one parent 'enforces' its own rhythm at a cost to the other parent).

Significance

Our results are of immediate interest to chronobiologists: we essentially fulfil their "wish-list" (see General introduction for the quote from Kronfeld-Schor, Bloch & Schwartz 2013). We report diversity that is unexpected from studies of individuals, we demonstrate high plasticity of rhythmic behaviour despite high heritability, and we both confirm and challenge the role of day-night cycles in entraining behaviour. The comparative aspect of our study, and the role of anti-predation strategy in shaping the behavioural rhythms, will also appeal to evolutionary biologists and ecologists, particularly because it solves a controversy about the relative importance of energetics vs. predation in shaping biparental incubation rhythms.

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Author contributions

Chapter 1: M.B. and B.K. conceived the study. M.B. coordinated the study. M.B and A.R. with help from B.K. and M.V. collected data. A.R. and M.B. managed the data, M.B. extracted the incubation/non-incubation, M.B. with help from M.V. analyzed the data. All authors discussed the results. M.B. and B.K. wrote the paper with input from all authors.

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- (10) **Bulla, M.**, Valuc, M., Rutten, A. L., Kempenaers, B. 2013. **Biparental incubation patterns in a high-Arctic breeding shorebird: how do pairs divide their duties? *Behav Ecol*. 129: 26-35.** Available at http://www.academia.edu/1500089/Eggshell_spotting_does_not_predict_male_incubation_but_marks_thinner_areas_of_a_shorebirds_shells
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PUBICATIONS – other

- Bulla M 2012. Skvrnění čejčích vajec: signál o kvalitě samičky nebo tloušťce skořápky? *Ptačí svět*. 2: 16.
- Dobes, V. & Bulla, M. 2006. EKODESIGN. *Environmentalni ASPEKTY podnikani*. 1: 5-7.
- Bulla, M. & Viltova, B. 2006. Interview: Christopher Day v České republice. *ERA21: more on architecture!*. 6(4): 8.

DATA & SCRIPTS

- Bulla M, et al. 2016. Supporting Information for 'Flexible parental care: Uniparental incubation in biparentally incubating shorebirds'. *Open Science Framework*. Available at <http://osf.io/3rsny>
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- Bulla, M. 2014. **R-SCRIPT and EXAMPLE DATA to extract incubation from temperature measurements** *figshare.com*. Available at http://figshare.com/articles/R_SCRIPT and EXAMPLE DATA to extract incubation from temperature measurements/1037545
- Bulla, M., Valcu, M., Rutten, A. L., Kempenaers, B. 2013. **Data from: Biparental incubation patterns in a high-Arctic breeding shorebird: how do pairs divide their duties?** *Dryad Digital Repository*. Available at <http://datadryad.org/handle/10255/dryad.54132>

PRESENTATIONS

2016	poster	Unexpected diversity in socially synchronized rhythms of shorebirds 16th congress of the International Society for Behavioral Ecology, UK
2015	talk	Incubation pattern of biparental shorebirds International Wader Study Group Conference, Iceland
2015	posters	Incubation pattern of biparental shorebirds: a comparative study Social Jet Lag Wild clocks: ecology meets chronobiology, Holland
2014	talk	Incubation pattern of biparental shorebirds: a comparative study International Wader Study Group Conference, Estonia
2013	talk	Biparental incubation-scheduling: no evidence for energetic constraint Evaluation Symposium of IMPRS for Organismal Biology, Germany International Wader Study Group Conference, Germany
2012	invited speaker	Biparental incubation patterns Czech University of Life Sciences Prague, Czech Republic
2012	talk	Biparental incubation: the division of duties 105th Annual Meeting of the German Zoological Society, Germany International Wader Study Group Conference, France
2012	poster	Unequal division of incubation in a High Arctic Shorebird 14th congress of the International Society for Behavioral Ecology, Sweden

TEACHING & SUPERVISION

2015 - 2016	Supervision of BSc student Daniela Tritscher , Technische Universität München, Germany
2014 - present	Supervision of MSc/PhD student Eva Vozabulova , Faculty of Agrobiolology, Food & Natural Resources, Czech University of Life Sciences Prague, Czech Republic
2012 - present	Supervision of MSc student Hana Vitnerova , Faculty of Science, Charles University, Czech Republic
2012 - 2014	Supervision of MSc student Sjoerd Hobma , Faculty of Mathematics and Natural Sciences, University of Groningen, the Netherlands
2011 - 2012	Supervision of MSc student Elias Stich , Department of Biology University of Tübingen, Germany
2009	Bird Identification Course University of Natural Resources and Applied Life Sciences, Vienna

REVIEWER

2016	Journal of Avian Biology
2016	Biology Letters
2015	The Auk
2014	Behavioral Ecology
2014	Naturwissenschaften
2014	Wader Study

AWARDS/SCHOLARSHIPS

2016	Marie Curie EU Grant
2014	IMPRS for Organismal Biology Student's Grant
2010	ERASMUS internship , University of Groningen
2009	Stipendium Verein der Freunde der Universität für Bodenkultur Wien International student excellence scholarship
2008 – 2009	ERASMUS , Universität für Bodenkultur Wien
2008 – 2009	Academic Excellence Scholarship Czech Uni. of Life Sciences Prague
2004 – 2006	Academic Excellence Scholarship Charles University in Prague
2002	Higher Education Support Program Mobility Grant Open Society Institute - Zug Foundation, Budapest, Hungary
2001 – 2004	Dean's Honours List (top 5% of students) University of New York/Prague
2001 – 2003	Academic Excellence Scholarship University of New York/Prague For the highest and the 2 nd highest GPA,

COURSES/SEMINARS

2012 - 2014	Various statistical, presentation, writing and visualisation workshops	IMPRS
2011	Generalised Linear Modelling – M. Crawley	Imperial College London
2008	Czech Bird Ringing License	
2007	Nesting Bird Survey Techniques in National Park Wattenmeer	
2004	Practice of Communicational Abilities for NGO Worker	
2003	Accounting for NGOs	

MEMBERSHIP and VOLUNTEERING

2011 – present	International Wader Study Group	International
2008 – present	Czech Ringing Association	Czech Rep.
2007 - present	Czech Society for Ornithology	Czech Rep.
2007	European Volunteer Service in Verein Jordsand, Management of natural reserves, bird monitoring, census, ringing	Germany
2004 – 2007	The Organization for Aid to Refugees Member of the Board of Directors	Czech Rep.
2004	Tereza, association for ecological education Volunteer of Fundraising Department	Czech Rep.
2004	NGO Alternative -V Dnipropetrovsk Volunteer at international project Ecological conservation work at Crimean mountains	Ukraine
2004	INEX - Association for Voluntary Activities, Leading international environmental project of voluntary service	Czech Rep.

WORK EXPERIENCE – science related

2010	Animal Ecology Research Group – Uni. of Groningen Field assistant in prof. Piersma's Ruff and Godwit Projects	Netherlands
2009	Uni. of Natural Resources and Applied Life Sciences, Vienna Field assistant in Alpine Biodiversity Project	Austria
2008	Czech Ornithological Society – Birdlife Partner Swift census	Czech Rep.
2005 – 2006	Project CzechKid - Charles University in Prague and British Council Member of a development and methodological group Multicultural education project http://www.czechkid.cz/	
2004 – 2005	Charles University in Prague – Civil Sector Department Translation of academic papers and projects Research of the umbrella org. within Czech nonprofit sector	Czech Rep.

WORK EXPERIENCE – other

2006 - 2007	Consensus Design Workshop with Arch. Christopher Day Invented, secured EU financing, organized	Czech Rep.
2005 – 2007	ENVIROS, s.r.o., Assistant to the Expert of Sustainable Production and Services Generated EU funds, organized seminars (e.g., EKODESIGN)	Czech Rep.
2005	Civil Society Development Foundation Translation of a Guide to EU Funds 11ed.	Czech Rep.
2004 – 2005	Tereza, association for ecological education Leader of Fundraising through volunteers	Czech Rep.
2003	Prague Business Partners Director's assistant	Czech Rep.

CARRIER BREAKS in RESEARCH

2015 April – 2016 December	Paternity leave	Germany
2014 October – 2015 April	Paternity leave: 80% employment	Germany
2014 August	Paternity leave	Germany

Statutory declaration and statement

Ehrenwörtliche Versicherung

Ich versichere hiermit ein Eides statt, dass die von mir vorgelegte Dissertation von mir selbstständig und ohne unerlaubte Hilfe angefertigt worden ist.

München, den

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Martin Bulla

Erklärung

Hiermit erkläre ich, dass die Dissertation nicht ganz oder in wesentlichen Teilen einer anderen Prüfungskommission vorgelegt worden ist. Im Weiteren erkläre ich, dass ich mich nicht anderweitig einer Doktorprüfung ohne Erfolg unterzogen habe oder ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich einer Doktorprüfung zu unterziehen.

München, den

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Martin Bulla