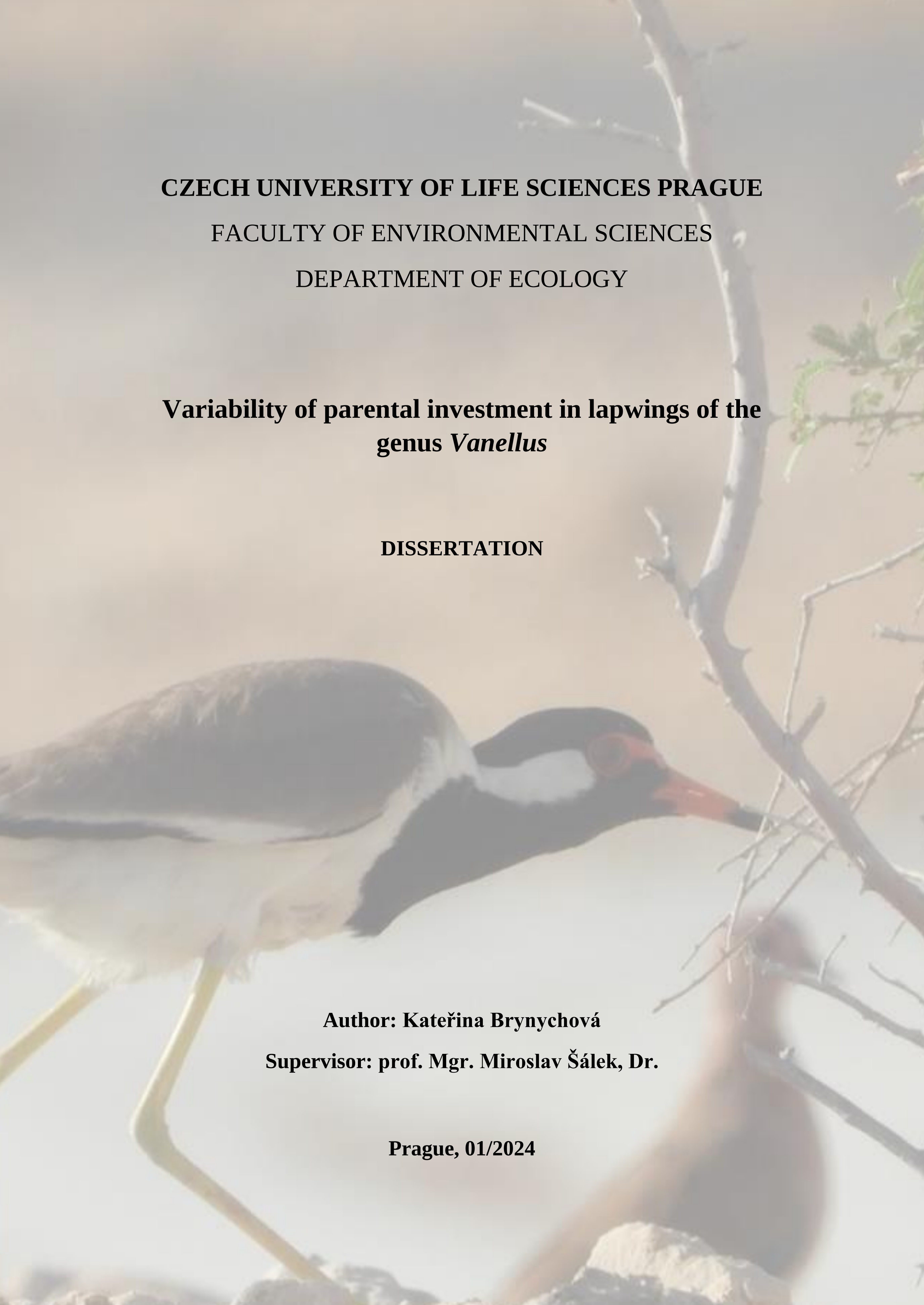

CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE
FACULTY OF ENVIRONMENTAL SCIENCES
DEPARTMENT OF ECOLOGY

Variability of parental investment in lapwings of the genus *Vanellus*

DISSERTATION

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Prague, 01/2024

For the most beautiful bird

The Lapwing

Declaration of originality

I declare that this thesis has not been submitted for the purpose of obtaining the same or any other academic degree earlier or at another institution. My involvement in the research presented in this thesis is specified in the statement of contributions and it is also expressed through the authorship order of the included publications and manuscript. All relevant literature sources used while writing chapters in this thesis have been properly cited.

Prague, ...

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Author contributions

This thesis contains three published articles and one unpublished manuscript. All articles were produced by a collaborative effort of researchers from the Behavioural Ecology Research Group at the Faculty of Environmental Sciences CZU. My contribution to each of the publications is listed below.

Chapter 1 - Sládeček, M., Vozabulová, E., **Brynychová**, **K**., & Šálek, M. E. (2019). Parental incubation exchange in a territorial bird species involves sex-specific signalling. *Frontiers in Zoology, 16,* 1-12.

Contribution: MS, EV and MŠ collected the data; MS, EV and KB extracted the incubation from videos; KB extracted vocalization and type of departure from videos; MS analyzed the data; MS wrote the original draft with input from MŠ. The final draft was read, commented on and approved by all authors.

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Contribution: KB and MŠ designed the experiment; KB, MS, LP, PCH, VF and MŠ collected the data; KB prepared data; MŠ, MS and PCH analyzed the data; KB and MŠ wrote the original draft. The final draft was read, commented on and approved by all authors.

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Contribution: MS, KB and MŠ designed the study; MS and EV collected the incubation data; KB extracted other behavioural data from the videos; MS analyzed the data; MS, KB and MŠ wrote the original draft. The final draft was read, commented on and approved by all authors.

Chapter 4 – (unpublished manuscript) Perennial monogamy is the preferred strategy for Red-wattled Lapwing breeding in a long seasonal hot environment.

Contribution: MŠ and KB designed the study; KB, MS, LP, PCH, VK, EE and MŠ collected the data; KB and MŠ prepared data; MŠ analyzed the data; KB and MŠ wrote the original draft.

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Abstract

Parental care in birds takes many forms and often requires the involvement of both parents. Although partners have the same aim to raise as many offspring as possible, their investment in parental care may differ, which can negatively influence the more involved parent. Therefore, communication or a kind of negotiation between the partners is important for successful reproduction. Parental care is not only energy and time consuming, but also difficult in coordinating the activities involved and risky due to the presence of predators. In this thesis, I investigated several aspects of parental care in the temperate Northern Lapwing *Vanellus vanellus* and the subtropical Red-wattled Lapwing *Vanellus indicus*. Both species are biparental, but with different lifestyles, and represent the genus of lapwings from the plover family, order Charadriiformes.

First, I focused on parental exchange at the nest and related communication in the Northern Lapwing with highly variable male contribution to incubation. In our study, we found that the incubating parent can communicate with the non-incubating partner using acoustic and visual signals, which helps to synchronize parental exchange at the nest. Thus, communication and negotiation between partners play an important role in parental care in a biparental species with unequal parenting.

Second, predation risk shapes the parental care behaviour. Ground-nesting birds use a variety of defence strategies to protect the offspring from predators, but little is known about a choice of strategy based on predator species and about the role of conspecifics in shared defence, especially in subtropical species. We experimentally confirmed that Red-wattled lapwings distinguish between different types of predators, and we found that both parents respond equally to the presence of predator and may share the nest defence with other conspecifics.

Third, many of the parental services provided for the benefit of the offspring are costly as they are carried out at the expense of parents' self-maintenance. In addition, the level of parental effort of one sex may influence such a behaviour of the counterpart. Therefore, we analyzed the daily rhythms of sleep and feather preening of incubating Northern Lapwing females and showed that male incubation effort affects female self-maintenance behaviour

on the nest. We also showed that the risk of predation modulates these behavioural rhythms.

Fourth, decisions for fidelity or divorce in birds are species specific but are also influenced by environmental conditions. The subtropical environment provides a long breeding season, which allows multiple breeding within a year and therefore more opportunities for frequent mate changes. We were interested to see the preferred strategy of Red-wattled lapwings, i.e., whether they prefer mate fidelity or more frequent partner changes. Despite the potential benefits of divorce in some aspects, we found that Red-wattled lapwings exhibit extreme mate fidelity both within and between seasons. We have tried to explain this extreme mate fidelity.

In sum, in this thesis I have investigated several aspects of shared parental care and the relationship between partners during reproduction in two biparentally breeding lapwing species. In particular, the importance of communication and cooperation between partners and other conspecifics during incubation period has been described and shown in detail, as well as the behaviours that can take place during incubation and in defence against predators. Whereas different roles of parental care are more divided between the partners in the Northern Lapwing, which may be related to partial polygamy of this temperate species, the parental roles are more equal in the Red-wattled Lapwing, which may be related to its extremely high partner fidelity and breeding in a hot long-seasonal environment.

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General introduction

"Discovery consists of seeing what everybody has seen and

thinking what nobody has thought."

- Albert Szent-Györgyi

Variability in parental care

Reproduction is the most important and the most demanding activity in the life of any organism. Before each reproductive attempt, individuals need to put questions, such as: when is the right time to breed? With whom to breed? Where is a good place for reproduction? How much energy invest in each breeding attempt? All these questions are closely related to parental care.

Most parental care in birds takes place on the nest where the parents care for the eggs and later (in altricial species) for the young (Royle *et al*., 2012). Therefore, avian parental care involves various aspects of behaviour, including nest building, incubation of the eggs, brooding of young, feeding of young and protecting offspring against predators (Clutton-Brock, 1991; Burley & Johnson, 2002; Deeming, 2002). However, parental care does not only bring benefits (in the form of offspring), but it is also hard work that costs a lot of energy, may reduce time for self-maintenance and time for extra-pair mating (Clutton-Brock, 1991; Williams, 2018). In addition, parental care can be dangerous in terms of various threats, in particular the risk of predation. In other words, parents may provide extensive parental care that enhances offspring's fitness but often at the cost of their own health and survival (Clutton-Brock, 1991; Royle *et al*., 2012). As a result, conflicts arise between male and female about how much care each should provide. There may be conflict between parents and offspring over the length and intensity of care and there is also a competition between siblings about how much care each should receive. Thus, the intensity of parental care may vary between sexes as well as across species, depending on species-specific life-history traits evolved, actual environmental conditions as well as individual characteristics of a given population (Martin, 1995; Royle *et al*., 2012; Remeš *et al*., 2015).

Forms of parental care in birds

There are several basic forms of parental care: no care, uniparental care by male or female, cooperative breeding and biparental care. Only ~1% of bird species show no parental care (Lack, 1968; Cockburn, 2006) as they practice brood parasitism or use geothermal heat (Spottiswoode *et al*., 2012; Harris *et al*., 2014; Soler, 2017). Uniparental care by males or females occurs mostly in species with sufficiently developed offspring already after hatching which do not require too much care (Lack, 1968). This fulfils the precocial offspring (most waterfowl, galliforms, shorebirds) which do not require provisioning as opposed to altricial offspring (most passerines, parrots, raptors, owls, woodpeckers). A comparative review showed that uniparental care occurs in 24% of precocial bird species compared to only 7% of altricial species (Cockburn, 2006).

Only female care may occur in species and conditions where mating opportunities for both sexes are abundant, and males have opportunities to acquire multiple mates. Only male care may occur where mating opportunities for both sexes, especially for males, are scarce (Owens, 2002). On the other hand, it is unlikely that male care is only response to unavailability of potential partners (Andersson, 1995; Cockburn, 2006). The possibility of single-sex care depends on the environmental conditions combined with other factors that must allow such form of care (Royle *et al*., 2012). Only male care is known in some megapodes (Birks, 1997), ratites (Valdez, 2022) and shorebirds (Székely & Reynolds, 1995; Oring *et al*., 1989). Within shorebirds, exclusive male care occurs in genera *Actitis* (Scolopacidae) and *Charadrius* (Charadriidae). In contrast with less common male care, there is much evidence that cumulative selection pressures due to previous investment in egg production have led to female care (Lack, 1968; Kokko & Jennions, 2008; Trivers, 2017). It is well known that across a range of taxonomic groups, females take more care for their offspring, while males invest more in obtaining additional mating opportunities (Clutton-Brock, 1991; Queller, 1997). If female does not need direct benefits of paternal provisioning, additional male care is not a crucial requirement for successful raising of offspring (Gowaty, 1996). Female care is known in many frugivory and nectarivory birds (Snow, 1971) and often is enabled in the environment with sufficient food resources, such as marshes with seasonal aquatic insects (Cockburn, 2006).

Cooperative breeding is a specific and interesting form of parental care. In this breeding system, more than two individuals are involved in the care of the offspring. Cooperative groups consist primarily of family members or non-breeding unrelated "helpers" (Koenig & Dickinson, 2004). Such a seemingly paradoxical behaviour is rare in species with precocial offspring but more common in species with altricial offspring e.g., Stripe–backed Wren (*Campylorhynchus nuchalis*), Long-tailed Tits (*Aegithalos caudatus*), White-browed Sparrow Weaver (*Plocepasser mahali*) (Price, 2003; Maccoll & Hatchwell, 2004; Voigt *et al*., 2021). Many cooperatively breeding birds are likely to have limited opportunities to breed independently which encourages cooperative breeding. The most common ecological constraints to independent breeding are lack of food and unavailability of nest sites (Arnold & Owens, 1998). The strongest explanation for the participation of relatives in cooperative breeding is kin selection (Koenig & Pitelka, 1981). In this way, individuals can increase their inclusive fitness by helping their genetic relatives. However, unrelated individuals gain also a variety of benefits from group membership, primarily territory inheritance, connection to future mates or skills relevant to parental care (Riehl, 2013).

Despite the existence of various breeding systems without individual parental care or with care provided by a single parent, successful reproduction in most species of birds requires shared care by both partners - female and male. Therefore, biparental care is the most widespread form of care in birds that occurs in more than 75% of bird species (Lack, 1968; Skutch, 1976; Cockburn, 2006). In general, biparental care is expected to evolve if it increases the offspring fitness, which outweighs other benefits such as additional reproduction with another partner (Smith, 1977). This is probably why in socially monogamous species, i.e., when the care is divided exclusively between two partners (male and female), a certain proportion of extra-pair offspring occurs (i.e., social but not genetic monogamy; Birkhead & Montgomerie, 2020). Therefore, when two parents cooperate to raise their offspring, a conflict arises over how much each parent should contribute to the care (Godfray, 1995; Houston *et al*., 2005). Some parental responsibilities are shared by both partners (not always evenly), but the roles of male and female may be specialized in particular tasks. For example, male may support his female partner by feeding during incubation (Matysioková & Remeš, 2014) or by defending territory or offspring (Van Rhijn, 1991). Females, on the other hand, may spend more time with egg incubation (Bulla *et al*., 2017; Sládeček *et al*., 2019; Conway & Martin, 2000). Despite the involvement of parents can vary dramatically between the species as well as between pairs within the species, detailed studies of the within-species variability in birds with highly variable male contribution to parental care are rare. If parental care is unevenly divided between partners, differences in parental effort will be reflected in behaviour, expenses and benefits, especially for the more burdened partner (Chase, 1980). Biparental care in birds thus involves many different solutions and provides an excellent model system for studying the division of parental roles and responsibilities, the balance of parental cooperation, and the trade-offs between offspring care and benefits to the parents themselves.

What makes a good partnership in biparentally caring species?

Breeding pair in a socially monogamous species represents a team where two unrelated individuals cooperate to produce as many offspring as possible (Roughgarden, 2012). In a good partnership, we should expect effective communication and cooperation in the division of roles between the partners. Although both partners share the aims in producing offspring, communication and cooperation may not always be brilliant. Compliance and compatibility in shared parental care depend on many circumstances including harshness of environment, personality, experience of each individual and others (Remeš *et al*., 2015). Furthermore, the quality of partner's relationships can grow over time, so a long-term partnership of stable pairs can also play a significant role (Auld *et al*., 2013).

One important question is how the partners divide their parental duties. McNamara *et al*. (1999) investigated how two partners achieve a division of workload by adjusting parental effort in response to the change in the partner's prior effort. Specifically, when one parent reduces his investment, the partner can either increase own workload to compensate this loss or, conversely, reduce workload to match the partner's reduced effort (Johnstone & Hinde, 2006). In general, there is higher but not exclusive support for the partial compensation model in which one parent tries to compensate the reduced effort made by his partner (Harrison *et al*., 2009), even though this compensating effort can have negative fitness consequences for the more investing parent.

Compensation by the increased effort of one parent for reduced activity of the partner is most evident in shared parenting responsibilities, which cannot be substantially reduced. Shared activities of breeding birds mainly include incubation and other care of the eggs and guarding the clutch against predators. In species where both parents share incubation duties, hatching success may be higher if the partners coordinate their incubation activities better (Spoon *et al.*, 2006, **Chapter 1**). The level of partners cooperation is obvious in a risky situation such as defending a nest or offspring against predators. Partners in such situations can cooperate and must choose an adequate defensive or offensive strategy because they are risking their own lives (**Chapter 2**). However, successful reproduction does not only depend on the partners cooperation and managing of risky situations such as confrontations with predators. Successful reproduction is also related to the good body condition and health of both partners. Sufficient sleeping and feather preening are important aspects of self-maintenance behaviour in birds (Amlaner & Ball, 1983; Delius, 1988) that undoubtedly contribute to the good condition of breeding parents. Thus, if two individuals are aligned and work together, it is desirable to study how more or less corresponding input of one parent affects the self-maintenance behaviour of the partner (**Chapter 3**). Most partnerships can last for several reproductive events because most bird species breed multiple times during their lifetime (Reichard & Boesch, 2003; Black, 1996). Therefore, before each breeding attempt, the individual must decide whether to stay with its current mate or exchange it for a new one (Choudhury, 1995; **Chapter 4**). Both decisions have their costs and benefits (Choudhury, 1995; McNamara & Forslund, 1996; Culina & Brouwer, 2022) which need to be investigated in each breeding system for a better understanding of the reproductive strategy of a given species. In general, only in long-term relationships, the partners may gradually fine-tune their coordination within the bond (Sánchez-Macouzet *et al.*, 2014) and divide their activities during reproduction more efficiently.

Communication of partners during parental care

Animals communicate with each other in many ways. In different species, olfactory, visual, and vocal communication is used to varying extents. Thus, communication can take many forms and often is accompanied by some extra displays (Wachtmeister, 2001) or by rituals, such as allopreening (Kenny *et al.*, 2017; Takahashi *et al.*, 2017), welcoming ceremonies (Eggleton &

Siegfried, 1979), or duetting (Boucaud *et al.*, 2017). These rituals are apparently important for partnership development and stability. In these rituals, we need to distinguish which component means positive communication between the partners and which represents a challenge to an enemy or competitor. For example, to avoid the risk of predation, birds have evolved antipredator communication and use alarm calls to inform each other of an approaching predator (Caro, 2005). However, there are other reasons why birds vocalize at the nest. Potential benefits of calling around the nest include elimination of harassment by males, deterring other birds from colonizing one's own territory, promoting mate vigilance against predators, signalling willingness to copulation, or luring potential predators away from the nest (Yasukawa, 1989; McDonald & Greenberg, 1991). However, the negotiation process through vocalization between partners during parental care has been rarely described to date (Benedict, 2008; Elie *et al.*, 2010).

Biparental incubation represents a specific situation where communication between incubating and non-incubating parent is necessary. Both parents are mostly involved in the communication process because interactive communication between the partners can shorten the exchange gaps (i.e., the intervals between one parent leaves the nest and the partner sits on the clutch) which reduces the risks of depredation or cooling the eggs (Ball & Silver, 1983; Boucaud *et al.*, 2016). Therefore, the parents need to negotiate about timing of their exchange at the nest. However, it largely depends on where the non-incubating parent spends its off-duty time and who initiates the exchange at the nest. If non-incubating parent is far from the nest, effective communication between partners is almost excluded. Many seabirds make long foraging trips whereas the incubating partners must wait until the partner's return (Weimerskirch, 1995; Guinet *et al.*, 1997; Jakubas *et al.*, 2018). Thus, the termination of the incubation bout is determined simply by the physical presence of the returning partner (Boucaud *et al.*, 2016). On the other hand, the species where the parent remains within the territory near the nest, the incubating parent may signalize the need for an exchange on the nest. This seems to be done often by the leaving the nest, thus visually showing the need to be exchanged (Deeming, 2002; **Chapter 1**). In reality, it may be a more complex but still unexplored process with clearly defined rules in different species to ensure smooth cooperation of partners during breeding process.

In addition to visual signals, vocalization plays an important role in communication between bird partners. Male vocalization, and particularly song, has been frequently studied in birds and especially in passerines (Mikula *et al.*, 2021). Song in passerines is highly conspicuous and shows a great variability across species. It plays an important role in the life of birds during courtship, in territory defence and undoubtedly also in communication in other stages of reproduction, for example in warning of danger (Kroodsma & Byers, 1991; Leavesley & Magrath, 2005; Riebel, 2016). It has been proven that the male song repertoire in passerines is significantly correlated with the size of song control area of the brain (HVC) (Székely *et al.*, 1996, Pfaff *et al.*, 2007). In contrast, much less is known about female vocalization (Gorissen & Eens, 2005; Riebel *et al.*, 2005; Riebel, 2016) and particularly its role in sharing and synchronizing parental care. Specifically, a little is known about the role of vocalization in the communication between breeding partners to ensure their synchronization during incubation process in the system with prevailing female incubation care where males tend to be less willing to incubate (e.g., in polygynous species). In these species, the males may be forced more urgently by females to help to care for the clutch. In addition, if non-incubating individuals are present within the visual as well as acoustic range of incubating partner, the vocal signalling combined with a visual one can gain considerable importance (**Chapter 1**).

Cooperation of partners in nest defence

The role of predators in forming the breeding behaviour of birds is always crucial. Predators affect reproductive success and are responsible for the majority of nest failures (Ricklefs, 1969). It has been shown that predation pressure influence nest site selection (Martin, 1993), optimal clutch size (Martin, 1995), and many aspects of parental behaviour (Martin *et al.*, 2000; Ghalambor & Martin, 2002). This is why the birds have developed many adaptations including passive or active behavioural strategies to reduce the probability of nest predation (Larsen *et al.*, 1996). In any case, especially the parents of more vulnerable species (e.g., smaller or non-defending species) must behave discreetly at the nest and reduce the conspicuousness to minimize risk of nest predation. One way to achieve inconspicuous behaviour is for the parents to synchronize their movements and vocalization nearby the nest (Smith *et al.*, 2012; **Chapter 1, 3**).

When the incubating parent detects an approaching predator, it must quickly decide how to react. Parents adapted to the least risky passive strategy will try to leave the nest unnoticed, which not only reduces their risk of injury, but may also ensure that the predator does not register the presence of the nest at all (Smith & Edwards, 2018). In some species, this strategy is further strengthened with perfect camouflage and crypsis of the incubating parent on the nest located in structurally more diverse vegetation (Troscianko *et al.*, 2016). However, many other species use more active and conspicuous strategies in defence of their nests. One strategy with highly variable behavioural expression is distraction display. Through this strategy, the parent attempts to divert the predator's attention away from the nest or offspring to supposedly easy prey, thereby reducing the risk of nest or chicks detection (Gochfeld, 1984; Humphreys & Ruxton, 2020). Frequently performed distraction display include injury-feigning, crouched running, mimicking a rodent ("rodent run") and several others (Humphreys & Ruxton, 2020). By performing these displays, parents put themselves in a risky situation that can have fatal consequences. However, predators can learn to associate the distractive behaviours with the presence of a nest or offspring (Sonerud, 1988), so in some situations the use of distraction display may be counterproductive. Passive or distractive strategies are more frequent in uniparental species with smaller bodies because these birds usually pose no risk to predators (Larsen *et al.*, 1996), however, this behaviour is also known in biparentally breeding species of larger size such as plovers or skuas (Humphreys & Ruxton, 2020).

In addition to less prominent defence strategies such as hiding and distraction display, many birds respond aggressively toward the present predator. Aggression is expressed through direct physical attacks and is mostly used when defending individuals pose a threat to predators. This is allowed by a larger body size, by a shared defence of the parents or by a cooperation with other conspecifics (Larsen, 1991; Larsen *et al.*, 1996; **Chapter 2**). Physical attacks are energy-demanding form of active defence (Curio, 1978; Caro, 2005) and are always very risky. Parental aggression may vary with respect to the predator species and often has been more intense in advanced incubation stage or when predator approaches closer to nest (Brunton, 1990).

In addition to some other aspects of interspecific variability, there are considered differences in aggressiveness between temperate and tropical bird species due to different dynamic of hormonal levels (Hau *et al.*, 2000;

Goymann *et al*., 2004; Stutchbury & Morton, 2022). Tropical birds tend to have lower testosterone levels on average during the prolonged breeding season (Soma, 2006), which may mitigate the long-term negative effects of stress hormones on the physiology of the organism (Schoech *et al*., 2011; Blas, 2015). In contrast, temperate species have rather unimodal pattern of testosterone level with a peak (higher concentration) in the optimum period of shorter breeding season. Thus, temperate species are more likely to exhibit more aggressive nest defence behaviour in their shorter breeding period (Hirschenhauser *et al*., 2003; Stutchbury & Morton, 2008). Therefore, tropical species could be generally less aggressive than temperate species in the nest defence because they more effectively spread investments in aggressiveness over a longer breeding season (Stutchbury & Morton, 2022). In connection with a lower level of testosterone in subtropical males, the sexes (both parents) could therefore be more similar in aggressive behaviour than in temperate species, where the sex (usually male) with a higher level of testosterone tends to be more aggressive. However, detailed studies on the antipredatory tactics of biparentally incubating species living in low latitudes are relatively rare, especially experimental studies allowing a good comparison between the responses of both sexes and in regard of the response to different predator species (**Chapter 2**).

Trade-offs in self-maintenance

Self-maintenance behaviour is an integral part of life for most mammals and birds. Sleep is important component of self-maintenance behaviour that is necessary for proper function of the organism (Siegel, 2003). All animals need to rest or sleep because sleep saves energy and has a regenerative function for the brain (Cirelli, 2005). Birds also devote a certain amount of time to self-maintenance behaviour such as feather preening, bathing, anting, dusting, allopreening and others (Bush & Clayton, 2018). Main functions of these activities are body care, prevention or defence against external parasites and maintaining a social relationship (Bush *et al*., 2010; Kenny *et al*., 2017). Long-term unsatisfied these basic needs may have lethal consequences (Cirelli & Tononi, 2008).

The problem facing a bird when sleeping is the increased risk of predation as the bird is less alert to surroundings and therefore more vulnerable. Birds can eliminate this risk in several ways. They can change their daily routine to avoid the risk of predation. For example, the Blue Petrel (*Halobaena caerulea*) has adapted to a nocturnal life on its breeding grounds, as it is very vulnerable to predators during the day or by moonlight (Mougeot & Bretagnolle, 2000). Birds may also consider the safety of a sleeping place. Cavity-nesting birds often use cavities for resting because they are a safer choice than open canopies, especially at night when nocturnal predators are more active (Drent, 1987). Finding a safe place to sleep is important especially for monophasic sleepers who sleep once a day but for longer time (Amlaner & Ball, 1983). Several studies have shown that the degree of vigilance depends on group size and position within the group (Lima, 1995; Roberts, 1996; Rattenborg *et al*., 1999b). In general, individuals at the edge of the group tend to be more vigilant because they are at greater risk than individuals near the centre. The advantage of birds is that they can control how they sleep as they may involve either one or both brain hemispheres. In extreme cases, birds can completely avoid sleep during the reproduction period (Rattenborg *et al*., 1999b; Lesku *et al*., 2012). If the birds feel safe, they can sleep with both hemispheres simultaneously. However, in a dangerous situation or when the bird is on the edge of the group, it can use less effective but more vigilant unihemispheric slow-wave sleep (Rattenborg *et al*., 1999a). This type of sleep allows the birds to partially control their surroundings and possibly spot an approaching predator (Rattenborg *et al*., 1999a; Rattenborg *et al*., 1999b). The situation is similar in the nest, where the bird has to take extra care not only of itself but also of the incubated clutch.

Predation risk does not only affect sleep, but also other behaviours such as foraging or preening. It is always a trade-off between vigilance and other activities. Compared to sleeping, the timing of preening is not so directly influenced by the place of performance. Although preening is a time-consuming activity, it is usually carried out in short intervals at any time of the day or night. Nevertheless, birds tend to reduce the movement associated with preening when the risk of predation is high. For example, an experiment with ducks showed that artificially increased disturbance associated with higher predation risk reduced the time devoted to preening (Zimmer *et al*., 2011). Minimizing movement may reduce the probability of detection and thus the risk of predation (Lima & Dill, 1990, Smith *et al*., 2012). This is especially important during incubation. If the bird performs preening during incubation, it does not only draw attention to itself but also to the presence of the nest.

Environmental events such as predator activity are changing throughout the day and season, so the costs of self-maintenance behaviour will also vary in time (Piersma & Van Gils, 2011) and the birds will tend to respect this rhythm (**Chapter 3**).

During parental care, the parents have limited time available for their own needs because the time devoted to one activity is always at the expense of another activity. Thus, the parent must decide how best to divide the time between conflicting demands. In addition, the bird must consider how much time to devote to each self-maintenance behaviour, when there is an appropriate time for these activities, and where to perform them. In this respect, biparental species have an advantage over uniparental species because both partners share parental duties. Thus, the off-duty parent could use free time for self-maintenance. A detailed description of the Semipalmated Sandpipers' (*Calidris pusilla*) off-nest behaviour showed that individuals spend most of their free time feeding and remaining time resting and preening (Bulla *et al.*, 2015). However, such an approach may work well in species that provide parental care rather equally and the free time of both sexes is more balanced. It is much fewer studied, how the issue of division of activities is solved by the species in which the contribution of one sex varies considerably in some aspects of parental care and in which the more caring parent is consequently forced to carry out self-maintenance even during parental care (incubation). In these species, the reduced (male) care may force the more incubating sex (females) to carry out their self-maintenance much more on the nest compared with individuals (females) with higher partner's (male) care, but probably with limitations given the risks of predation. In this context, in the territorial species with biparental care, where the non-incubating parent stays near the nest and can thus inform the incubating mate of impending danger, it may be interesting to see if the incubating parent can afford some activity on the nest more by relying on the mate's proximity. These questions have not yet been addressed and especially nothing is known in detail for openly and biparentally ground-nesting waders of a temperate zone (**Chapter 3**).

The role of partners fidelity

Despite the high investment in parental care, birds can breed several times in their life, either within one year or over many years (Griffith, 2019). The possibility of multiple breeding is therefore closely related to the decision of mate choice. Birds may form pair bonds for one breeding attempt or for the entire breeding season, but many species form long-term bonds lasting several years or even a lifetime (Black, 1996; Black, 2001). In addition, some pairs maintain continuous partnerships throughout the year even in the non-breeding season (Black, 2001; McCowan *et al.*, 2015). In any case, each partnership can be terminated either involuntarily by death or voluntarily by divorce i.e., both individuals stay alive, but at least one of them starts breeding with a new partner (Black, 1996; Jeschke & Kokko, 2008). Preferences for mate fidelity or divorce depend on the costs and benefits of each alternative, which is related to the life history of the species (Choudhury, 1995) and additionally influenced by the environment (Kosztolányi *et al.*, 2009).

Why many bird species repeatedly breed with the same partner? One possible explanation is that breeding performance (e.g., laying date, clutch size, hatching success, chick survival etc.) is positively related to the longevity of the pair bond and increase individual fitness (Bradley *et al.*, 1990; Fowler, 1995; Sánchez-Macouzet *et al.*, 2014). Furthermore, shared experiences and interactions between partners lead to better cooperation and coordination during parental care (Van De Pol *et al.*, 2006; Griffith, 2019). Long-lasting pairs can better manage nest sites, defend against competitors or predators and they may provide extended parental care to their offspring (Black, 2001; Naves *et al.*, 2007). However, only species with low mortality rates may afford repeated interactions between mates. Short-lived species change the partners more often because they have less chance that their previous partner is still alive before a new breeding attempt, and it is not profitable for them to wait too long (Botero & Rubenstein, 2012). Therefore, higher levels of cooperation and lower divorce rates are preferred especially by long-lived species such as geese, swans and albatrosses, which breed repeatedly with same partner for several years or for a lifetime (Black, 1996; Rees *et al.*, 1996). Mate fidelity is also positively correlated with breeding site fidelity. Remating with the same partner at a known breeding ground brings the advantage of earlier egg laying because individuals do not waste their time with looking for a new partner and forming new bond (Lifjeld & Slagsvold, 1988; Real, 1990; Sánchez-Macouzet *et al.*, 2014). However, there is evidence that the partner´s fidelity is not always beneficial. The reproductive output of the pair may increase in the first years but not for later so that such partnership may be not advantageous from a long-term perspective, as found e.g., in the Eurasian Oystercatcher (*Haematopus ostralegus*). Specifically, long lasting pairs of oystercatchers had a lower reproductive output after ~7 years of pair bonding than did newly formed pairs (Van De Pol *et al*., 2006).

There are two ways how to solve the unsatisfactory partnerships: either divorce or copulate with extra-pair mates (Choudhury, 1995; Botero & Rubenstein, 2012). Thus, divorce is a strategic decision, which may improve individual's fitness and bring additional benefits. By divorcing, the individual can obtain a partner of higher quality, more appropriate territory, or can produce genetically diverse offspring (Choudhury, 1995). All these benefits may potentially improve the fitness of the divorcing bird. In particular, unsuccessful breeding is the most common cause of divorce in birds (Ens *et al*., 1993; Dubois & Cézilly, 2002). Usually, it is the female, who leaves the territory and searches for another partner, as this is a way to increase the breeding success and individual fitness (Dhondt & Adriaensen, 1994; Dubois & Cézilly, 2002; Culina *et al*., 2015). Another reason for divorce may be an attempt to speed up breeding and thus produce more clutches within a season. Females of Kentish Plover (*Charadrius alexandrinus*) leave their mates after hatching of chicks and immediately initiates another clutch with a new partner to produce as many chicks as possible. However, the decision to leave the partner depends on availability of potential mates in the population (Ens *et al.*, 1993; Choudhury, 1995).

High densities of breeding birds occur in colonies. In colonies, it is easier to assess qualities of neighbouring individuals and there is a better chance of getting a new partner. Thus, higher divorce rates would be positively associated with high degree of coloniality (Dubois *et al*., 1998). However, searching for a new partner and associated change of the breeding site always involve some risks. The most common risks include loss of the previous partner and territory status (Choudhury, 1995; McNamara & Forslund, 1996). Moreover, courtship is a costly activity that can lead to an increased risk of injury (Real, 1990). These risks are stronger if the individual decides to divorce within the season or if the breeding season is too short (Choudhury, 1995; Culina & Brouwer, 2022). The short breeding season does not provide enough time to find a new mate, so mate fidelity across years is preferred strategy in short season environments (Green *et al*., 1977; Saalfeld & Lanctot, 2015).

Thus, latitude and environmental severity may play a significant role in mate fidelity and divorcing rates among birds, but most studies to date have been conducted in short-seasonal temperate or Arctic regions (Sandercock *et al*., 2000). In contrast, significantly fewer studies come from long-seasonal low latitudes, especially from the challenging environment of hot deserts (Kosztolányi *et al*., 2009). In hot environment, especially the incubation care of both partners is desirable, but a longer season also offers a reason for an increased divorce rate, all the more if there were enough potential (non-breeding) partners in the population. However, it has never been properly shown how partnership longevity is resolved in bird species that live in this demanding hot environment (requiring biparental incubation), with enough potential partners available, and with a long breeding season that allows repeated partner changes during the year as well as between years (**Chapter 4**).

Charadriiformes: comparison of two key groups

Shorebirds form a large order of birds distributed over the globe from high Arctic in the north through the equatorial tropics to Antarctica in the south (Del Hoyo *et al*., 1996; Székely, 2019). They possess a wide range of migratory, foraging, mating, and breeding strategies and are therefore a popular group for revealing the drivers and mechanisms of life histories diversification in birds (Colwell, 2010; Székely, 2019).

Two most numerous groups (clades) of shorebirds are Scolopaci and Charadrii, which have diametrically different life histories that reflect their global distribution and environments in which they preferably breed (Gibson, 2010). Scolopacids have the core of breeding distribution from boreal forests to high Arctic in the north hemisphere from where they undertake usually long-distance migration to southerly wintering grounds (Del Hoyo *et al*., 1996; Delany *et al*., 2009). For example, Bar-tailed Godwit (*Limosa lapponica*) performs with almost 11,000 km long trip, which is the longest known non-stop flight to date among all terrestrial birds (Hedenström, 2010). In contrast, Charadriids are more widespread in lower latitudes in tropics and subtropics, where they lack the need for long-distance migration. Instead, many of them tend to be year-round resident with only short-term or nomadic movements (Conklin, 2019).

There are many other differences between these two groups. Scolopacids mainly use the tactile bodies at the tip of the beak to find food (Sustaita *et al.*, 2018). They have a longer and narrow bill, but its shape and length are highly variable among species. For example, long bills of Eurasian Woodcock (*Scolopax rusticola*) and Eurasian Curlew (*Numenius arquata*) with specific sensitive nerve ending helps to probe deep in soft (muddy) ground. On the other hand, most Charadriids use a completely different strategy. They rely more on sight to hunt insects dwelling on the ground surface and, depending on habitat structure, they usually apply run-and-stop method rather than probing the ground continuously. Many Charadriids use shaking the legs or tapping the substrate, presumably to detect and scare the prey hidden beneath the surface (Colwell *et al.*, 2019). This different foraging strategy reflects the most inhabited environment. Whereas Scolopacids prefer a more hidden life in closed habitats (high tussock tundra, scrubs, wet forests, grasslands with taller vegetation), Charadriids breed rather open terrains (low mossy tundra, open wetlands, stony beaches, lake margins and farmland), although, of course, there are large overlaps between species of these clades (Colwell *et al.*, 2019). However, the general differences in their foraging and breeding habitats mirrors their defending and breeding strategies including parental behaviours.

Most shorebirds including Scolopacids as well as Charadriids breed on the ground where they dig a small hole that they may or may not line with an additional material (grass, leaves, small stones, shells etc). Only three Scolopacids, i.e., Green Sandpiper (*Tringa ochropus),* Solitary sandpiper (*Tringa solitaria*) and Nordmann’s Greenshank (*Tringa guttifer*), but no Charadriid species are tree-nesting shorebirds (Oring, 1973; Žďárek, 1999; Houston, 2012; Maslovsky *et al.*, 2023). Nests on the ground are much more vulnerable to predators (Angelstam, 1986) and shorebirds have therefore developed various antipredation strategies including inconspicuous behaviour and elaborated communication between the biparentally incubating partners in taking exchanges at the nest. However, in accordance with their preferred habitats, Scolopacids and Charadriids may differ in these tactics and behaviours. During the breeding season, Scolopacids tend to hide and breed secretly in moist habitats, where they prefer mosaic grasslands with taller vegetation (**Figure 1A**). They rely more on body crypsis during incubation (**Figure 1B**) and leave the nest immediately under threat from a predator. Furthermore, Bulla *et al.* (2016) showed that Scolopacids have longer incubation bouts and that the partners exchange on the nest less frequently than Charadriids to limit activity near the nests as much as possible. Communication between the partners during incubation period is generally not well known but has probably a wide repertoire across species (Bulla *et al.*, 2015, Boucaud *et al.*, 2016; **Chapter 1**). When they take turns at the nest, hidden in confusing vegetation, they probably inform each other mainly by silent voice (Bulla *et al.*, 2015). However, for example, in a Green Sandpiper parent who flies to replace the partner on the nest, this call is loud, but given over a long distance, i.e., without alert the nest location, while the incubating partner is ready in time for fast exchange (Žďárek, 1999). The variability in this behaviour is therefore large, even within a group of related species. However, virtually nothing is known about these tactics and their variation in the clade of Charadriids.

Charadriids breed more openly in low and sparse grass or on bare ground (**Figure 1C**), usually very close to water. The Northern Lapwing (*Vanellus vanellus*) and the Little-ringed Plover (*Charadrius dubius*) also use agricultural landscapes in Central Europe. They rely more on sight and cryptic egg coloration while less on own body crypsis and therefore must leave the nest usually at a greater distance in case of imminent danger. Correspondingly, they move more often and more conspicuously near the nests. They have shorter incubation bouts and the partners exchange on the nest more frequently and more visibly then Scolopacids (Bulla *et al.*, 2016). The communication of biparentally incubating Charadriids on breeding grounds nearby nests can therefore differ from Scolopacids with respect to the good visibility of breeding habitat and frequent exchanges on the nest. However, we know much less about the communication between the partners in these species due to the main distribution range of most species in the little-explored areas of lower latitudes. Similar to Scolopacids, some Charadriid species prefer to fly safely away from the nest in danger situations (smaller species) or use distraction display (Humphreys & Ruxton, 2020). Large-body Charadriids such as lapwings actively repel approaching predators. However, little we know about the division of duties and roles between the partners of different Charadriid species during the events of nest defence.

Figure 1. (A) Pectoral Sandpiper (*Calidris melanotos*) sitting on the nest hidden in tall grass tundra in Barrow Alaska; (B) nest of Eurasian Woodcock with hiddenly incubating female in dense cover of sedges (*Carex* sp.) and bog billbery (*Vaccinium uliginosum*) in the Krušné hory Mts, North Bohemia; (C) visibly incubating Kentish Plover in open saltmarsh in Ras Al Khor Wildlife Sanctuary, Dubai. Photo Miroslav Šálek.

Scolopacids show higher diversity of mating systems compared with Charadriids, but the care of offspring is frequently uniparental (Reynolds & Székely, 1997). Many species are monogamous but simultaneous polygyny was also recorded (Miskelly, 1989). Phalaropes (*Phalaropus* spp.) and Spotted Sandpiper (*Actitis macularia*) are polyandrous with reversal sex roles (Lank *et al*., 2002). This suborder also includes several lekking species such as Ruff (*Philomachus pugnax*), Pectoral Sandpiper (*Calidris melanotos*) or Great Snipe (*Gallinago media*). Lekking system with no parental care of males may occur in these species because hidden females are able to care for their offspring alone already from the beginning of incubation (Kokko & Jennions, 2012; Kempenaers, 2022). In addition, multiple mating system may occur within a single population of the same species. For example, the mating system in the Sanderling (*Calidris alba*) is characterized as socially monogamous and both partners share incubation duties, however, a detailed study of Reneerkens *et al*. (2014) shows a high proportion of uniparental incubation within the same population and at least several cases of polygamy. In contrast, monogamy and biparental care of offspring strongly prevail in Charadriids, although polygamy may occasionally occur in some species. For example, Eurasian Dotterel (*Charadrius morinellus*) is sequentially polyandrous. Females of Mountain Plover (*Charadrius montanus*) lay two subsequent clutches, of which the first is cared by male while the second by female. It indicates that mating system in shorebirds may be flexible and more complex in many species. Thus, also the associated feature, the mate fidelity, can be highly variable among shorebirds and may generally differ between Scolopacids and

Charadriids. Most of the studied shorebird species showed mate fidelity but most of the species studied to date were Scolopacids from higher latitudes where mate fidelity is considered crucial due to limitations given by the harsh climate and short breeding season (Pierce & Lifjeld, 1998). However, this does not allow consideration of other possible aspects that can be reflected in Charadriids (lapwings) living in lower latitudes with moderate climate and longer breeding season.

The lapwings of genus Vanellus

The genus *Vanellus* (suborder Charadrii) consist of 24 species including the almost certainly extinct Javan Lapwing (*V. macropterus*) which has not been seen since 1940 (but I still hope that it lives happily hidden somewhere in Java, Timor or Sumatra). Lapwings have cosmopolitan distribution excluding Nearctic region, with the core of their distribution in the Afrotropical realm (11 species). Four species occur in the Palaearctic, and three in the Indomalayan region. Neotropics are inhabited with three species and, finally, Australasian realm has two representatives (Cramp *et al.*, 1983; Howard & Moore, 1991; Del Hoyo *et al.*, 1996; Shrubb, 2010). Most lapwings live sedentarily or do only short seasonal movements. Only seven species are migratory (Shrubb, 2010) and one species is nomadic, depending on foraging conditions. In my thesis, I focus on two species, the Palearctic Northern Lapwing and the Indo-Malayan Red-wattled Lapwing (*V. indicus*). While there is no subspecies differentiation in the Northern Lapwing, the Red-wattled Lapwing consists of four subspecies (Del Hoyo *et al.*, 1996).

These long-legged princesses are typical for their shrill voice but also for fantastic appearance. Lapwings are medium-sized and brightly coloured, with specific morphological traits such as red or yellow wattles (11 species), wing spurs (15 species) and crest (3 species), but each species has a unique ornamentation. Specific morphological traits are absent only in the White-tailed Lapwing (*V. leucurus*), Senegal L. (*V. lugubris*), Crowned L. (*V. coronatus*), Sociable L. (*V. gregarious*) and Black-winged Lapwing (*V. melanopterus*). The most strikingly coloured is the Sociable Lapwing, which is quite unique among lapwings because it is the only one without red or yellow legs, bill, coloured iris or eye ring, wattle, or spur. Generally, lapwings have not a pronounced sexual dimorphism, except for the Northern Lapwing, in which the size of the crest and expressiveness of the head and throat pattern distinguishes males from females. Apparently, there are minor sex differences in other species as well (for example longer wing and carpal spur in males, females may be less intensely coloured than males etc.), but the possible role of coloration and other ornamentation has not been explored so far.

Lapwings are known as generally monogamous except for partially polygynous Northern Lapwing (Walter, 1982; Parish *et al.*, 1997b; Šálek, 2005). One explanation for polygamy in this species is higher potential for colonial or semi-colonial breeding in areas with higher population densities (Kis, 2003). In this case, there is less pressure on both partners to protect individual nests than in solitary breeders, because predation is shared by a larger number of birds (Larsen, 1991). Parental care in lapwings include antipredatory protection, brooding and guarding of chicks, and food showing (at least in the case of the African Crowned Lapwing; Shrubb, 2010). In addition, all activities are accompanied with demanding parental vigilance and frequent warnings. Partners therefore need to share most of the parental duties and had to develop tactics for mutual communication and division of parental roles. In general, raising offspring is time and energy consuming and depends on the offspring number. It often requires a tight cooperation of both parents and may play an important role in evolution of mating systems (Larsen, 1991). The high cost of parental behaviour may also lead to cooperative breeding, which was described, for example, in the Masked *V. miles* (Lees *et al.*, 2013) and Southern Lapwing *V. chilensis* (Cerboncini *et al.*, 2020). The offspring of the Southern Lapwing from previous nests share with the parents not only territory defence but also incubation, and chick rearing. Double brooding (production of a new clutch after hatching of chicks from previous clutch) has also been documented in lapwings, e.g., in Northern Lapwing (Parish *et al.*, 1997a) and in Red-wattled Lapwing (our observation). Double brooding is generally mentioned in other lapwing species as well, but no details are known (Del Hoyo *et al.*, 1996).

Lapwings usually lay three to four cryptic eggs on the ground (**Figure 2**). The Northern Lapwing usually lays one clutch per (short) breeding season and may only replace the clutch if the eggs or chicks fail. The incubation period in lapwings is relatively long (27-30 days), but detailed studies concerning the length of the incubation process are rare (Dann, 1981; Galbraith, 1988; Sládeček *et al.*, 2019; Elhassan *et al.*, 2021). The partners change on the nest quite often, which is one of the facts that show the need for elaborate communication between them.

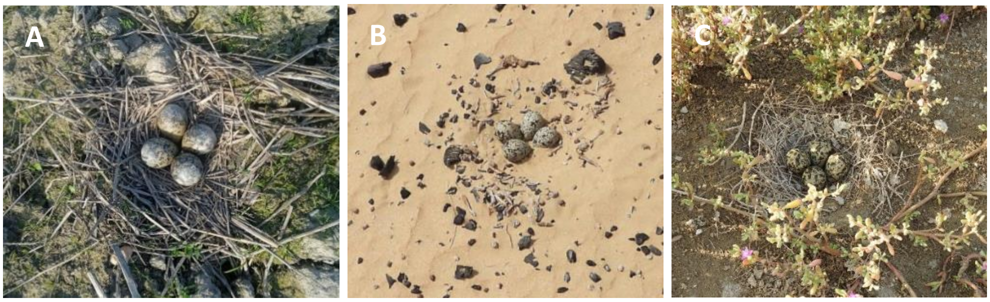

Figure 2. The nests of (A) Northern Lapwing, (B) Red-wattled Lapwing, (C) White-tailed Lapwing. Photo Miroslav Šálek (A, B) and Lucie Pešková (C).

Lapwings may breed in loose colonies, especially the Northern Lapwing and Sociable Lapwing (Šálek & Cepáková, 2006; Kamp *et al*., 2009). Since they are quite conspicuous, they are known for their aggressive behaviour. Their wings are wider and more rounded than in other Charadriids, allowing them to manoeuvre quickly in flight. Aggressive displays may also be related to the prevailing monogamy, as monogamous species tend to be more aggressive than polygamous ones (Larsen, 1991). Mobbing of potential enemies has been observed in several species including Northern Lapwing and Red-wattled Lapwing (Walters, 1979; Elliot, 1985; Rose, 2002; Delfino & Carlos, 2022; Brown & Brown, 2004; Mishra & Kumar, 2022). However, the extent to which the partners and the neighbours cooperate with each other in defending the nest or offspring against predators or who defends the nest more, whether male or female, remains unclear in most lapwing species. In the temperate Northern Lapwing, defending territory and defending offspring against predators is more in the role of the male (Kis *et al*., 2000), but what about other species of lapwings such as the subtropical, Red-wattled Lapwing? Subtropical and tropical lapwings may have different life histories related to the slow pace of life (Wikelski *et al*., 2003), which may be reflected in their behaviour and aggression.

In sum, even though the temperate Northern Lapwing is a well-studied species, in many ways it does not have to represent other Charadriids or all other lapwing species living in subtropics or tropics. Although we know a lot about lapwings in general, there are still gaps in knowledge of specific details such as division of parental roles, cooperation between the partners during incubation, their communication during breeding period, defence against predators as well as partner´s fidelity. The under-exploration of these beautiful birds may be due to their current predominance in the tropics (Conklin, 2019), where they are difficult to study, which is a great pity.

Aims

The general aim of this thesis was to elucidate hitherto little-studied aspects of breeding behaviour in biparentally incubating lapwings of the genus *Vanellus*, a representative group of the suborder Charadrii, order shorebirds (Charadriiformes). Using continuous video recordings of incubating adults, experimental approach with stuffed predators and multi-year monitoring of individually marked parents, we focused on several behavioural aspects in two species, the temperate Northern Lapwing (**Chapter 1** and **3**) and the subtropical Red-wattled Lapwing (**Chapter 2** and **4**). We tried to find out the circumstances of the communication between the breeding partners during the incubation period and revealing whether the partners use specific signalling system to coordinate exchange on the nest to ensure a smooth incubation process (**Chapter 1**). As frequent occurrence of nest predators on breeding grounds of lapwings raises the need for mutual cooperation of birds during the breeding process, we addressed the forms of partners' cooperation in defending their nests from avian and mammalian predators (**Chapter 2**). With intensive incubation care, individuals may suffer from insufficient care for their own body. Therefore, we tried to evaluate whether the intensity of male cooperation with the female partner during incubation can be reflected in the self-maintenance activities performed on the nest during the incubation process and we discuss how it can affect the female fitness (**Chapter 3**). The mutual knowledge of the partners can influence both the quality of parental care and the level of cooperation between the partners. Thus, in the last part of the thesis we asked whether the lapwings belong rather to the more faithful species that enjoy the benefits of long-term partners' fidelity similar to Scolopacids studied in higher altitudes or prefer to strengthen the individual fitness by frequent partners' exchange at the cost of losing the experience gained with one long-term previous partner similar to Kentish Plover (**Chapter 4**).

Communication and cooperation during incubation

Specifically, the goals of **Chapter 1** were to find out whether vocalization combined with visual signalling in the Northern Lapwing may play a role in **communication between the partners to ensure synchronization during their incubation care**. First, we determined the events of partners' exchange during incubation process. Next, we analyzed what behaviour accompanied the parent's departure from the nest, i.e., whether the departing bird vocalizes immediately before leaving the nest and how it leaves the nest, i.e., by flight or walk. Subsequently, we were interested in the reaction of the social partner, i.e., whether and when it comes to sit on the clutch. A total of 63 nests were used for this analysis. Specifically, we tested whether **(a)** the exchange of partners is more likely to occur after the vocalization signal of the incubating parent, possibly reinforced by flight from the nest; **(b)** the vocalization signal shortens the time of partners exchange during incubation; **(c)** the incubation break will be longer whenever the off-duty parent will ignore the incubating parent's vocalization signal, as a result of a mismatch in the communication between the partners. We analyzed this separately for females and males assuming greater binding of females to their clutches. Because the proportion of male incubation effort in Northern Lapwing varies considerably among nests, we were able to examine how the male incubation effort follows the efficiency of female vocalization signals. This study allowed us to expand our knowledge about the mutual communication of bird partners during shared incubation care and about the importance of female signaling in a system of partial polygyny of a predominantly monogamous species.

Then, in **Chapter 2** we experimentally tested what behaviour use the parents of Red-wattled Lapwings in **nest defence against different predators and how the breeding partners share or divide their defending roles**. We used three stuffed models of predators posing different risks to the nest and to the adult (a cat dangerous to the nests and to adults, a raven dangerous to the nest, and a moorhen as a reference harmless model). We placed the stuffed models (in a random order) in alert position two meters in front of each nest and recorded the responses (on a semi-quantitative scale) of individually colour-ringed lapwing parents for 15 minutes. In addition, we recorded the number of other conspecifics present at the nest during the experiment. In total, the experiment we performed with all three stuffed models on 32 active nests. We were particularly interested **(a)** whether the Red-wattled Lapwings distinguish between different predator species; **(b)** which nest defence strategies they use; and **(c)** whether both parents participate in nest defence in a similar extent or whether males are more active like in the temperate Northern Lapwing (Kis *et al.*, 2000). Finally, we investigated **(d)** whether conspecifics in this socially living species will share nest defence against predators.

In **Chapter 3**, we analysed self-maintenance behaviour of incubating parents and a link of this behaviour with the diel pattern of predation risk and sex-unbalanced incubation care in Northern Lapwing. This species is a good model species in this respect. As females incubate much more than males in some nests, the system allowed us to examine whether **male contribution to incubation influences the females in their self-maintenance behaviour (sleep and preening) on the nest**. From continuous 24-hour video recordings, we extracted behaviours of nesting females at 55 nests and registered the time of predation events as well as the predator species. Specifically, we were interested **(a)** what is the timing distribution of nest predation events in our study population; **(b)** whether sleeping and preening follow a daily rhythm, and if so, **(c)** whether this rhythm is consistent (i.e., is potentially affected) with the daily rhythm of predation events (i.e., activity of predators). Finally, we focused on testing whether **(d)** sleeping and preening of females on the nest vary according to the male's contribution to incubation.

Fidelity or divorce: what is more profitable in the Arabian desert?

In **Chapter 4**, we chose the Red-wattled Lapwing as a model species to compare **fidelity and divorce rates in a socially monogamous species inhabiting low-latitudinal demanding environment** (hot Arabian desert). The population has a good opportunity to use both strategies. First, living in demanding environment requires a good coordination of biparental care and a tight cooperation of the partners (which supports preference for fidelity). Second, long breeding season and availability of non-breeding potential mates creates opportunities for mating with additional partners and multiple breeding (which supports preference for divorces). We asked **(a)** which strategy is more profitable (mate fidelity or divorce) in this population and tested **(b)** how mate fidelity or divorce affect breeding performance and success.

General discussion

This thesis has shed further light on hitherto lesser-known aspects of parental behaviour in birds, specifically in biparental shorebirds (lapwings) in which both partners share their responsibilities during reproduction. As much of the parental care is devoted to the incubation process, this dissertation was aimed at a deeper study of parental investment, cooperation and a comparison of the contribution of both sexes to the process during this important period in the birds' lives. The following discussion is centred on these key findings:

We found that Northern Lapwing females use both visual and vocal communication to ensure smooth exchanges on the nest with a mate during the incubation period **(Chapter 1)**. This scheme of communication has not been previously described and appears to have evolved in close association with the attributes such as mating system, breeding arrangement (i.e., on the ground in open habitat), home range size (which is relatively small in this species) as well as anti-predation tactics (to draw as little attention as possible to the location of the nest). Particular attributes, their role in the communication scheme and reasons for appearance are discussed.

Ground nests are exposed to a high risk of predation, so in addition to parental behaviour during the exchanges on the nest (**Chapter 1**), the parents have to deal with situations of imminent threat from a predator. We experimentally determined how lapwings react to avian and mammalian predators in nest defence (**Chapter 2**). While previous studies in the temperate Northern Lapwing have shown that the male has a preferential role in nest defence, we were the first to show that this role is shared equally by both sexes in subtropical lapwings. We further described the presence of conspecifics at the nest during its defence by parents and depending on the threatening predator species. We discuss these findings in the wider context of the range of defence strategies in shorebirds as well as the climate zone in which the populations were studied.

Further, we revealed that self-maintenance of incubation females is a necessary part of their behaviour on the nest, and that this behaviour is shaped by predation risk (**Chapter 3**). It may imply that insufficient male care in biparental species that prevents females from engaging in more of these activities outside the nest may have negative fitness consequences. Therefore, we discuss the variability of this behaviour in the context of existing knowledge on this topic in birds.

Finally, consistent with the need for partners to know each other in order to coordinate their parental duties during the demanding incubation period in a hot desert climate, we confirmed very strong partner fidelity in the Red-wattled Lapwing (**Chapter 4**). In the following discussion, we look for a rationale for this partner´s fidelity that goes beyond the previous explanations given so far for temperate species and the Arctic species, on which most studies to date have been conducted.

The importance of mutual communication to synchronize parental duties

Bird parents usually use acoustic communication to synchronize parental duties. We found that the incubating Northern Lapwings actively communicate with the off-duty partners and use both acoustic and visual signalling **(Chapter 1)**. Especially females often combined vocal and visual signals before leaving the nest. Probably just the vocal signals helped to improve the synchronisation of mate exchange on the nest, because the exchange gaps after female vocalization were shorter than those without vocalization. Moreover, when female vocalization was accompanied by flight departure, mate exchange was more likely to take place. However, if the female vocalized when she wanted to be exchanged and the male did not come to switch the female, the incubation breaks before the female returned to the nest were longer. This more complex communication may be the result of the evolution of polygamy in this lapwing species.

The Northern Lapwing female can negotiate with the male to some extent, but she usually has higher responsibility for incubation. We revealed that the exchanges of males by females occurred most often after the male quietly flew away from the nest and that female vocalization frequency did not correlate with male incubation effort. This complex behaviour, including sex differences during exchanges at the nest, suggests that Northern Lapwing female (but not males) are prepared to take responsibility for the care of the clutch at any time, whereas it is a matter of male individuality how he responds to the female's call to take turns at the nest.

It is possible that this is a more general feature of (at least partially) polygamous species (such as the Northern Lapwing), where females sometimes incubate the clutch exclusively (Sládeček *et al*., 2019), but it is not a general feature of all lapwings, because the subtropic Red-wattled Lapwing does not behave in this way (own unpublished data). Therefore, this difference might be more likely related to the harshness of the breeding environment than to the systematic affiliation. In temperate zone, females are able to care for the clutch themselves, whereas in hot climates where the Red-wattled Lapwing breeds, increased care by both parents can be expected (Vincze *et al*., 2017). It can be an interesting evolutionary feature of species spreading from the tropics and adapted to temperate conditions, to show an increasing tendency towards polygamy with a more complex communication system with new elements of negotiation between the parents during parental care. A similar phenomenon such as an increase of extra-pair paternity (EPP) from the tropics to the temperate zone (but without corresponding data on partner´s communication) has also been observed in passerine birds (Brouwer & Griffith, 2019). We do not assume such a complex communication mechanism in the subtropic Red-wattled Lapwing, since the partner´s attendance at the nest in this species is obligatory for successful reproduction and negotiation similar to that of the Northern Lapwing is not necessary. However, a detailed analysis of communication during the exchange of partners at Red-wattled Lapwing has not yet been carried out. This phenomenon thus requires further and deeper investigation.

There are also risks associated with acoustic communication near the nest because any activity or sound alerts predators to the presence of the nest (Martin *et al*. 2000, Smith *et al*. 2012). Bird parents must address the trade-off between staying undisclosed and communication with the partner to better coordinate the care. So, it depends on whether the incubating parent needs to rely on crypticity and better inconspicuousness (thus he vocalizes less) or can afford to be more prominent and more easily detectable. This is general rule among the birds, but it is probably unlikely the case of lapwings and similar species, which are usually always conspicuous in open habitat. Their size and aggressiveness put them in the category of species that do not need to be so inconspicuous and can therefore afford to use a more pronounced combination of vocal and visual signalling when carrying out parental duties, if necessary. It would be interesting to analyze across bird species whether the complexity of communication between breeding partners is correlated with predation risk and the ability to actively defend the progeny against predators.

Of course, acoustic communication is more pronounced in species where the off-duty parent stays close to the nest (in territory) and can therefore communicate with its mate (Smith *et al.* 1978; Hawkins, 1986; Glutz von Blotzheim, 1999). But how do birds communicate when their mates are far away from the nest and vocal range? There is only one detailed study by Bulla *et al.* (2022) who found that incubating Scolopacid shorebird, the Semipalmated Sandpiper, relying on nest crypsis to avoid nest predation and whose partner does not move near the nest at a time when they do not need to incubate eggs, performs rapid but acoustic mate exchanges during incubation. However, this is a slightly different communication strategy to that of the Northern Lapwing. The Semipalmated Sandpiper calls but does not fly away from the nest until the partner returns, so in this case the off-duty bird initiates the exchange on the nest. In contrast, it is probably the incubating parent in the Northern Lapwing, who initiates the exchange on the nest and leaves the nest even without the presence of its mate. There are also huge differences in the frequency of mate changes during incubation between these two species. While the Northern Lapwing partner´s exchanges at the nest are quite frequent (even several times a day), Semipalmated Sandpiper sits on the nest for 11 hours and changes with partner only twice a day. The preference for vocalisation in these sandpipers, which have a very different breeding system from lapwings, suggests that vocalization is a central tool for communication between partners during parental care, even in species that rely on crypsis and inconspicuousness at the nest. For species that can afford to be more conspicuous such as Northern Lapwing, visual signalling can then be effectively added.

Only few studies investigated how partner's communication affects the coordination of parental responsibilities. Kavelaars *et al.* (2019) found that the parents of Lesser Black-backed Gulls (*Larus fuscus*), which were more vocal, shared incubation duties more evenly. Negotiation process between partners was also showed in the Great Tit (*Parus major*). Great Tit males contributed to incubation indirectly by feeding the female on the nest. Boucaud *et al.* (2016) found that the incubating Great Tit female was able to signal her needs through specific calls and even modified the calling rate. Through this communication, the male adjusted feeding intervals and reduced or increased his visits at the nest. In this way, the parents may affect nest attentiveness and thus breeding success. However, the signals associated with calling at the nest may have also another reason. For example, females of Red-winged blackbirds

(*Agelaius phoeniceus*) use specific vocalisation when leaving the nest, which stimulates their mates to defend the nest more strongly (Yasukawa, 1989). Thus, acoustic communication appears to benefit females also by keeping males vigilant against nest predators. Acoustic communication is therefore a fundamental aspect of avian behaviour, which plays a crucial role in coordinating of parental duties and maintains successful reproduction. It seems that in urgent cases this acoustic signalling can be combined with visual signalling aimed at increased stimulation of the partner as we found in the polygamous Northern Lapwing.

Nest defence strategy of the Red-wattled lapwings

Lapwings actively defend their nests and have a number of morphological and behavioural predispositions for this strategy (described in the introduction). However, antipredatory strategies may vary between species within the genus *Vanellus*. For this reason, we used a controlled experiment to assess nest defence behaviour of subtropical Red-wattled lapwings towards different stuffed models (**Chapter 2**).

We found that the Red-wattled Lapwings distinguished between different types of predators (feral cat, Brown-Necked Raven, and Common Moorhen) and reacted to them differently. Parents reacted most aggressively to the cat and least to the harmless moorhen. The responses of breeding Northern Lapwings to stuffed models of the Carrion Crow, Great Black-backed Gull and Red fox varied similarly but with slight differences (Elliot, 1985). The Northern Lapwing directly attacked in most the egg predator (crow), which is, however, not consistent with the behaviour of Red-wattled lapwings. Surprisingly, in the case of the Red-wattled Lapwing, direct attacks were not frequent toward ANY of the stuffed models. Red-wattled Lapwings reacted to the presence of raven (egg predator) with a wide range of behaviours (from silent alerting on the ground to loud flying without attacks or with attacks) and parents' reactions were enhanced by presence of other conspecifics that could support these reactions (see below). Thus, if Northern lapwings have the opportunity to scare off avian predators, they behave more bravely, take more risks and attack the enemy. In contrast, Red-wattled lapwings do not take risks at all costs, preferring a more cautious, less demanding strategy. The responses of the lapwings to the mammalian predators were more similar to each other. The Northern Lapwing reacted more gently to the fox by flying around and trying to lure it away from the nest. The reaction of the Red-wattled Lapwing parents to the cat was the most aggressive compared with other models, however, intense alarming on the ground prevailed. In addition, during cat experiments the highest number of conspecific visitors were present, which did not increase the parents' reactions in this case. In contrast, in the Northern Lapwing, only one bird (probably a male) responded to the fox at a time, and conspecifics did not participate in the fox experiment (even though in the crow experiment, conspecifics participated in a shared defence). In sum, in both species the responses to mammalian predators that pose a risk to both the nest and the adults are more cautious, and lapwings tend to use a strategy of distraction from the nest rather than direct attacks toward the predator. Also, the Red-wattled lapwing was generally less aggressive than Northern Lapwing.

There are other studies that analyzed responses of lapwings to different stimuli. Unfortunately, these are always very specific stimuli that do not allow comparison between the species within the genus *Vanellus*. Cruz-Bernate (2020) found that the breeding pairs of Southern Lapwings reacted most strongly to the rider and less to the walking person and the tractor. Masked Lapwings reacted more aggressively to a person pushing a lawnmower than to a pedestrian. They also stayed closer to the nest in the presence of the lawnmower. In addition, eye stickers on the back of the neck of the pedestrian reduced mobbing behaviour, whereas the presence of eye stickers on the person pushing the lawnmower increased mobbing behaviour (Lees *et al.*, 2013). It is therefore clear that the degree of aggression shown by lapwings depends on the type of intruder and that they are able to adjust their anti-predatory behaviour to the danger posed by the intruder. In addition, there may be an effect of previous individual experiences, which is difficult to consider in most studies. In addition, aggressive reaction may vary between the sexes, which is a methodological problem in the field research especially in species without significant sexual dimorphism, where sexes are not individually marked.

In our experiment, individually marked males and females participated in nest defence to a similar extent, which is not consistent finding with other studies. In the temperate Northern Lapwing males defended the nest more intensively than females (Elliot, 1985; Kis *et al.*, 2000; Królikowska *et al.*, 2016). In addition, the intensity of defence behaviour increased in males over the course of the season (Kis *et al*., 2000). Thus, Northern Lapwing males invest more in aggressive behaviour than females. However, these results were only obtained for this temperate lapwing. It may indicate that temperate birds may afford to divide parental roles more and each partner can concentrate more on his part of parental care. On the other hand, the extremely hot environment of the Arabian desert may force Red-wattled Lapwings into more balanced parental care, where both partners must share equally all activities (including incubation and nest defence) to ensure successful breeding. There are few studies showing equal investment in male and female defence behaviour in tropical and subtropical biparental species (Fedy & Stutchbury, 2005; Stutchbury & Morton, 2022). However, in the Southern Lapwing, which breeds in the tropics (Colombia), males respond more aggressively than females (Cruz-Bernate, 2020). In the Red-wattled Lapwing, female responses varied over the course of our experiment. Female responses were initially milder and tended to intensify over the course of the experiment, approaching male levels. It suggests that differences between male and female behaviour need to be studied in more detail, for example that the length of the experiment must always be considered in analysis. However, for a more thorough analysis and comparability, it is necessary to standardise experiments across species and to observe marked individuals with known sex, which calls for further research.

Other factor that can influence the intensity of parental aggression is incubation stage. In many species, the intensity of nest defence usually increases as the incubation period progresses (Elliot, 1985; Knight & Temple, 1986; Viñuela *et al*., 1995; Brown & Brown, 2004). However, in our case, the incubation stage did not affect the strength of the parents' reaction to stuffed models. Similarly, in the study by Kis *et al.* (2000), the reactions of the Northern Lapwing were not related to the incubation stage. There are several reasons why the intensity of nest defence did not increase as the incubation period progressed in Red-winged Lapwings. One explanation is that nest defence may be related to the conspicuousness of eggs or chicks rather than to the incubation period; thus, if the conspicuousness of the nest and eggs does not change during incubation, there is no reason why the intensity of defence behaviour should increase (Dale *et al*., 1996; Kis *et al*., 2000). Secondly, the embryonic vocalisation itself (before the chick's hatch), which did not occur in our experiment, may provoke parents to be more aggressive (Kostoglou *et al*., 2021). Both aspects, the degree of nest concealment as well as the pre-hatching chick vocalisation, may or may not play a role in intensity of nest defence in lapwings and it would be useful to target further investigation in this direction.

Joint defence seems to be an important part of the lapwing's antipredatory strategy. Conspecific visitors we regularly observed at the nests of defending Red-wattled Lapwing parents in our experiments. Unfortunately, we did not record their reactions individually. However, individual marking allowed us to determine the origin of at least some conspecific visitors at the nests. Most of them were non-breeding birds but there appeared also parents from nearby active nests and chicks (of unknown parents) from previous years, which may have different reasons for sharing this nest defence events. First, non-breeders can behave mutualistic and share the defence of the young (Rabenold, 1985; Larsen & Moldsvor, 1992). Secondly, parents from nearby active nests can share the defence of nests reciprocally with a time lag between costs incurred and future benefits from shared protection of their nests (Rabenold, 1985; Clutton-Brock, 2009). Third, the offspring (helpers) from previous successful nests may be related to each other and can act in the role of kin cooperation. However, the motivations of conspecifics in joint defence may not be entirely positive, as non-breeding floaters may scout and subsequently acquire breeding territories that become available in the event of adult predation. Unraveling these alternatives is a topic for further research. Our more detailed insight into the composition of individuals in groups in places threatened by a predator indicates that social relations between individuals in these situations are not trivial or random.

It appears that the joint defence of lapwings may be related to the semi-colonial breeding that lapwings sometimes practise at higher densities. Indeed, nesting in loose aggregations increases the efficiency of the lapwings' responses to predators, which is beneficial to everyone involved (Elliot, 1985). Cooperation in joint defence is known not only in Red-wattled lapwing, but was observed also in Northern Lapwing, Crowned Lapwing, Southern Lapwing, Masked Lapwing and Yellow-wattled Lapwing (**Chapter 2**; Kis *et al.*, 2000; Brown & Brown, 2004; Maruyama *et al.*, 2010; Lees *et al.*, 2013, Chavan *et al.*, 2016; Kostoglou *et al.*, 2020; Cruz-Bernate, 2020; Cerboncini *et al.*, 2020). For each of these species, the motivations for co-occurrence during potential predation events may differ.

Furthermore, Masked Lapwing was described as cooperatively breeding species based on the joint defence of the territory and nests (Lees *et al*., 2013). This system assumes that some females in a social group do not regularly breed, but instead provide alloparental care to the offspring of breeding females (Koenig & Dickinson, 2004). The extent to which this is a cooperative breeding in the Masked Lapwing, however, is not entirely clear to me, as the authors only wrote about chicks from previous breeding taking part in territory defence. At the same time, these young can only be present passively at the nest without active participation in parental care. If the parents initiate a new clutch in same territory before the chicks from previous successful nest have fledged, the chicks will be present in the territory as part of a double brooding system without necessarily being involved in cooperative breeding. In my opinion, the presence of young at the nest in this case can only be a side effect of double brooding, unless the active care of the clutch (egg-laying, incubation) has been explicitly confirmed. The "our" Red-wattled Lapwing breeding system suggests rather the variant of double-brooding without subsequent cooperative breeding with the matured offspring. For this reason, future research needs to be focused more on the behaviour and motives of conspecifics involved in joint defence, or to observe more the behaviour of older chicks present in the territories of their repeatedly breeding parents.

Self-maintenance behaviour of incubating Northern Lapwing

Self-maintenance behaviour (sleeping, preening) has been poorly studied in animals living under natural conditions. The importance of these studies is underlined by the findings of Rattenborg *et al*. (2008), who noted that the sleep behaviour of captive animals differs significantly from that of wild animals. Therefore, in **Chapter 3**, we investigated the self-maintenance behaviour (sleep and feather preening) of incubating Northern Lapwing females under natural conditions.

During parental care, animals cannot sleep or preen themselves whenever they want, because they have to combine these activities with the needs of their offspring, and they also must take into account the risk of predation. Predation risk is a key ecological factor which may explain the timing of sleep and feather preening in birds (Curio, 2012; Stuber *et al*., 2014). In our study we revealed a strong daily rhythmicity in self-maintenance behaviour of incubating Northern Lapwing females. We found that the female sleep frequency had a bimodal rhythm with two peaks after sunrise and before sunset, whereas preening had a unimodal rhythm with one peak in the middle of day. In addition, we found that most predation events in our population occur at night, which also has an impact on self-maintenance rhythm of incubating females. Both activities (sleep and feather preening) were suppressed at night, when risk of predation is highest, particularly by mammalian predators.

Birds react to the increased risk of predation in completely different ways: they either sleep more or remain more alert. Reactions may vary depending on the vegetation cover in which individuals are found and also on the activity (e.g. incubation, foraging) they are currently engaged in (Lima, 1987; Amat & Masero, 2004). The reaction also certainly depends on the predator species. Stuber *et al*. (2014) demonstrated the plasticity of sleep behaviour in Great Tit (*Parus major*). They experimentally increased the risk of predation by the presence of the Tawny Owl *Strix aluco* (predator dangerous outside the nestbox), which caused Great Tits to spend more time sleeping inside the nest box. If there is a threat from avian predator, the Great Tits prefer to stay in the safety of the cavity and and it's more profitable for them to sleep. However, during the Pine Marten *Martes martes* experiment (a predator dangerous for birds inside the nestbox), Great Tits did not reduce the time spent sleeping inside the nestbox, but they did wake up less often during the night. Authors suggest that waking less frequently may reduce noise and movement inside the nestbox, making individuals less conspicuous at night, which may be an antipredator strategy (Curio, 2012; Ruxton, 2009). A similar study in which the risk of predation was artificially increased was carried out by Zimmer *et al*. (2011). They recorded the time spent on sleeping, preening, foraging and vigilance in three species of Anatidae: the Mallard (*Anas platyrhynchos*), the Common Teal (*Anas crecca*) and the Tufted Duck (*Aythya fuligula*). After the artificially increasing predation risk, they compared behaviour before and after the stressful situation. In all species, exposure to the increased predation risk caused a change in behaviour. While the time spent on preening and foraging decreased, the time spent on sleeping increased. These studies showed that birds are able to assess the level of predator threat and adjust their behaviour accordingly.

The lapwings nesting in open agricultural landscapes must be vigilant at night to escape mammalian predators in time, so they sleep minimally and do not draw attention to themselves by any movement (including preening).

Similarly, openly living Greater Flamingos (*Phoenicopterus roseus*) have been observed to increase their vigilance at night in response to increased mammalian predator activity (Beauchamp & McNeil, 2003). However, after and before sleepless nights, the Northen Lapwing females probably need to sleep, which may explain the two sleep peaks before and after sunset. Thus, the rhythmicity of the lapwing's self-maintenance behaviour may be adapted to nocturnal predators but also to diurnal predators, albeit with a different manifestation. Avian predators hunt mainly during the day and the peak of their activity is similar to the sleep peaks of an incubating female (Rutz, 2006; Roth & Lima, 2007). During sleep, the female is immobile, which may be an efficient antipredatory strategy against visually oriented avian predators during the day. Conversely, avian predator activity may be lower at midday, allowing females to use this time for preening. In addition, the female lapwing usually has a mate nearby to warn her if a predator is approaching, and the birds are generally able to mobilize quickly (Elliot, 1985; Kis et al., 2000). Also in this regard, the mutual cooperation of lapwing partners can play an important role for successful reproduction.

Beauchamp (2007) suggested that reduced nocturnal vigilance may result from unfavourable light conditions during which the bird has no chance of detecting an approaching predator anyway. This idea is supported by Javůrková *et al.* (2011), who focused on factors affecting sleep and vigilance in incubating Mallard. Incubating Mallard females were more vigilant during the day and the level of their vigilance decreased as the night progressed. This finding does not support the idea that females adjust their vigilance to the expected increased predation pressure at night, nor is it consistent with the behaviour of lapwing females. The authors suggest an alternative explanation, namely that mallards nesting in dense vegetation at night may orient themselves by hearing, rather than seeing, an approaching predator. They can therefore afford to be less vigilant at this critical time. However, lapwings nesting in open habitats may not be able to rely on acoustic cues. Thus, behaviour of birds nesting in boxes or on the ground in different vegetation conditions cannot be reliably comparable because the perception of predation risk is different. It is clear that birds need to sleep and preen themselves, but the way how they do this on the nest is strongly influenced not only by the predator community but also by the habitat in which they breed.

The rhythmicity of self-maintenance behaviour is influenced not only by ecological factors (predation risk), but also by environmental factors (such as latitude, daylength, season, weather conditions, ambient temperature) and, in biparental species, by the parental contribution of one sex (Amlaner & Ball, 1983; Dominguez, 2003; Steinmeyer *et al*., 2010). Our study provides first evidence that the male contribution to incubation is related to the self-maintenance behaviour of female partners. We assumed that the more the male helped with incubation, the less time the female spent sleeping and preening on the nest, as she would have enough time for these activities outside the nest. The male contribution to incubation affected the strength of the female self-maintenance rhythms, but in a different way than we thought. Females that were paired with more contributing males had a stronger sleep rhythm during day and night and a weaker preening rhythm. We explain this finding by the fact that if the female has a more supportive male during incubation, the male may also put more effort into other aspects of parental care, such as guarding the female, defending against predators, and warning in case of danger. The female can therefore afford to sleep more during incubation because she can rely more on the male. At the same time, the female has more time to herself because the male incubates more, so she can preen herself outside the nest. These explanations are speculative as we do not know how much time the females spend sleeping and preening when they are away from the nest. However, we know that females, especially those with less supportive males, spend a significant part of the day on the nest (around 18 hours), and that they must find time to forage, which may severely limit the time available for self-maintenance outside the nest.

Till death do us part

Despite many existing studies on avian mating systems, the reasons for, and advantages or disadvantages of, mate fidelity or divorce in birds are still unclear in some respects. In **Chapter 4**, we investigated mate fidelity and divorce rates in a subtropical population of Red-wattled Lapwings breeding sedentary in a hot desert environment. We found that the predominant strategy of most breeding pairs was strong mate fidelity within season as well as between-seasons. Out of 328 nesting attempts by individually marked Red-wattled lapwings, there were 41 cases of pair broke up. Of these, only nine divorces and two widowhoods were documented. In the remaining 30 cases, unfortunately, we do not know the cause of the pair break-up because one of the partners disappeared from the study area and we are therefore unable to say whether it was divorced or widowed.

Maintaining a long-term partnership over several breeding attempts is a useful strategy that has been recorded in at least 33 families belonging to 14 avian orders (Black, 1996). However, this strategy is surprising for a Red-wattled Lapwing living in an environment with a long season and a sufficient supply of potential mates (Elhassan *et al*., 2021). For example, a Snowy Plover (*Charadrius nivosus*) studied in Mexico that may attempt to breed with the same or a different partner several times per season (i.e., has the same options as our Red-wattled Lapwing) prefers divorce to mate fidelity (Halimubieke *et al*., 2019). Not only the Snowy Plover but also the Kentish Plover tends to divorce after successful breeding to maximize fitness and, conversely, tends to stay with the same partner after unsuccessful breeding (Kosztolányi *et al*., 2009; Halimubieke *et al*., 2020). This controversial finding is not consistent with the general assumption that divorces are more likely to be caused by lower reproductive success in the previous breeding attempt (Choudhury, 1995; Culina & Brouwer, 2022). In our study, however, the success or failure of previous breeding did not influence mate choice in the Red-wattled Lapwing. It is not uncommon for many species such as the Cassin's Auklet (*Ptycorhampus aleuticus*), White-chinned Petrel (*Procellaria aequinoctialis*), Kittiwake (*Rissa tridactyla*) and Red-tailed Tropicbird (*Phaethon rubricauda*) to show strong mate fidelity regardless of previous breeding success (Sydeman *et al*., 1996; Bried & Jouventin, 1999; Naves *et al*., 2006; Sommerfeld *et al*., 2015).

Further, the timing of the breeding failure and the length of the breeding season may play a role in the decision to stay or change partner in the next breeding attempt. Naves *et al*. (2006) found that late failed pairs of kittiwakes were more likely to stay together in next season than early failed pairs. If a pair fails to hatch eggs early in the breeding season, this may indicate a low-quality partner and may lead to divorce. In addition, at the beginning of the season, birds have a better chance of finding another mate or a change of territory. However, if a pair reaches the hatching stage and loses young towards the end of the breeding season, this does not necessarily lead to pair dissolution due to low reproductive quality of one of the partners. The reasons for breeding failure vary (due to predation, weather conditions, disturbance at the breeding site, etc.) and are not necessarily indicative of the reproductive quality of the pair.

In Red-wattled Lapwing, the benefits of mate fidelity very probably outweigh the costs of mate replacement, regardless of previous breeding success or failure, and despite a long season and thus ample time to change mates.

We expected that newly formed pairs would invest more in egg size, in line with the Coolidge effect (Beach & Jordan, 1956; Vance & Shackelford, 2022). Most authors claim that divorce cause improvement of next breeding performance (Choudhury, 1995; Dubois & Cézilly, 2002; Culina & Brouwer, 2022). However, we did not find any support for the assumption that the change of mate would lead to a larger first clutch or higher reproductive success in these pairs. It is unlikely that newly formed pairs of Red-wattled Lapwing would have larger first clutches or breed more successfully, as divorce was quite rare in our study population. Similarly, the breeding performance (timing of breeding, clutch and egg size) of e.g., the Western Sandpiper (*Calidris mauri*) and the Semipalmated Sandpiper has not changed with divorce because their divorce rate is low (Sandercock *et al*., 2000). Moreover, some authors have also failed to find evidence that breeding performance affects staying in a pair (Black, 1996; Murphy, 1996). More important factors affecting breeding performance may be the age and experience of both partners. Breeding performance tends to improve with age, but at least in some species it decreases with senescence (Daunt *et al*., 1999; Espie *et al*., 2000). Unfortunately, we do not know the exact age in Red-wattled Lapwings, so we cannot take this potentially important factor into account.

We found that faithful pairs started nesting non-significantly earlier than newly formed pairs. However, in an environment with a long breeding season, earlier breeding in the order of individual days may not be a crucial factor affecting breeding success. The short breeding season in temperate or Arctic regions limits the possibility of repeated breeding and it is preferable to breed as soon as possible (Perrins, 1970; Fowler, 1995). In contrast, long season in the tropics and subtropics allows multiple breeding and therefore a bit earlier start may not be influential. Moreover, in Dubai it may not be advantageous to start nesting early in March, because Marsh Harriers (*Circus aeruginosus*) are still wintering here at that time before their departure to their more northern breeding grounds. Harriers are frequent predators of bird nests on the ground (e.g., Opermanis, 2001), and their appearance in March can be a big risk for early nests. More important than the early start of breeding in this case may be the variability of food supply, which may change over the season, or perhaps the changing risk of predation within the season (Both, 2010; Kosztolányi *et al*., 2006; Sládeček *et al*., 2021). Conversely, it has been suggested that chicks of plovers hatched later in the season may grow faster than chicks hatched earlier in the season (Kosztolányi *et al*., 2009). However, this cannot be taken as a general rule acting across regions.

Slightly earlier initiation of breeding and egg size did not appear to be significant factors in the decision to remain faithful or change mates in Red-wattled lapwings. Furthermore, we expected the advantage of faithful pairs to consist in the total number of clutches per season, which would be higher for faithful pairs than for newly formed pairs. Due to the 'mate familiarity effect', one would expect better cooperation in parental care and higher reproductive success from faithful pairs, who could therefore afford to practice double brooding and increase their reproductive output (Fowler, 1995; Black, 1996; Ens *et al*., 1996; Sánchez-Macouzet *et al*., 2014). Indeed, we found a difference in the total number of breeding attempts during the season between faithful and newly formed pairs. While faithful pairs initiated two to four clutches per season, newly formed pairs usually nested only once per season. We also confirmed 15 cases of double brooding. In eight cases, the double brooding was performed by faithful pairs from the previous season, while no newly formed pair in the early season continued to nest with multiple attempts in the same season. However, in seven cases the status of the pair was unknown.

Decision makings about mate fidelity or mate changes across taxa are certainly influenced by some environmental conditions such as ambient temperature and precipitation (Halimubieke *et al*., 2020; Székely *et al*., 2023). For example, in Arctic birds that breed in harsh and cold environments with limited time to multiple nests, mate fidelity regularly prevails. Tropical and subtropical regions are referred as mild and stable environments providing more time for breeding and therefore mate exchange (Halimubieke *et al*., 2020), but I think that mild environment cannot be applied universally to the tropics and subtropics in this respect. Desert environment may represent a completely different weather extreme in the form of high ambient temperatures. In areas such as the deserts, where temperatures can achieve 40 °C or more and where not only eggs are at risk of overheating, but also parents often must shade the chicks (Kolešková *et al*., 2023), mate fidelity may be just as important as in Arctic. So, it is possible that the harsh conditions of the Arabian desert push Red-wattled lapwings to prefer high mate fidelity. If they change mates frequently, they would not be as good at parental care (incubation or chick care), would not be able to perform double brooding, and would be far less successful in total reproduction. Even in the Kentish Plovers studied near Abu Dhabi, which prefer divorce to mate fidelity, biparental care was more common than in other temperate populations (Kosztolányi *et al.*, 2009). This finding only highlights the fact that extreme environments may push birds to greater cooperation, which may or may not result in stronger mate fidelity.

Mate fidelity is often found closely related to high nest site fidelity (Cézilly *et al.*, 2000; Friedrich *et al.*, 2015; van Leeuwen & Jamieson, 2018; Seyer *et al.*, 2023). Gill & Stutchbury (2006) found that young Buff-breasted Wrens (*Thryothorus leucotis*) first find a mate and then start breeding near the parental territory. They do not change partners or territories, even if there is an opportunity to get a better territory at the site. This finding underlines the fact that new local breeders can assess the quality of mates and territories prior to nesting, based on parental experience. While floaters that are new to the breeding site first occupy any available territory, start nesting, and then evaluate the quality of the partner and the territory they have acquired, so they may change partners more often. Divorce is also more common among young birds in Buff-breasted Wren (Gill & Stutchbury, 2006). Sporadic cases of divorce in the Red-wattled Lapwing population may be caused by just such floaters. They are new at the breeding site, young, and thus inexperienced birds, who just recognise their potential mates and territories, while most already nesting birds are of local origin with the tactic to start breeding near the parental territory and to remain site- and partner- faithful.

Despite a number of possible explanations, we still do not know exactly why mate fidelity is so advantageous for Red-wattled lapwings and what the disadvantages of divorce are in this population. We think that the main reason for mate fidelity in this population is the opportunity for repeated breeding with the possibility of double brooding. Lapwings simply stay together (with few exceptions) in all the circumstances we know of. Interestingly, both partners of some pairs temporarily stopped nesting together for the entire breeding season without at least one partner initiated a new nest with a new partner. For this reason, the 'till death do us part' rule probably applies to them. In fact, I think that Red-wattled Lapwings should be presented not “only” as socially monogamous, but rather as perennially monogamous species, because many pair bonds last over several (in our data set six) breeding seasons.

Synthesis of findings

Lapwings with a core distribution at lower latitudes are birds with a generally biparental care for offspring but showing variability in mating and parental behaviour. Although there is a clear need for biparental care, the degree of parental cooperation may vary between lapwing species. Differences between parental care of males and females are more apparent in the Northern Lapwing representing the species of higher latitudes, whereas at lower latitudes, where typically the Red-wattled Lapwing breeds, equally shared parental care is more pronounced.

The variation in parental care and male contribution to reproduction in lapwings can be fundamentally determined by the demands of the environment. Female compensation for variable and in some pair bonds low effort of male incubation in temperate Northern lapwings is unlikely to be acceptable in hot desert environments in the case of Red-wattled lapwings, where nesting is extremely challenging due to high ambient temperatures and thus requires elaborate cooperation between both partners. The necessity for equal parental effort may be then related to mate fidelity, which may be stronger (even perennial) in the harsh hot desert, similar to birds breeding in the climatically challenging Arctic.

Mutual knowledge and cooperation between partners are well represented by the Red-wattled Lapwing, as faithful pairs have a higher potential for multiple breeding within a season than new, inexperienced pairs. In terms of equally shared parental care for offspring (eggs) and strong mate fidelity, the Red-wattled Lapwing appears to be consistent with the probably prevalent strategy in tropical and subtropical birds (both passerines and non-passerines). On the other hand, the Northern Lapwing has a different lifestyle with a variable willingness of males to invest in parental care and the tendency towards polygamy. A more pronounced division of parental roles, such as more intense incubation by females, may be associated with sexual dimorphism. As a result, the unequal sharing of parental care in Northern Lapwing may require more developed communication between partners during incubation. In fact, the Northern Lapwing female has to use more elements of insistence and negotiation with her partner in order to be exchanged by the male at the nest, so that she can devote at least part of the day to self-maintenance behaviour. As a result, there may be much more variability in fitness impacts in temperate

Northern Lapwing females compared to the more balanced parental care of subtropical Red-wattled lapwings.

The breeding ecology of lapwings is strongly influenced by the risk of predation. Cooperation between partners is therefore crucial not only for the incubation process, but also for nest defence, as especially ground nests are very vulnerable to various visual and olfactory predators. Although lapwings usually defend their nests actively and aggressively, they also use other antipredator tactics, such as trying to be immobile and therefore inconspicuous (sleeping on the nest), or collectively attracting attention away from the nest, which may be a form of distraction display. It appears that their antipredator behaviour may vary between species and according to various circumstances. Whereas in the Northern Lapwing the male is more active in defending the nest, in the Red-wattled Lapwing the nest defence is more shared between the parents. Breeding in colonies (Northern Lapwing) or at least semi-colonies (Red-wattled Lapwing) is a common strategy in lapwings, so they are close to some form of shared nest defence. Surprisingly, Red-wattled lapwings with different social status (e.g., birds from the neighbourhood nests or non-breeding individuals) participate in joint nest defence, which suggests that these individuals have different motives for this behaviour.

The difference between temperate and subtropical species can reflect their life history traits. A tropical species (Red-wattled Lapwing) with a slower lifestyle tends to have more shared parental care, spread out over a long breeding season, and a greater tendency toward perennial bonds. On the other hand, a temperate species (Northern Lapwing) with a faster lifestyle has a greater tendency to polygamy (and to a sexual conflict) and more divided parental roles (the female takes more care of the clutch while the male defends the territory). Therefore, females need more tactics for a more developed form of parental care negotiation.

Future research

Every study raises more questions than it answers. Also, our research has revealed several interesting topics that could be the subject of future investigation on the behavioural ecology of shorebirds. In general, detailed behavioural research on lapwings living at lower latitudes has so far been neglected, while most studies to date have dealt with the temperate Northern Lapwing. To compare how different species behave in different parts of the world, we need to use consistently the same research methods for all species and focus on less studied species of lower latitudes.

Communication between partners who share parental care equally

Focus on the complexity of communication between partners in the tropics and subtropics where cooperation is required: Do partners help each other automatically or is there a negotiation process between them? The system may not be as complex as in temperate regions because their roles are more balanced, and negotiation may not be necessary. The complexity of communication between partners may vary depending on the mating system.

Female compensation in desert extremes

It would be interesting to experimentally test the extent to which Red-wattled Lapwing females are able to compensate for their partner's lack of activity in such a demanding environment, for example during egg incubation. However, such an experiment would need to be carefully prepared as it raises ethical issues and poses a risk to nesting birds and their eggs.

Why do conspecifics co-defend nests?

To better understand complex antipredator behaviour, we should focus our attention on the drivers and motivations of conspecifics in shared nest defence. It is important to focus on their origins and to record in detail their responses to predators.

Fitness consequences

Our research has shown that the incubation effort of males influences the self-maintenance behaviour of females. Further research should focus on the consequences of variability in sleep behaviour between individuals. In particular, we know nothing about the fitness consequences of females receiving less help from males.

Is it always cooperative breeding or is double brooding more common?

To look more carefully at studies of cooperative breeding in lapwings and try to find out whether it is always an active contribution of the offspring to parental care or not. In fact, in some cases it may only be the passive presence of offspring from a previous breeding without active contribution to incubation or nest protection, so that the definition of cooperative breeding would not be met.

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Chapter 1

Sládeček, M., Vozabulová, E., Brynychová, K., & Šálek, M. E. (2019). Parental incubation exchange in a territorial bird species involves sex-specific signalling. *Frontiers in Zoology*, *16*, 1-12.

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Parental incubation exchange in a territorial bird species involves sex-specific signalling

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Abstract

Background: Effective communication between sexual partners is essential for successful reproduction. Avian parents with biparental incubation need to know how to negotiate, when and who will incubate, and how to harmonize partner exchange at the nest. Although considerable effort has been dedicated to studies of incubation rhythms, few studies have investigated how behavioural signals serve to tighten cooperation between parents. Moreover, existing studies are almost exclusively restricted to species in which long distances between incubating and non-incubating parents prevent continuous communication during incubation. Thus, the most frequently described parental exchange system is a simple model characterized by the return of the non-incubating parent to the nest itself. Here, we propose more complex parental exchange behaviour in the Northern Lapwing (*Vanellus vanellus*), a territorial species capable of continuous partner communication during incubation and with a highly variable male contribution to incubation.

Results: Northern Lapwing females regularly vocalized shortly before departing from the nest, while males mostly left the nest quietly. Responsiveness of the male to female vocalization, perhaps in combination with her flying away from the nest, helped to synchronize incubation care by increasing the probability of exchange, and also by shortening the exchange gaps. In contrast, a male-to-female exchange gap most often occurred after the male quietly flew away from the nest. The frequency of female vocal signalling was not correlated with the male incubation effort on a between-nest scale, but the highest probability of a female-to-male exchange occurred after vocal signalling by females with the most nest-attentive males. Conversely, lowered effort by females to vocalize in the night was accompanied by lower willingness of males to incubate.

Conclusions: Our results suggest that (1) that the incubating parent can communicate with the non-incubating partner using sex-specific behavioural signals, and this helps to synchronize parental exchange on the nest, (2) this signalling may combine acoustic and visual cues, and (3) the efficiency of this signalling might influence the overall nest attendance. The presumption that the repertoire of behavioural signals during reproduction will be much more complex in territorial species that are capable of continuous communication between the partners during the incubation period should be further tested.

Keywords: Biparental incubation, Incubation rhythms, Parental care, Shorebirds, Nest relief, *Vanellus vanellus*, Waders

Background

Effective communication between sexual partners is essential for successful reproduction. In biparental species, in particular, acoustic and visual communication between the partners can tackle issues of sexual conflict [1, 2] and also issues of tighter cooperation [3, 4]. In many avian species, both parents take part in incubating the eggs [5], and this increases the demands on communication between incubating and non-incubating partners. A variety of incubation patterns have been described, ranging from exchanges between partners at the nest every few minutes [6] to incubation sessions lasting several weeks [7–9]. However, a question remaining almost unstudied concerns how parents communicate on the scale of particular exchanges.

Most studies targeting the question of partner exchange at the nest have been carried out on species in which the non-incubating parent spends its off-duty time far from the nest [9–12], and thus the parents are

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unable to communicate continuously. The only feasible way to make a synchronous partner exchange in these cases is therefore probably for the off-duty parent to return to the nest itself [8]. In seabirds, such as albatrosses [9], penguins [13] and skuas [14] with extremely long incubation bouts and hundreds of kilometres long foraging trips, the incubating bird waits until the partner returns. Any failure in this return can therefore lead to a critical decline in the body condition of the incubating bird, and even to abandonment of the nest [7, 8, 11]. However, even in species with much more frequent nest relief, the exchanges usually take place while both parents are present at the nest. This is frequently accompanied by some kind of displays [15] or by other rituals, such as allopreening [3, 16].

There is much more opportunity for communication between the partners and for negotiating about the timing of their exchange on the nest in species where the non-incubating parent spends most of its off-duty time near to the nest, or if it frequently visits the nest even during its off-duty time. Multiple visits preceding an exchange were observed in captive ringed doves (*Streptopelia risoria*) [3]. These regular contacts enable tight cooperation between the parents. Only 13% of nest reliefs were initiated by nest abandonment by the incubating bird before the partner returned. Similarly, in zebra finches (*Taeniopygia guttata*) such regular visits are accompanied by repeated acoustic duets, through which the sitting bird signals its need to be exchanged [4, 17]. In these cases, both birds are probably involved in the negotiation process about when it is time to exchange incubation duties. This can help in achieving tight coordination of incubation care [3, 4, 18].

However, in many species it is not unusual for the incubating parent to leave the nest before the arrival of its partner, and thus the incubation sessions are separated by so-called “exchange gaps” [19, 20]. It is undesirable for the exchange gaps to be too long, because they may increase the risk of nest depredation [21] or cooling of the unattended eggs [22]. Even species that have exchange gaps as a regular part of their incubation schedule should therefore use some request signalling for nest relief. However, the mechanisms for communication between the partners in these species aimed particularly at motivating the non-incubating parent to return to the nest and engage in incubation duties are poorly understood.

The Northern Lapwing (*Vanellus vanellus*) is a biparentally incubating shorebird with a highly variable male contribution to incubation [23–26], and with irregular frequency of parental exchanges [25–27]. The male contribution to incubation is ordinarily smaller than the contribution of the female. The male contribution peaks during the day, while it is almost totally absent in the night [26, 28]. The Lapwing has intermittent incubation, with about 13% of the time when the nest is not attended by either parent [26]. However parental exchange occurs only during a relatively small part of the incubation recesses (Actograms in: [25], this paper). Northern Lapwings are territorial, and the birds spend most of the time in their territories, usually in open habitats [29, 30], which enables continuous contact and communication between partners [30].

In this paper, we analyse behavioural patterns associated with incubation gaps in breeding Northern Lapwings. We hypothesized that the incubating parent communicates with the non-incubating partner using behavioural signals, and that this helps to synchronize parental exchange on the nest. Specifically, and based on our direct observations, we suggest that when intending to exchange with the partner, the incubating parent vocalizes briefly (i.e. for a few seconds) before departing from the nest. The urgency of this signal can be reinforced by flying away from the nest, a more pronounced action than walking away. If this is true, we would expect that 1) partner exchange will occur more probably during the recesses after the departure of the on-duty parent, after issuing a vocalization signal, perhaps reinforced by flying away; 2) there will be shorter recesses accompanied by nest relief coming after these signals (i.e. the signals increase partner synchronization); 3) if the off-duty parent ignores the signal, the subsequent recess will be longer than the recesses without signalling, as a result of partner disagreement within the negotiation process.

Based on the fact that the male contribution to incubation varies strongly among the nests [23–26], we further investigated whether the variation in the male contribution to incubation 1) is predicted by the vocal signalling effort made by the female, or 2) reflects the efficiency of these signals (i.e. more incubating males exchange the female more probably after her signalling). Similarly, because the male contribution to incubation shows strong daily rhythmicity, being highest during the day (with peaks after sunrise and before sunset) and is almost absent in the night [25, 26], we further tested: 3) whether the effort put into signalling by the female changes in the course of the day, and 4) whether the signalling efficiency (i.e. male willingness to exchange) changes in the course of the day.

Methods

General field procedure and data extraction

We monitored the incubation of Northern Lapwings in the České Budějovice basin, Doudlebia, Czech Republic (49.25°N, 14.08°E), on approximately 40 km^2 of agricultural landscape, during April and May 2016. We searched for nests by thoroughly scanning fields and meadows with telescopes, or by walking through areas with high nest densities. We monitored incubation with a small camera (Ø 2 cm, length 4 cm) placed approximately 1.5 m from the nest in a southward direction, in order to minimize the time that the lens faced the sun (which would have overexposed the videos and made individuals hard to recognize). The digital recorder stored videos at 10 frames per second with 640 × 480-pixel resolution. The system was powered by a 12-V, 44-Ah battery buried together with the recorder under the ground. The target was to obtain ~ 2–3 days of recordings from each nest.

We extracted the incubation behaviour using AVS Media Player (http://www.avs4you.com/AVS-Media-Player.aspx). First, we determined each arrival or departure of incubating birds with precision of 1 second. The sex of the birds was determined on the basis of sex-specific plumage traits, such as crest length and the extent of the melanin ornaments on the breast and on the face [31]. Then, we thoroughly scanned the last 5 seconds before each departure in order to identify whether or not the incubating bird had vocalized. Vocalization was clearly identifiable on the videos by specific head movements and by bill opening. As two of the video sets that were used were additionally provided with a small microphone, we were able to validate the linking of specific head and bill movements with vocalization.

For each departure from the nest, we scored vocalization as a binomial variable (1 = at least one call; 0 = without a call), and we noted whether the bird flew away or walked away. Because the recordings from some nests were damaged or ended early due to nest depredation, we excluded from the analysis any nests with less than 10 scored incubation recesses.

We defined an **'incubation recess'** as any period of time for which the nest was unattended by either of the parents. Subsequently, we classified the incubation recess as a **'break'** (the same parent came back and continued incubation) or as an **'exchange gap'** (parents exchanged during the incubation recess) [19]. In order to relate female vocal signalling with the between-nest variation in the male contribution to incubation, we introduced a term **'male incubation effort'**, calculated as the ratio of male nest attendance at the nest to the overall time for which the nest was attended by either of the parents (i.e. excluding all incubation recesses). **'Female vocalization effort'** was then defined as the proportion of female departures accompanied by vocalization (per particular nest/hour), and **'female vocalization efficiency'** was defined as the probability that the male will come to incubate after female vocalization.

Validation of the assumptions, to avoid confounding effects

In order to correctly interpret the results of this study, we first explored the vocalization pattern of incubating Northern Lapwings with a particular focus on the context of departure from the nest. We investigated whether vocalization can occur frequently at any time during incubation (and might thus confound our interpretation of partner behaviour) or whether it is concentrated just before departure from the nest (as predicted for the purposes of this study). We therefore specifically analysed a subset of 40 nests (~ 960 h) with 1 day of continuous (i.e., completely uninterrupted) videotaping, which enabled us to determine in detail all vocal sessions throughout a one-day incubation course. The set consisted of 30 nests collected in another study in 2015, and a subset of 10 nests from 2016 that were included in this paper.

We found that although vocalization events could take place at any time during the incubation bouts in both sexes, the frequency steeply increased in few minutes prior to departure. Whereas in males the pattern is weak, in females it is much more pronounced. The vocalization of females peaks immediately before the departure, with more than 60% probability of vocalization during the last 30 s. It contrasts with strongly decreasing probability up to 1.3% (mean probability of vocalization for any thirty-second interval five or more minutes prior to departure; Fig. 1a, b). Secondly, using this dataset, we investigated whether more attentive males (i.e. those that made a greater incubation effort) could have been (positively) assortatively mated with more vocal females, which would confound our interpretation of female vocal signalling efficiency. We observed no positive correlation, and we conclude that the incubation effort in males is not directly positively associated with the vocalization frequency of their female mates (Additional file 1: Figure S1, Table S1).

Statistical analysis

All statistical analyses were performed in R version 3.3.0 [32]. For the model-based parameter estimates (or for the contrasts between these estimates) we report the effect sizes as medians and Bayesian 95% credible intervals (95%CrI) represented by the 2.5 and 97.5 percentiles from the posterior distribution of 5000 simulated values obtained by the 'sim' function from the 'arm' R package [33].

Binomial response variables were fitted with generalized mixed-effect models with a binomial error structure and the logit link function, using the "glmer" function from the "lme4" R package [34]. In particular, in order to explain the probability of an exchange gap (i.e. the probability of nest relief during an incubation recess) we used three binomial predictors: "sex", "vocalization" (yes or no) and "departure type" ("flight" or "walk"). All these effects were used both as main effects and in interactions (including three-way interaction). To explain the probability of vocalization before departure, we also used

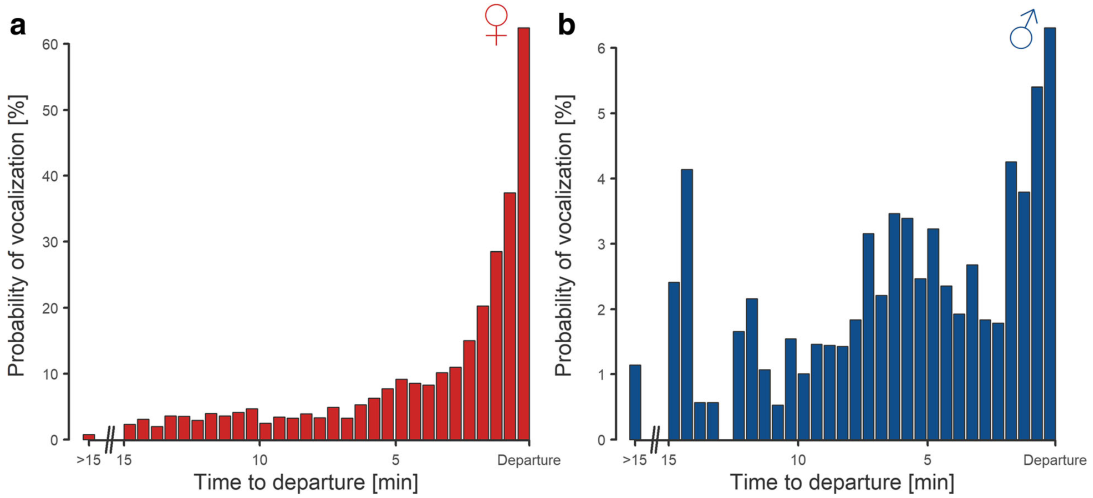

Fig. 1 Vocalization in relation to the time prior the end of incubation bout. Bars represent 30 s periods before leaving the nest (departure) and depict the probability that female (**a**; red) or male (**b**; blue) vocalized at least once within a period. The left-most bars (> 15) depict probability of vocalization (mean value per 30 s periods) more than 15 min before the departure. Note that Y-axis range differs between the sexes. Presented data include complete 24-day incubation footages for 40 nests. Ten of these nests are a part of the dataset presented in this paper while other 30 nests used in this figure were collected using the same method in the same area in 2015

"sex" and "departure type" as predictors in terms of main effects and in interaction.

In order to test the daily rhythmicity in the female vocalization effort, we also used vocalization before female departure (yes or no) as a response in the model, with time as a predictor. We used time transformed to radians (2*time * π/period of interest) and subsequently fitted it as the sine and the cosine of the radians. We used 24 h as a period of interest and, due to the obvious bimodality of the response variable, with peaks in the morning and in the late afternoon, we also used 12 h as a period of interest. Similarly, the "departure type" binomial response was fitted with time (24-h rhythmicity) in interaction with sex.

The length of the incubation recesses was fitted with the mixed-effect model with a Gaussian error structure using the "lmer" function from the "lme4" R package [34]. The response variable was log-transformed to approach the normality of the model residuals. Binomial variables "sex", "vocalization" (yes or no) and "departure type" ("flight" or "walk") were used as predictors in the model. We fitted nest identity as a random intercept in all the models described above, and in models using temporal information as a predictor we also fitted time (sine and cosine) as random slopes [35].

To analyse the between-nest differences in female vocalization effort, we used the male incubation effort as a response variable. Female vocalization effort and vocalization efficiency were then z-standardized (centered and mean-divided [36]), and were used as predictors in a general linear model fitted using the "lm" function [32]. The model was weighted by the square-rooted number of analysed female departures from the nest.

Because of the overall scarcity of male incubation in the night (and thus the small sample size of exchange gaps in the night), we were unable to use models to test the night efficiency of female vocalization or the male responsiveness to these signals. We therefore divided all incubation recesses into those started during the dark part of the day (i.e. when the sun was more than 6° below the horizon) and those started during daylight. We then tested 1) whether female vocalization in the night raised the probability of nest relief, and 2) whether the probability that the male would comply with the signalling is the same for both day and night. We tested these hypotheses using the Boschloo test, a technique from a group of unconstrained exact tests for two binomial proportions, which is suitable for use when small expected values occur. This approach using the *p*-value from Fisher's exact test as a test statistic is explicitly recommended by Mehrotra et al. [37] as convenient in cases of unbalanced designs. In particular, we used the "exact.test" function from the "Exact" R package [38].

Results

A total of 63 nests were monitored for 2854 h (12 to 116 h; median = 41.37, sd = 18.2) and 5033 nest departures were scored (23 to 242 from particular nests; median = 77, sd = 36.4). Females departed in 3367 cases (66.8%) and males departed in 1666 cases (33.1%). Overall, an exchange gap occurred in 25.6% of incubation recesses (CrI: 22–30%), and was on an average 17% (CrI: 14–20%) more likely after male departures (710 out of 1666; 37.6%; CrI: 34–41%) than after female departures (719 out of 3367; 20.3%; CrI: 17–24%).

Patterns of nest departures and vocalization

The use of departure types (flight or walk) and also the probability of vocalization before departure differed between the sexes and varied with the time of day. Males flew away (1415 cases; 87.1% of flight departures; CrI: 84–89%) more often than females (2317 cases; 70.4%; CrI: 67–74%), and females accompanied their departures with vocalization much more often (1385 cases; 41.5%; CrI: 37–46%) than males (193 cases; 10.3%; CrI: 8–12%). Females (but not males) vocalized much more frequently when they flew away from the nest than when they walked away (52 vs. 18%; Fig. 2a, Additional file 1: Table S2). In the daily pattern of females, flight departures prevailed during the night, while they dropped to less than 50% around midday (Additional file 1: Figure S2a, Table S3). In males, this drop was less pronounced, albeit still significant (Additional file 1: Figure S2b, Table S3). The daily pattern of female vocalization during nest departures was bimodal, with peaks after sunrise and before sunset, and followed the ratio of the male contribution to incubation (with the minimum during the night; Fig. 3, Additional file 1: Table S4).

Probability of exchange gaps with sex-specific signalling

The probability of parental exchange after an incubation recess was associated with vocalization by an incubating female, but not male. In females, the probability of being exchanged by a male was enhanced by previous vocalization, both when the female flew away (36% vs 9% without vocalization; Fig. 4, Table 1) and when she walked away (26% vs 12% without vocalization; Fig. 4, Table 1). In addition, an exchange after female vocalization was more likely after she flew away than after she walked away (see non-overlapping CrIs in Table 2). Nevertheless, female flight departure itself (i.e. without vocalization) did not increase the probability of an exchange gap. Out of 719 exchange gaps after female incubation, 478 (i.e. 66%, Fig. 2b) were preceded by female vocalization, and of these 421 (58%, Fig. 2b) were also followed by flight departures. In contrast, in males the vocalization before flight departure decreased the probability of male-to-female exchange (Fig. 4, Table 1).

Effect of vocalization on the synchronization of exchange gaps

Female vocalization before departure from the nest helped to synchronize the exchange gaps, since the

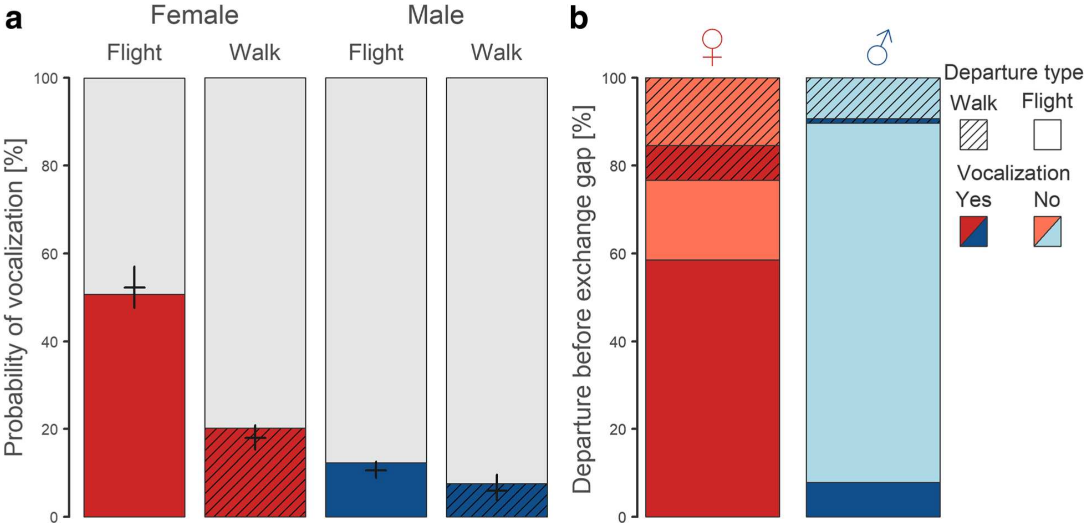

Fig. 2 **a** Vocalization in relation to sex and type of a bird's departure. Bars show the probability of a female (red) and male (blue) vocalization before the bird left the nest by flight (solid bar) or walking (hatched bar). Horizontal lines of black crosses denote estimates from a mixed-effect model with nest identity as a random intercept (Additional file 1: Table S2). The vertical lines denote 95% credible intervals of the estimates. **b** Sex-specific departure type before an exchange gap. Bars represent the relative proportions of exchange gaps (i.e. parents exchanged during the incubation recess) after female (red) and male (blue) incubation bouts with distinction between walk (hatched bars) and flight (solid bars) departures. In addition, dark colours indicate vocalization of a departing bird

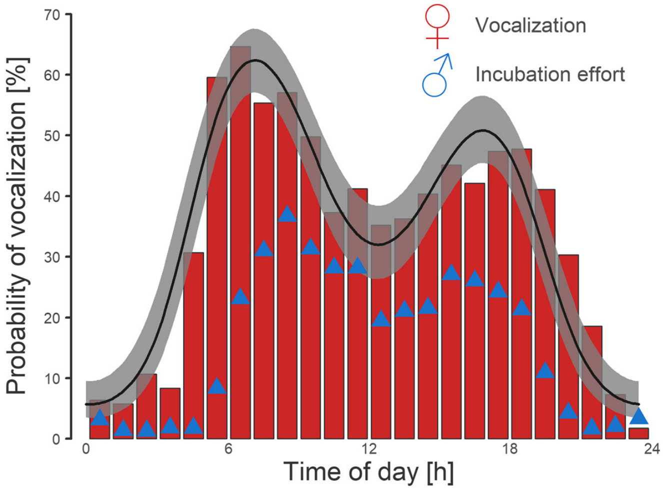

Fig. 3 Daily pattern of female vocalization before leaving the nest and male incubation effort. Red bars depict real proportions of female departures accompanied by her vocalization for a particular hour of the day. The curve with shaded area indicates the model prediction with a 95% credible interval (Additional file 1: Table S4). Blue triangles illustrate the proportion of male contribution to incubation in our dataset for a particular hour of day

exchange gaps coming after female incubation bouts were better synchronized (i.e. they were 1.25 min shorter; CrI: 0.85–1.71 min., Fig. 5) after vocalization than without vocalization. The opposite was true if the recess resulted only in a break (i.e. if the male did not come to exchange the female). The breaks coming after female departure accompanied by vocalization were 1.29 min longer (CrI: 0.93–1.68 min.) than those without vocalization (Fig. 5, Tables 3 and 4). Conversely, the incubation recesses of males were generally shorter than those of females, and the length of the exchange gaps coming after male incubation bouts was not affected by whether or not the male vocalized.

On a between-nest scale, the male contribution to incubation in a particular nest was not enhanced by the female vocalization effort (i.e. the proportion of departures accompanied by vocalization per particular nest/hour). However, in nests with a higher male contribution to incubation, the males were more likely to come and incubate after female vocalization (Fig. 6, Additional file 1: Table S5).

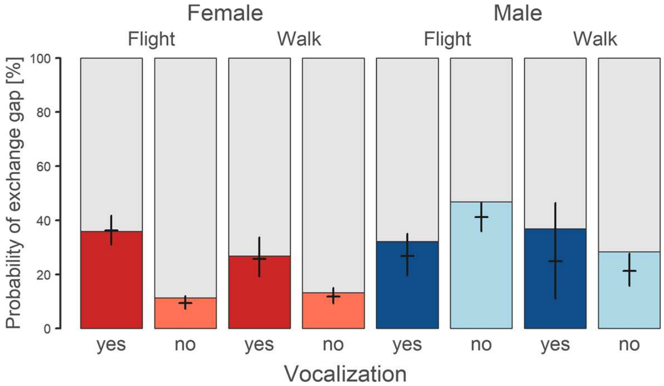

Fig. 4 The probability of an exchange gap during an incubation recess. Bars show the probability that a female (red) or male (blue) is exchanged by the partner. Dark colour indicates, that the departing bird vocalized before the departure. Labels above the plot distinguish if the nest was left by flight or walking. The horizontal lines of black crosses denote estimates from the mixed effect model with nest identity as a random intercept (Table 1). The vertical lines indicate 95% credible intervals of the estimates

Table 1 Probability of exchange gap during incubation recess

					95% CrI	
Level	sex	Vocalization	Type of departure	Estimate	Lower	Upper
1	F	YES	FLIGHT	0.36	0.31	0.42
2	F	NO	FLIGHT	0.09	0.07	0.12
3	F	YES	WALK	0.26	0.19	0.34
4	F	NO	WALK	0.12	0.09	0.15
5	M	YES	FLIGHT	0.27	0.2	0.35
6	M	NO	FLIGHT	0.41	0.36	0.47
7	M	YES	WALK	0.25	0.11	0.47
8	M	NO	WALK	0.21	0.16	0.28

Daily pattern in vocalization efficiency

Although the overall frequency of female vocalization in the night was very low (10.7% of departures) and there were only 17 subsequent exchange gaps from 8 nests, female vocalization before departure strongly increased the probability of her being exchanged even in the night (Boschloo test; $p < 0.001$). Nonetheless, the efficiency of female vocalization signalling (i.e. the probability that a male will come after female vocalization) was significantly lower in the night than in daytime (Boschloo test; $p = 0.017$).

Table 2 Probability of exchange gap during incubation recess

		95% CrI	
Contrast	Estimate	Lower	Upper
1–2	**0.27**	**0.22**	**0.31**
1–3	**0.1**	**0.03**	**0.17**
3–4	**0.14**	**0.08**	**0.21**
2–3	**−0.16**	**−0.24**	**−0.1**
2–4	−0.02	− 0.05	0.01
5–6	**−0.14**	**− 0.21**	**− 0.07**
5–7	0.02	− 0.2	0.18
7–8	0.03	−0.11	0.25
6–7	0.16	−0.05	0.3
6–8	**0.2**	**0.14**	**0.25**
1–5	**0.1**	**0.02**	**0.17**
2–6	**−0.32**	**−0.36**	**−0.27**
3–7	0.01	−0.21	0.16
4–8	**−0.09**	**−0.16**	**− 0.04**

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrI) from a posterior distribution of 5000 simulated values generated by the 'sim' function in R [33]. Variance components were estimated by the 'glmer' function for binomial errors with logit link function [34]. **1)** Estimates for particular factor combination levels (see Fig. 4). **2)** Estimates for selected contrasts (number in column "contrast" refers to level number in Table 1). Note that presented values were back-transformed. Those contrasts whose 95% credible intervals do not contain 0 are highlighted in bold

Discussion

In this study, we have revealed several aspects of partner communication in the Northern Lapwing during the incubation period: 1) females (but not males) combine acoustic and motion signals in an attempt to ask the partner for nest relief, and these signals, together with male willingness to exchange with the female, shape the length of the incubation recesses; 2) scarcity of male incubation at night is associated with a lower female vocalization effort, and also with lower male readiness to incubate; 3) the between-nest differences in male incubation effort are shaped by the willingness of the male to provide nest relief, rather than by the female vocalization effort. We discuss these topics below.

Use of signals

Unlike many other related species with biparental incubation [19, 39, 40], Northern Lapwings have an incubation rhythm that is characterized by frequent but relatively short incubation recesses, only a minority of which (i.e. 25% in our sample) serve as an exchange gap (Fig. 4). Some of the incubation recesses without nest relief therefore have other functions, e.g. leaving the nest unattended during a disturbance or a predator approach (and relying on nest crypsis) [41], a direct predator attack [41, 42], or just a short foraging break. For example, females often took a break around the noon, walked and foraged nearby the nest (our direct observations both in video recordings and in the field).

In addition to the reasons mentioned above, we suggest that a proportion of incubation breaks can also result from failures of the negotiation process about partner exchange at the nest [3]. We show that females had a far higher probability of being exchanged by a male when they vocalized shortly before departing from the nest, and this pattern was more obvious when the female flew away (though the pattern could still be observed when she walked away). This suggests that female vocalization could serve as a signal to the male partner requesting an exchange of incubation duties. The patterns in the length of incubation recesses were also consistent with our predictions; exchange gaps were shortened (i.e. better synchronized) whereas breaks (i.e. recesses without parent exchange) were prolonged when there was female vocalization. Thus, we can assume that when the male does not fulfil the female's exchange request, the female waits within the negotiation process for a considerably longer period, then returns to continue in incubation.

However, an alternative explanation can be put forward, at least in some events, i.e. that prolonged breaks after female vocalization can occur in cases when the female signals a perceived danger, such as an approaching predator, rather than a need to be exchanged. At the

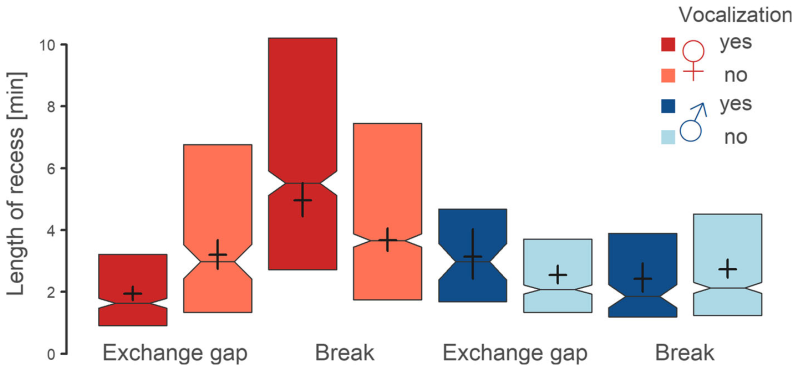

Fig. 5 Length of incubation recess in relation to sex, vocalization and type of a bird's departure. The boxplots summarize lengths of the recesses after female (red) and male (blue) incubation bouts, colour intensity indicates whether the bird vocalized before leaving the nest (dark colours) or did not (light colours). Recesses are classified either as an "Exchange gap" (parents exchanged during the incubation recess) or as a "Break" (the same parent returned and continued incubation). The median length of the recess is depicted by the vertical line inside the box, its 95% confidence interval by the notch, and the 25–75% quantiles by the box. The horizontal lines of black crosses denote estimates from the mixed effect model with nest identity as a random intercept (Table 2). The vertical lines indicate 95% credible intervals of the estimates

same time, the voice activity of the female often graduates for several minutes before she leaves the nest (see Fig. 1a), and such conspicuous behaviour in the presence of a predator could be counterproductive in terms of nest protection. Moreover, long female breaks after a disturbance (accompanied by vocalization), contrasting with really short female-to-male exchange gaps on the nest in the same situations, seem to be cumbersome and difficult to explain (Fig. 5). Finally, it seems improbable that there would be a rapid female-to-male exchange after a disturbance when the male-to-female exchange is slower, in a species where the main role of a male is to protect the territory from predators and the male participates considerably less than the female in incubation care (Fig. 5). There is a need for further studies to determine the roles of both alternatives suggested here, and their effects on the length of incubation recesses in avian incubation.

Table 3 Length of recess

					95% CrI	
Level	sex	Vocalization	Type of gap	Estimate	Lower	Upper
1	F	YES	EXCHANGE	1.94	1.74	2.17
2	F	NO	EXCHANGE	3.19	2.75	3.7
3	F	YES	RECESS	4.96	4.42	5.52
4	F	NO	RECESS	3.67	3.33	4.04
5	M	YES	EXCHANGE	3.15	2.45	4.03
6	M	NO	EXCHANGE	2.54	2.28	2.86
7	M	YES	RECESS	2.42	2.02	2.93
8	M	NO	RECESS	2.73	2.45	3.05

We documented also a considerable proportion of exchange gaps (33%; Fig. 2b) after female departure without previous vocalization. We cannot rule out that vocalization occurred in these cases immediately after leaving the nest, when the female was already out of camera view. On the other hand, it might indicate that the negotiation process also involves other signals, made away from the nest, but note that these exchanges were

Table 4 Length of recess

		95% CrI	
Contrast	Estimate	Lower	Upper
1–2	**– 1.25**	**−1.71**	**−0.85**
1–3	**−3.02**	**– 3.46**	**– 2.6**
3–4	**1.29**	**0.93**	**1.68**
2–4	**−0.48**	**−0.88**	**– 0.03**
5–6	0.6	−0.1	1.47
5–7	0.72	−0.07	1.65
7–8	−0.31	−0.74	0.17
6–8	−0.19	−0.46	0.07
1–5	**−1.21**	**– 2.05**	**−0.52**
2–6	**0.65**	**0.23**	**1.11**
3–7	**2.53**	**1.96**	**3.1**
4–8	**0.93**	**0.67**	**1.21**

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (CI) from a posterior distribution of 5000 simulated values generated by the 'sim' function in R [33]. Variance components were estimated by the 'lmer' function in R [34]. **3)** Estimates for particular factor combination levels (see Fig. 5). **4)** Estimates for selected contrasts (number in column "contrast" refers to level number in Table 3). Note that response variable was log-transformed in the model, but presented values were back-transformed. Those contrasts whose 95% credible intervals do not contain 0 are highlighted in bold

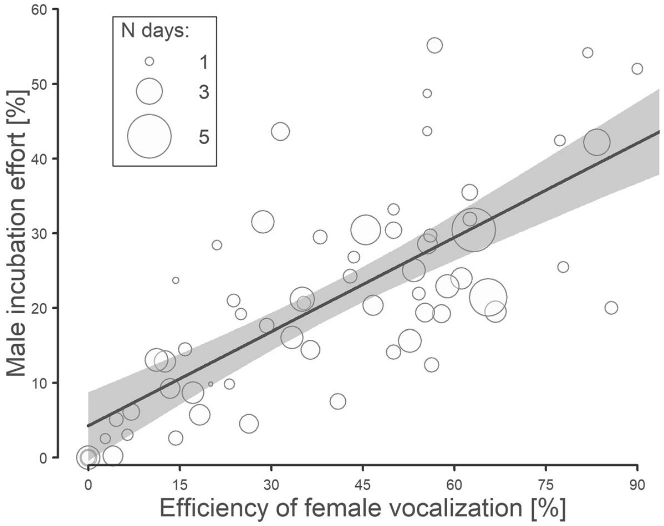

Fig. 6 The relationship between male incubation effort and the efficiency of female vocalization. The male incubation effort is taken as the ratio of male nest attendance at the nest to the overall time, for which the nest was attended by either of the parents. The efficiency of female vocalization is the proportion of female departures accompanied by her vocalization after which the male came to incubate (i.e. "Exchange gap" took place). Circles represent the individual nests and their size the number of days with incubation data. The line with shaded area indicates the model prediction with a 95% credible interval (Additional file 1: Table S5)

generally worse coordinated (Fig. 5). Some less common alternative ways of communicating, or failures of usual patterns regarding the exchange process, could exist in the Northern Lapwing, as is also found in other species. For example, although regular nest reliefs in Ringed Doves and Herring gulls *(Larus argentatus)* take place in the presence of both parents on the nest, it has been documented that some smaller proportion of the nest reliefs in these species are accompanied by exchange gaps [3, 20], even though such exchange gaps can be accompanied by a severely enhanced risk of egg depredation [21].

We observed different signalling patterns in males than in females. Vocalization was observed in only 11.6% of males, and was even accompanied by a decrease in the probability of an exchange gap. We suggest several possible explanations for this different pattern. Firstly, males may not need any specific requesting signal to negotiate an exchange with the female partner. As parental exchange occurs much more often after male departure than after female departure, the departure of a male who generally incubates less than the female can itself serve as a signal for the female to negotiate an exchange, even without a male call. Furthermore, Lapwing male acoustic signalling during incubation may serve primarily as a warning in response to an approaching predator [43]. We know that Lapwings avoid incubating in the presence of a predator, leaving the nest for the necessary period of time and relying on egg crypsis [41]. The male behaviour described here may therefore be seen as an aspect of the key role of the male in guarding the nest against predators. This could explain why males more frequent fly away from the nest than walk away from it, which would enable the male to attack the predator faster and more effectively [43].

Our findings could suggest that, in contrast with most of the previously studied species [3, 4, 7, 12, 20], the timing of nest reliefs in Northern Lapwings might be induced by the bird that is currently incubating, particularly by females. However, revealing who really initiates the exchange on the nest would require simultaneous recording of both partners (on the nest and away from it), which is a topic requiring further observational research.

Night incubation

Females greatly lowered their vocalization effort before departing from the nest in the night. This could be because male incubation in the night is very rare in the Northern Lapwing [25, 28, 44], and thus the possibility of being exchanged can be negligible for a female. However, despite the overall scarcity of male night incubation in our sample (17 cases), the probability of an exchange gap after female vocalization during nest departure was still almost 20% (in comparison with 35% during the day), while it was reduced to only 1.6% after a "silent departure" (in comparison with 15% during the day). Thus, although the males showed significantly lowered willingness to provide night nest relief, there was still a substantial chance for a female to get male help on the nest in the night after vocalization signalling.

So, why did the females lower their vocalization efforts so much in the night? We suggest that this pattern could mirror the response to increased predation pressure during the night, when mammalian predators are most active ([45, 46]; own observation). This explanation is justified by the observation that the nests of Northern Lapwings are depredated almost solely by nocturnal mammals ([47]; all 11 cases of known depredations in the study population). Firstly, vocalization during the night can attract nest predators, and females may face a trade-off between sitting quietly for most of the night and loudly highlighting the position of her nest. Our results indicate that most females probably prefer to bear the incubation bout for a whole night in order to be as inconspicuous as possible. Secondly, it could be more beneficial for females to leave the vigilant males to guard the nest in the night, rather than to ask for exchange. In future research, we therefore propose to test the significance of acoustic cues, such as bird calling, on mammal predator orientation in the night. We also need to describe Northern Lapwing male behaviour in the night, with respect to their ability to warn the sitting female about the approach of a predator, which is a strong characteristic feature of Lapwing males during the day [29, 42].

Between-nest differences in male incubation attendance

As can be found elsewhere [24, 26, 28], the male contribution to incubation is a strong predictor of overall nest attendance in the Northern Lapwing. This could be because of female energy limitations to fully compensate reduced male care [48], or it could be a result of negotiations over parental care [1]. Predictions from theoretical models assume that an evolutionarily stable strategy in response to the reduced parental effort of one partner is for the other partner to compensate to some extent ([1, 49, 50], but see: [51]). This explanation has also been supported by empirical data [52, 53]. Our study suggests a possible extending of this previous knowledge with a new finding in the behaviour of partners in this mechanism: it was found that better incubating males were more willing to come and incubate after the female had signalled her departure from the nest, but that the female signalling effort itself did not affect the extent of male care in a particular nest. This finding, together with the fact that the subsequent recess is longer if a female "exchange request" is not fulfilled by the male, suggests that it is the negotiation process associated with the fine-tuning between the partners that can influence the total nest attendance, rather than an energetic constraint [1]. On the basis of our data, we are not able to quantify the importance of this partnership mechanism and to compare it with the effect of energetic constraints. However, the negotiation process resulting from tuning and compliance between the partners appears to be a possible proximate mechanism that modifies the overall incubation attendance in biparentally nesting birds.

Conclusion

To conclude, we have documented that, in a territorial species capable of continuous communication between the partners during incubation, vocal and motion signals could be used for better synchronization of nest relief. Because it seems that the effectiveness in negotiating about exchanging parental duties influences the length of incubation recesses, we have also suggested how the negotiation process could influence overall nest attendance. Since we found vocalization signalling only in females, we suggest that behavioural signals serving parental cooperation and negotiation in birds can be sex-specific.

Additional file

Additional file 1: Figure S1. Frequency of female hourly vocalization in relation to male incubation effort. **Figure S2.** Daily pattern of flight away from the nest during a bird's departure. **Table S1.** The relationship between male incubation attendance and female vocalization effort during the incubation. **Table S2.** Patterns of probability of vocalization. **Table S3.** The probability of flight away during departure. **Table S4.** Circadian pattern of female exchange requesting. **Table S5.** Between nest differences in male contribution to incubation. (DOCX 132 kb)

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Availability of data and materials
The raw data and R codes that enabled replications of all analyses performed in this paper, and that were also used for generating all of the figures, are available from Open Science Framework: https://osf.io/zmd8g/.

Authors' contributions
MS, EV and MŠ collected the data; MS EV and KB extracted the incubation from videos, MS analysed the data and wrote the paper, with input from MŠ All authors read, commented on and approved the final manuscript.

Ethics approval and consent to participate
The study was conducted in accordance with the current laws of the Czech Republic, where it was performed under the ringing licence (1082) of the Czech Ornithological Society.

Competing interests
The authors declare that they have no competing interests.

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Chapter 2

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RESEARCH ARTICLE

AGGRESSIVE BEHAVIOR | WILEY

Aggressiveness in a subtropical shorebird's nest defense is adjusted to the predator species and shared by conspecifics

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Abstract

Aggression is an important component of an animal's defense when protecting offspring from predators. Ground nesting birds use a variety of defense strategies. However, their choice according to situation context is poorly known, especially in nonpasserines and in the subtropics and tropics. The ability to distinguish between differently dangerous predator species and the opportunity to share defense with conspecifics are potentially important but little-studied aspects of nest defense strategy. We experimentally studied the nest defense of Red-Wattled Lapwing in an individually marked population in a desert area near Dubai, UAE. We used three stuffed models representing 1) a predator dangerous both to adults and to nests (a cat), 2) a nest predator (a raven), and 3) a harmless reference model (a moorhen). We confirmed that the lapwings distinguished between predator species (being most aggressive toward the cat, and least aggressive toward the moorhen) and adjusted their defense strategy accordingly. In addition, conspecific visitors play a variety of roles in parents' defense strategy. They can strengthen the parental reaction, or they can assist in distracting a predator. The visitors included not only nesting neighbors but also nonbreeding floaters. Both parents participated in nest defense to a similar extent, regardless of incubation stage and ambient temperature. This study provides new insight into the complexity of the defensive patterns in ground-nesting birds inhabiting a hot environment. Comparative experimental research on a range of environments, with various bird species and predator models, can help us to understand the drivers of these defensive behavioral patterns.

KEYWORDS

antipredator behavior, distraction display, predation, Red-Wattled Lapwing, shared defense, *Vanellus indicus*

1 | INTRODUCTION

Defending offspring against predators is an essential part of parental care (Caro, 2005). The importance of successful defensive behavior for individual fitness is high, especially because predation is the prevailing cause of death in most species (Lima & Dill, 1990). Parents need to trade off the risk of injury to themselves, or even death, because predators may pose a risk not only to offspring but also to the parents (Caro, 2005). In birds, various antipredatory strategies have evolved for defending their nests (Larsen et al., 1996), in which other conspecifics are often involved (Caro, 2005; Koenig & Dickinson, 2004). However, the choice of a defense strategy according to the situation context has been scarcely studied. Most studies addressing the defensive behavior of breeding birds have been conducted in the temperate zone (Caro, 2005), and much less is known about this behavior in the subtropics and tropics.

In principle, breeding birds use two main groups of antipredator defense strategies. The first group consists in avoiding conflict with the predator. It involves making a passive escape with a small risk of danger, masking the nest in vegetation or using egg crypsis, and/or plumage crypsis (Šalek & Cepáková, 2006). The second group of strategies includes risky elements of active defense, ranging from distraction display when the predator is still far from the prey (Humphreys & Ruxton, 2020), through various alarm calls (Caro, 2005), to direct physical attacks. Physical attacks are the most aggressive and most energy-demanding form of active defense (Caro, 2005; Curio, 1978). As birds must consider the costs and benefits of such behavior (Cunha et al., 2017), the type of predator and its hunting tactics can fundamentally influence the choice of a defense strategy. Birds should, therefore, choose a more cautious tactic against a predator that is a threat both to the nest and to the parents than against a predator that threatens only the nest. However, experimental tests of this hypothesis are relatively scarce and have been conducted primarily on passerines *(Passeriformes)* (Class & Moore, 2010; Němec & Fuchs, 2014; Strnad et al., 2012).

Antipredatory behavior at the nests may be exhibited not only by the parents from endangered nests but also by other conspecific visitors. First, help in defending the nest is common in cooperatively breeding birds, where the helpers (usual offspring from previous breedings) can assist in all aspects of parental care (Cerboncini et al., 2020; Koenig & Dickinson, 2004; Walters & Walters, 1980). Second, birds breeding in high densities, such as colonial species, can share the defense of the offspring with neighbors from the surroundings. With the participation of multiple defenders, the sensory concentration of the predator can become confused, and the risks may be diluted among the defenders. This may increase their willingness to get involved in greater aggression (Larsen & Grundetjern, 1997; Larsen & Moldsvor, 1992). Such group defense may be more effective and less risky for the engaged individuals. It is assumed that these group defenders are currently breeding neighbors, but this has not yet been directly verified through uniquely marked individuals in a population. The presence of conspecifics, however, does not necessarily prove their participation in nest defense, as they can only wait for the opportunity to acquire territory (Bruinzeel & Van de Pol, 2004; Smith, 1978).

There are a number of other variables that can affect nest defense behavior. In many bird species, one sex (typically male, but see Emlen & Wrege, 2004) tends to be involved more in the territory and nest defense activities (Brunton, 1990; Kis et al., 2000; Liker & Székely, 1999; Tryjanowski & Goławski, 2004), while the other (typically female) bears a greater incubation responsibility (Sládeček et al., 2019). However, in some species, parents may share parental duties, including defense against predators, more equally (Cardilini et al., 2015; Fedy & Stutchbury, 2005). The effect of sex, therefore, needs to be considered.

Finally, nest defense tactics may vary with the incubation stage and ambient temperature. The willingness to take a risk may increase with the incubation stage, due to the investment already made in the clutch (Andersson et al., 1980; Brown & Brown, 2004; Montgomerie & Weatherhead, 1988; but see Forbes et al., 1994; Gunness & Weatherhead, 2002). There are also indications that extreme ambient temperatures may make it much more demanding for birds to perform any type of activity (Albright et al., 2017; Gudka et al., 2019; Streicher et al., 2017). Defensive behavior may be generally less vigorous at extremely high temperatures. The incubation stage and the ambient temperature should, therefore, always be taken into consideration in analyses of nest defense behavior, even if they are not the main research topics.

Shorebirds (Charadriiformes) are an order that is globally distributed and serves as a model group for studies on mating systems, life histories, and parental care in birds (Reynolds & Székely, 1997; Thomas et al., 2007). Shorebirds also show great interspecific variation in defense strategies (Larsen et al., 1996; Walters, 1990), but detailed insight into the intraspecific variation of nest defense behavior is lacking. Lapwings (genus *Vanellus*) belongs to a group of shorebirds, which openly incubate their nests on the ground. Their good maneuverability in flight is favorable for the use of aggressive physical attacks toward nest predators (Grønstøl, 1996; Larsen et al., 1996). Some shorebirds, including lapwings, form loose nest aggregations, where shared breeding may improve nest defense and nest success (Kis et al., 2000; Meilvang et al., 1997; Šálek & Šmilauer, 2002). One study on Northern Lapwing (*Vanellus vanellus*) in temperate conditions showed that parents distinguished between fox and crow when defending the nests and that the males were more involved in this defense (Elliot, 1985). However, it is still not clear whether and how lapwings distinguish differently dangerous predators in the tropics, and when other conspecifics are involved.

In this study, we experimentally investigated the nest defense behavior of subtropical Red-Wattled Lapwings (*Vanellus indicus aigneri*) in an arid and hot environment in the Arabian desert. Since predator visits to nests are rarely observed in the field (Sládeček et al., 2021), stuffed models were used to ensure standardized conditions similar to previous experimental studies (e.g., Elliot, 1985; Hinde, 1954; Kis et al., 2000). Specifically, we monitored the reactions of breeding adults to stuffed models placed near the nest. Based on the species composition of the fauna in the study area, we used the following models: feral cat (*Felis silvestris f. catus*, referred to as cat), a predator dangerous both to nests and to adults; Brown-Necked Raven (*Corvus ruficollis*, raven), a predator dangerous to nests but not to adults; and Common Moorhen (*Gallinula chloropus*, moorhen), as a nonthreatening sympatric species. Although episodic reports have shown that Red-Wattled Lapwings chase away potential predators and can share nest defense with conspecifics (Narwade & Fartade 2011; Narwade et al., 2010; Mishra & Kumar, 2020), detailed nest defense studies of this species (and of other tropical lapwings) are lacking.

We tested the following predictions. First, we expected lapwings to adjust their defense strategy to the model species, and to be least aggressive toward the harmless moorhen. At the same time, we expected fewer physical attacks toward the cat (dangerous to both the nests and to adults) than toward the raven (nest predator). Second, we expected that both parents would participate in nest defense to a similar extent because they share the incubation duties evenly (own unpublished results). Third, we expected that nest defense against the two predators would be shared with conspecifics. We assumed, that these conspecific visitors would be mostly parents from nearby nests and that the number of conspecific visitors would correlate positively with the density of active nests in the surroundings. Finally, we included the incubation stage and the ambient temperature as additional possible factors influencing the nest defense behavior.

2 | METHODS

2.1 | Study area

The study was conducted in the Al Marmoom Desert Conservation Reserve (24°50′N, 55°21′E), United Arab Emirates, 30 km south of Dubai. The reserve is in a primarily desert area and includes a system of artificial lagoons with small islands, built for recreation and in support of biodiversity. On an area of 6.63 km^2, there is a stable population of ~250 adult individuals of Red-Wattled Lapwing, of which roughly 60% breed there from February to August (Elhassan et al., 2021). The lagoons also provide suitable habitats for other species, many of which are potential predators of adult lapwings, for example, feral cat, Red Fox (*Vulpes vulpes arabica*), and Desert Monitor (*Varanus griseus*), or potential predators of lapwing nests, for example, Brown-Necked Raven (*Corvus ruficollis*) and Marsh Harrier (*Circus aeruginosus*). The studied population faces predation pressure spread throughout the day and night (Sládeček et al., 2021).

2.2 | General field procedure

Nests were systematically searched for throughout the study area. Incubating adults were readily visible from a distance, and we were, therefore, able to find nearly all active nests (Elhassan et al., 2021; Sládeček et al., 2021). Whenever a nest was found, the GPS position was recorded and the incubation start date was estimated based on an egg flotation test (van Paassen et al., 1984). Adults were trapped on nests using spring traps and were marked with a unique combination of a metal ring, four colored rings, and a green flag so that individuals could be recognized remotely. In addition, unfledged chicks were ringed with metal rings without color combinations, and these individuals were recognizable as fledged chicks. A small (ca. 50 µl) blood sample was taken for DNA sexing (Fridolfsson & Ellegren, 1999) because females and males cannot be distinguished in the field. The ambient temperature at the nest was measured using continuous temperature loggers (ZAYDA 1.1, http://berg.fzp.czu.cz).

2.3 | Design of the experiment

The nests where both parents were ringed with a unique color combination were selected for the experiment. The incubation stages of the treated nests ranged from 1 to 28 days (median = 14 days, mean = 14.3 days, SD= 6.2 days), which is 3%–93% of the total incubation time (30 days; Sládeček et al., 2021). The experiment consisted of three 15-min trials at each nest with each of the three stuffed models (cat, raven, and moorhen). Only one randomly selected model was exposed at each nest within 1 day, with a rest day between subsequent trials. The order of the stuffed models in each nest was randomized. The stuffed models were mounted in an alert posture facing toward the nest at a distance of about 2 m. The experiment started 5 min after the installation. This time was sufficient for the person installing the stuffed models to move out of sight and for the lapwing parents to return to the vicinity of the nest (own observations). To prevent disturbance, the reactions of the lapwings were monitored from a car at a sufficient distance. The monitoring included continuous video recording of parental activities around the nest by one observer and parallel identification of individuals by a second observer, using cameras (Nikon Coolpix P1000) with a focal length up to 3000 mm (optical zoom ×124). During each minute of the 15-min trial, the strongest reaction to the stuffed model on a semiquantitative scale (Table 1) was recorded for each parent. In addition, the number of conspecific visitors presents within a particular minute was recorded. Among the conspecific visitors, nonringed, metal-ringed, and color-ringed birds were distinguished, and the color-ringed birds were individually identified, to assign them later to specific nests. Overall, the experiment was performed with all three stuffed models on 32 active nests. Two other active nests were treated with raven and moorhen only (the cat trial could not take place due to nest predation).

TABLE 1 The semiquantitative scale of lapwing reactions.

Category	Reaction
0	Ignoring the predator/sitting on the nest
1	Silently alerting on the ground
2	Sporadic alarm calling on the ground (≤5 calls/min)
3	Intensive alarm calling on the ground (>5 calls/min)
4	Silently flying without attacks
5	Loudly flying without attacks
6	Attacks with alarm calling

2.4 | Statistical analysis

For the purpose of statistical modeling, the reaction to the stuffed model was treated as a continuous (numeric) variable. We chose to do so because 1) the reaction had seven levels and followed the Guttman scale ($C_R = 0.87$) and 2) we expect a linear relationship between the reaction and the predictors (which is unlikely for ordinal variables). The data are missing completely at random, which provides consistent and unbiased parameter estimates, even when the reaction is treated as numerical (Robitzsch, 2020).

In total, three regression models were performed. The first model aimed to explain the variation in overall reactions of each individual during the 15-min trial. This reaction could be expressed 1) by the highest scores (maximum reaction) and 2) by the mean of the scores (mean reaction) during the 15-min trial. As the two variables were strongly correlated (Spearman's rank correlation test, $r_s = 0.90$, $p < .001$), the maximum reaction was selected as a response variable of the model, fitted as a general linear mixed-effects model. As predictors, we included the stuffed model species (cat, raven, and moorhen), the sex of the parent, the incubation stage (i.e., the day of incubation), the ambient temperature (°C), and the number of conspecific visitors during the trial. The stuffed model species was included also in interaction with the sex of the parent and with the number of conspecific visitors. As three trials (one for each model) were conducted at each nest and reactions of two parents were assessed separately, parent identity nested in the nest identity was included as a random intercept. However, because the nesting of random intercepts led to model singularity (i.e., "parent" nested in the "nest" explained zero variance), we present models with only the nest identity as a random intercept.

To reveal the patterns of change of the individual reactions within the 15 min of the trial, we fitted the second general linear mixed-effects model. As a response variable, the maximum reaction of a particular parent within each minute of the trial was used, while the order of minutes within the trial (1–15), the sex of the parent, the stuffed model species, and the day of incubation were included as predictors. The minute of the trial was included also in the interaction with the stuffed model species and the sex of the parent. Nest identity was included as a random intercept and the minute of the trial as a random slope.

Finally, to explain what affects the number of conspecific visitors present during the trial, a generalized linear mixed-effects model with Poisson error distribution and log link function was fitted. As a response, the maximum number of conspecific visitors present during the 15-min trial was used, while the stuffed model species and the number of active conspecific nests up to 200 m from the treated nest (i.e., the "local nest density") were included as predictors. Nest identity was included as a random intercept.

All statistical analyses and visualizations were performed in R version 3.6.3. (R Core Team, 2019). The linear mixed-effects models were fitted using the "lmer" function, and the generalized linear mixed-effects models were fitted using the "glmer" function, from the "lme4" R library (Bates et al., 2015). The model assumptions were visually inspected from diagnostic plots (see https://osf.io/bfvgj/). The dispersion parameter in generalized linear mixed-effect models was checked using the "dispersion_glmer" function from the "blmeco" library (Korner-Nievergelt et al., 2015). All continuous covariates in the models were z-transformed (mean-centered and divided by SD). For all models, the "sim" function from the "arm" R package and noninformative prior distribution (Gelman & Hill, 2006; Gelman et al., 2016) was used to create a sample of 5000 simulated values for each model parameter (i.e., posterior distribution). Then, the effect sizes were reported as the medians and Bayesian 95% credible intervals (95% CrI) represented by the 2.5 and 97.5 percentiles of the posterior distribution of the 5000 simulated values.

3 | RESULTS

3.1 | Variation of parents' reactions

All considered reaction categories (Table 1) were observed, from ignoring to attacking the predator (Figure 1). The strength of the reaction varied considerably between the stuffed model species (Table 2). The lapwings were more aggressive toward the cat than toward the raven (estimate: 0.82, 95% CrI: −0.02 to 1.65, Table 2, Figures 1 and 2a) and toward the moorhen (estimate: 1.59, 95% CrI: 0.78–2.40). The lapwings also reacted more strongly toward the raven than toward the moorhen (estimate: 0.76, 95% CrI: 0.04–1.51).

Apart from general differences in the strength of parents' reactions to the predators, there are also several other considerations. First, while the reactions toward the cat were generally strong,

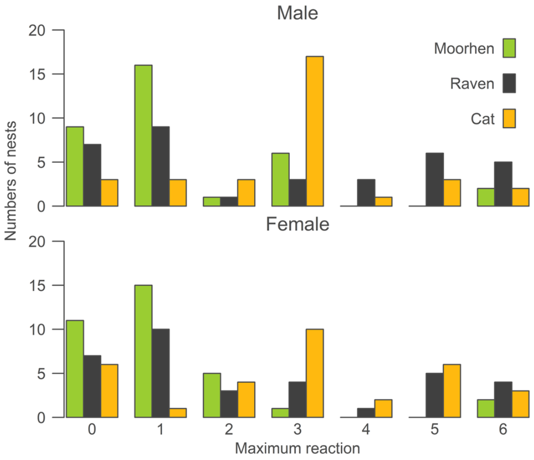

FIGURE 1 Strength of Red-Wattled Lapwing parent's reaction to moorhen, raven, and cat stuffed models during experimental trials. The length of each bar reflects the number of parents from the focal nests that produced a particular behavioral reaction (0–6, see Table 1) as the strongest reaction to the presence of the model near the nest (for moorhen and raven, $N = 34$ nests and for cat, $N = 32$ nests). [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 2 The maximum reaction of a parent within the 15-min trial.

Fixed effects	Estimate	95% CrI Lower	95% CrI Upper
Intercept	**0.898**	**0.345**	**1.425**
Raven	**0.764**	**0.038**	**1.51**
Cat	**1.589**	**0.746**	**2.379**
Sex male	0.225	−0.447	0.911
Incubation stage	0.238	−0.014	0.5
Ambient temperature	−0.043	−0.28	0.187
Number of conspecific visitors	**0.63**	**0.323**	**0.921**
Raven: Sex male	0.079	−0.887	1.054
Cat: Sex male	−0.359	−1.332	0.662
Raven: Conspecific visitors	0.136	−0.24	0.516
Cat: Conspecific visitors	**−0.408**	**−0.741**	**−0.083**
Random effects	% Explained variance		
Nest (intercept)	10		
Residual	90		

Note: There are shown the posterior estimates (medians) of the effect sizes with 95% credible intervals (CrI) from the posterior distribution of 5,000 simulated values generated by the "sim" function in R (Gelman et al., 2016). The variance components were estimated by the "lmer" function. The response variable was the maximum reaction (0-6, see Table 1) of the parent during a particular minute (1-15) of the trial. The incubation stage was z-transformed (mean-centered and divided by SD). Estimates with 95% CrI not containing 0 (i.e. which are statistically significant) are highlighted in bold.

Abbreviation: 95% CrI, 95% credible interval.

TABLE 3 Changes in the strength of Red-Wattled Lapwing parent's reaction to moorhen, raven, and cat stuffed models in the course of the trial.

Fixed effects	Estimate	95% CrI Lower	95% CrI Upper
Intercept	**0.315**	**0.006**	**0.649**
Minute	0.022	−0.004	0.049
Predator raven	0.403	0.180	0.634
Predator cat	0.170	−0.065	0.404
Day of incubation	0.001	−0.125	0.123
Sex male	**0.319**	**0.137**	**0.509**
Minute: Predator raven	0.022	−0.003	0.047
Minute: Predator cat	**0.100**	**0.075**	**0.126**
Minute: Sex male	**−0.019**	**−0.040**	**0.000**
Random effects	% Explained variance		
Nest (Intercept)	28		
Minute	<1		
Residual	72		

Note: There are shown the posterior estimates (medians) of the effect sizes with 95% credible intervals (CrI) from the posterior distribution of 5,000 simulated values generated by the "sim" function in R (Gelman et al., 2016). The variance components were estimated by the "lmer" function. The response variable was the maximum reaction (0-6, see Table 1) of the parent during a particular minute (1-15) of the trial. The incubation stage was z-transformed (mean-centered and divided by SD). Estimates with 95% CrI not containing 0 (i.e. which are statistically significant) are highlighted in bold.

Abbreviation: 95% CrI, 95% credible interval.

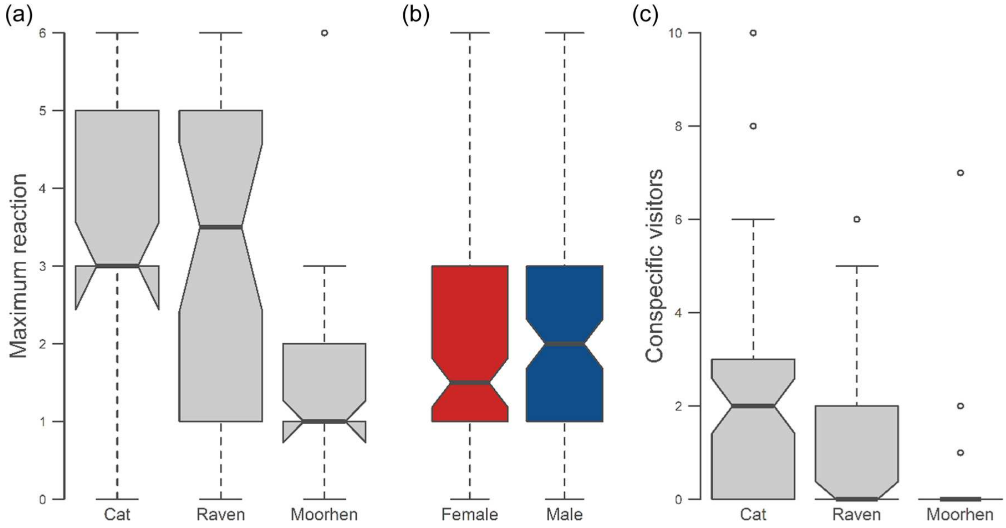

FIGURE 2 Variability in maximum reactions between nests with respect to the stuffed model species (a), sex of the parent (b), and the variability in the number of conspecific visitors present near the nest in the course of the trial with respect to the stuffed model species (c). Boxes depict the median (horizontal line inside the box), the 25th to 75th percentiles (box), the 25th and 75th percentiles minus or plus the 1.5× interquartile range, respectively, or the minimum and maximum value, whichever is smaller (whiskers), and outliers (circles). For moorhen and raven, $N = 34$ nests and for cat, $N = 32$ nests. [Color figure can be viewed at wileyonlinelibrary.com]

regardless of the number of conspecific visitors, the reactions toward the raven and the moorhen were enhanced by the presence and the number of conspecific visitors (Table 2). This pattern probably causes a somewhat greater diversity of reactions toward the raven than toward the cat (see the shape of the boxplots in Figure 2a). Second, over the course of the 15-min experiment, the strength of the reaction increased sharply during the cat trials but changed only slightly in the moorhen and raven trials (Table 3, Figure 3).

Both parents participated to a similar extent in nest defense (Figures 1 and 2b, Table 2). However, the females tended to start with a less forceful reaction than the males, but they later caught up with the reaction of the male (Figure 3, Table 3). The strength of the

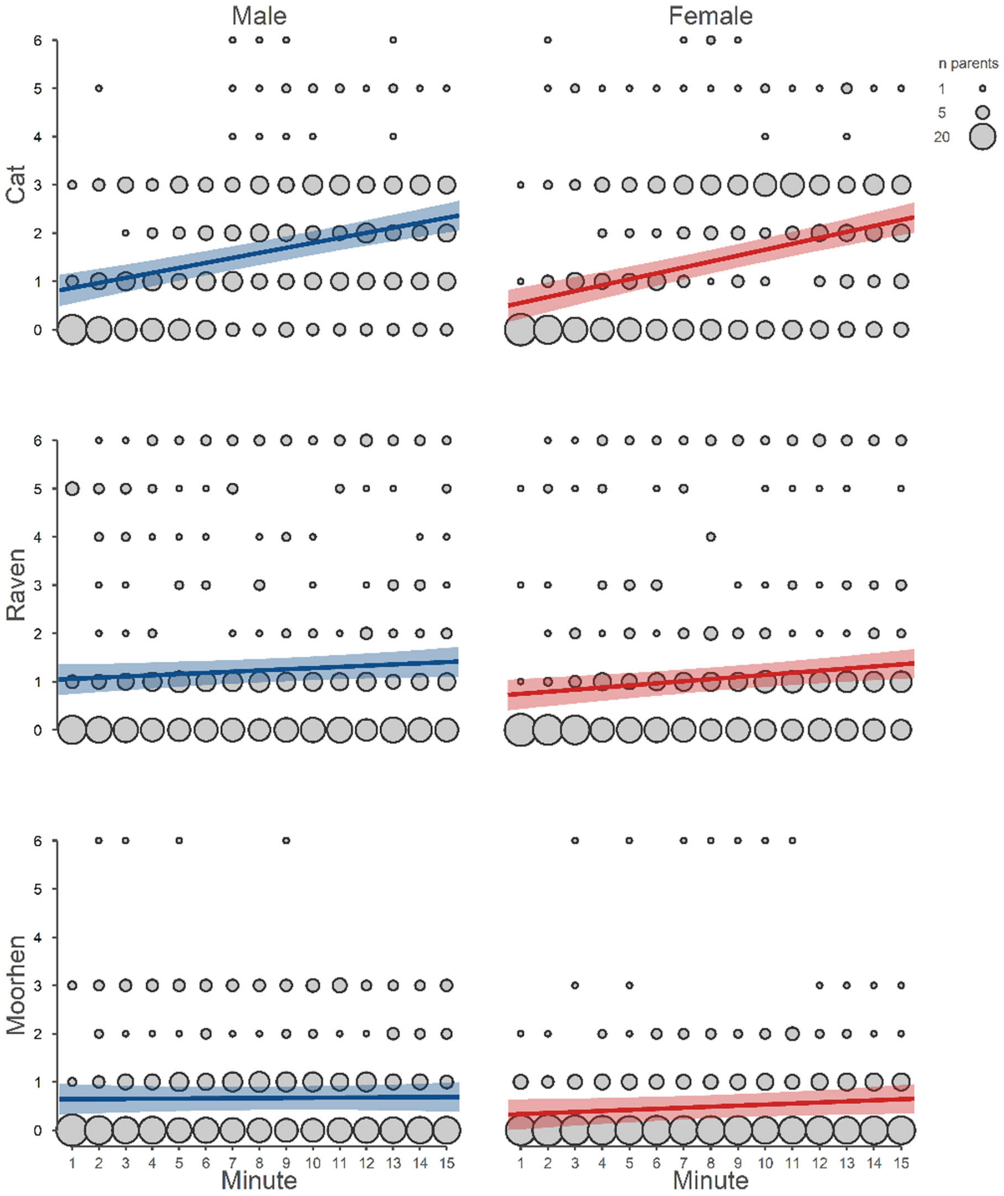

FIGURE 3 Changes in the strength of Red-Wattled Lapwing parent's reaction to moorhen, raven, and cat stuffed models in the course of the trial. Point size represents the number of males (left) or females (right) performing the particular reaction (1–6) as a maximum reaction during a particular minute of a trial (1–15). The line with the shaded area represents the model prediction with 95% CrIs based on the joint posterior distribution of 5000 simulated values generated by the "sim" function in R (Gelman et al., 2016), based on model outputs (Table 3). For moorhen and raven, $N = 34$ nests and for cat, $N = 32$ nests. 95% CrI, 95% credible interval. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 4 The number of conspecific visitors presents near the nest during the trial in relation to the stuffed model species and the density of neighboring nests.

Fixed effects	Estimate	95% CrI Lower	95% CrI Upper
Intercept	**−1.158**	**−1.974**	**−0.364**
Predator raven	**0.661**	**0.044**	**1.258**
Predator cat	**1.664**	**1.123**	**2.195**
N nests to 200 m	0.072	−0.234	0.383
Random effects	**% Explained variance**		
Nest (Intercept)	44%		
Residual	56%		

Note: There are shown the posterior estimates (medians) of the effect sizes with 95% credible intervals (CrI) from the posterior distribution of 5,000 simulated values generated by the “sim” function in R (Gelman et al., 2016). The variance components were estimated by the “lmer” function. The response variable was the maximum number of conspecific visitors observed during the trial in the immediate vicinity of the focal nest. Estimates with 95% CrI not containing 0 (i.e. which are statistically significant) are highlighted in bold.

Abbreviation: 95% CrI, 95% credible interval.

reaction was not affected by the incubation stage, or by increasing ambient temperature (Table 2).

3.2 | Number of conspecific visitors

In 39 trials (39% of a total of 100 trials), the parents were accompanied by 1–10 conspecific visitors (median = 2, mean = 3.2, SD= 2.14, Figure 3c), which became actively involved in alarm calling and attacking the stuffed models. At least one conspecific visitor was present in 22 trials (69%) with the cat, in 9 trials (26%) with the raven, and in 8 trials (24%) with the moorhen. The mean number of conspecific visitors present in the cat trials was higher than in the raven trials (estimate: 1.01, 95% CrI: 0.47–2.13), and also higher than in the moorhen trials (estimate: 1.31, 95% CrI: 0.65–2.65). The raven trials were also on average accompanied by more conspecific visitors than the moorhen trials (estimate: 0.28, 95% CrI: 0.01–0.76). However, contrary to our expectations, the number of conspecific visitors that were present was not related to the local density of active nests (Table 4).

3.3 | Origin of conspecific visitors

Among the conspecific visitors, 13 uniquely color-ringed, 12 metal-ringed, and 96 nonringed birds were observed. Several findings indicate that a substantial proportion of these birds were not breeding at the time of the experiment. First, among the 13 color-ringed birds, 11 were parents from nearby active nests (39– 185 m from the focal nest; median = 66), while the remaining 2 were not breeding at the time of the experiment. Second, the low proportion of color-ringed birds among the conspecific visitors (13 out of 121; 11%) contrasted with the high proportion of color-ringed parents (68 out of 108; 62.9%) breeding at the time of the experiment up to 200 m from the focal nest ($\chi^2 = 68$, $df = 1$, $p < .001$). Finally, the 12 metal-ringed conspecific visitors (i.e., 10%) were (in the context of the study population) almost certainly nonbreeding chicks from previous seasons.

4 | DISCUSSION

In this study, we have experimentally confirmed that Red-Wattled Lapwing parents defending their nests distinguish between predator species (they reacted most aggressively toward the cat, and least toward the moorhen), and they are often accompanied by conspecific visitors. First, we have revealed that the reaction of the parents to different predators varied not only in overall strength but also in intensity during the trials. Second, the parents at the nest during the experiments were accompanied by conspecific visitors, a substantial proportion of which were nonbreeding individuals. Third, both parents participated in nest defense to a similar extent. Finally, we found no significant effect of incubation stage and ambient temperature on nest defense effort.

4.1 | Choice of antipredator tactic

In line with our prediction, the Red-Wattled Lapwings adjusted their nest defense according to the potential predator model. They were most aggressive toward the cat and least aggressive toward the harmless moorhen. Contrary to our expectation, direct attacks were infrequent toward any of the models, including the raven, a nest predator, against which attacks could have been used with a lower risk of injury. The low proportion of attacks on the raven is in contradiction with the results obtained in a similar experiment on a related species, the Northern Lapwing (Elliot, 1985), breeding in the temperate zone. Whereas the Northern Lapwings used aerial attacks in almost 70% of the experimental nests (Elliot, 1985), we observed attacks by Red-Wattled Lapwings in less than 20% of the nests. We suggest that the more even (and thus generally lower) testosterone production of birds over the longer reproductive period in subtropics (Class & Moore, 2010; Goymann & Landys, 2011; Sandoval & Wilson, 2012) may result in a generally lower level of aggression during nest defense in these species. However, this assumption requires further detailed research across bird species and latitudes.

The overall reactions of lapwing parents to the raven and to the moorhen were milder and remained relatively stable during the experiments. In addition, the overall reactions to these models were associated with the participation of other conspecifics, which may explain the wider range of reactions to the raven and the moorhen. The presence of other conspecifics may condition the greater willingness of parents to react more strongly (Elgar, 1989; Tvardíková

& Fuchs, 2011). It may also have provoked irritability and led to an exaggerated reaction even to the moorhen, which would otherwise have been ignored. In addition, the diverse reactions of the parents to the raven may have resulted from confusion and panic. The raven is a visual predator looking for prey while in flight (Conover et al., 2010). If a raven lands near a nest, it has probably already located the position of the nest and poses an immediate threat to the nest, but not to the parents. The parents, therefore, have various options for repelling him.

The lapwings reacted most strongly to the cat, and their aggression escalated during the course of the experiments. However, the reactions were unaffected by the number of conspecifics, although the number of conspecifics was highest in the presence of the cat. The significantly increasing reaction of the parents may be due to the danger that the cat poses to nesting lapwings, or, alternatively, due to a reduction in fear in the presence of an immobile stuffed model (Hinde, 1954). The most common reaction toward the cat was intensive alarm calling on the ground. We offer two possible explanations for this reaction. First, birds avoid using direct attacks, which supports the prediction that the benefit of repelling the cat by direct attacks does not exceed the risk of injury or death to the adult (Amat & Masero, 2004). Second, this nest defense behavior may also reflect the predator's strategy for prey (nest) detection. The cat is a ground mammal that uses olfactory cues for short-distance nest searching (Conover, 2007). It can, therefore, be more confused by the additional visual and acoustic cues if lapwings move intensely and alarm on the ground, rather than fly around. By drawing attention to themselves, the lapwings may be applying a form of distraction display, diverting attention from the nest, which the predator has not yet located (Humphreys & Ruxton, 2020; Weston et al., 2018). In addition, the effectiveness of this tactic may lie in the presence of multiple conspecifics that increase the predator's confusion. It is, therefore, surprising that the number of conspecific visitors did not significantly affect the lapwing reactions.

To sum up, nest defense strategies of lapwing parents may be adjusted according to the predator species, and conspecific visitors may take on various roles. For example, the presence of conspecific visitors may induce a stronger reaction to the predator, in cases when the parents alone would have reacted less aggressively. On the other hand, if the main nest defense strategy of parents is to distract the predator, the presence of conspecific visitors attracted by a parent's calls may be an important part of the parent's strategy, aimed at increasing the efficiency of the nest defense (Humphreys & Ruxton, 2020). Untangling the role of conspecific visitors in different nest defense strategies will require further research on a broader range of bird species and predator models.

4.2 | Origin of conspecific visitors

The presence of conspecific visitors at the nests of defending parents was regularly observed in our experiments. The behavior of the conspecifics was similar to that of the parents defending the nest, but we did not quantify their activities during the experiments individually. However, individual marking enabled us to identify the origin of at least some of the conspecific visitors.

In agreement with our prediction, some conspecific visitors were recruited from the parents breeding in the neighborhood. Shared nest defense is a common feature among birds, typically in colonially breeding species (Kazama & Watanuki, 2010; Sandoval & Wilson, 2012). We found that the Red-Wattled Lapwing is capable of joint nest defense in the study population, where the distances between neighboring nests varied between 39 and 414 m (median = 105 m). Therefore, the behavior of birds breeding nearby can be mutualistic to defend offspring together (Krams et al., 2009; Larsen & Moldsvor, 1992). These immediately shared benefits may have helped to maintain the long-term relationships between individuals that are known in many social animals (Clutton-Brock, 2009).

A small proportion of metal-ringed individuals might represent matured chicks from previous successful nests. Nonbreeding offspring from previous breedings may remain in the territories and, although it may not help to incubate, it may help defend the territory. Kin cooperation shared by the young (helpers) is known in lapwings, specifically in the Southern Lapwing (*Vanellus chilensis*), in which the offspring from previous nests participate in territory defense, incubation (Lees et al., 2013), and chick care (Cerboncini et al., 2020). Indeed, the helping individuals among birds are usually offspring from previous nesting or other relatives (Cerboncini et al., 2020; Koenig & Dickinson, 2004). Were we to prove the relatedness of these metal-ringed individuals with nesting parents, it would be another example of helper kinship cooperation in birds.

A substantial proportion of conspecific visitors at the nests of defending parents were nonbreeding adults. It is unlikely that all these visitors without color rings were closely related to the parents defending the nests, and that they were currently breeding. In fact, nonbreeding conspecific floaters were common across the area throughout the breeding season (Elhassan et al., 2021) and could easily move among the breeding territories. We suggest additional possible explanations for their presence at the nests during experiments. First, the floaters can be attracted by the adult alarm calls, simply because predatory events could be an opportunity for them to acquire a breeding territory (Bruinzeel & Van de Pol, 2004; Smith, 1978; Stutchbury & Zack, 1992). The fact that the reactions of parents increased with the number of visitors and, exceptionally, there were also skirmish with conspecifics, may indicate an effort to defend the territory against the potential competitors. Second, as we observed some conspecific visitors attacking the stuffed models, the participation of nonbreeding floaters in joint nest defense can be motivated by the expectation of future benefits (reciprocity) in similar situations during their own breeding in this settled population, where they all know each other (Clutton-Brock, 2009; Krebs & Davies, 2009; Nowak, 2006). Third, the nonexperienced bachelors may be learning how to assess the risks that they will face. Therefore, further detailed research is required to untangle the various possible causes of joint nest defense by individuals with different breeding and social status.

4.3 | Roles of sex, incubation stage, and ambient temperature

We did not find a significant difference in reactions between the sexes. Although the females tended to start with a less aggressive reaction than the males, they later caught up with the male reaction. This result is not consistent with the findings for many birds, particularly in the temperate zone, where the defense of territories and nests are typically a matter for males rather than for females (Brunton, 1990; Elliot, 1985; Kis et al., 2000; Tryjanowski & Goławski, 2004). A possible explanation for the similar defense behavior in the Red-Wattled Lapwing males and females studied here is that the extremely hot environment of the Arabian desert may force the birds into equally shared parental roles, including incubation and nest defense against predators (Cardilini et al., 2015; Fedy & Stutchbury, 2005). In addition, the reduced level of testosterone in birds breeding in the subtropics may reduce the difference in aggression between males and females (Class & Moore, 2010; Goymann & Landys, 2011; Sandoval & Wilson, 2012).

We did not find a significant relationship between the behavior of the parents and the incubation stage of their eggs. Although some studies have found such a relationship (Brown & Brown, 2004; Galeotti et al., 2000; Mallory et al., 1998; Meilvang et al., 1997) in various bird species, the relationship is ambiguous (Cruz-Bernate, 2020; Forbes et al., 1994; Gunness & Weatherhead, 2002; Kis et al., 2000). In addition, the increased aggression in later incubation stages found in some species in some areas might result from the accumulative disturbances to which the birds had been exposed before, and not from the stage of incubation itself (Burger, 1981). In addition, the effect of the incubation stage may be minor in comparison with other more important factors (e.g., negative experience from previous unsuccessful breeding attempts; Caro, 2005). Certainly, a more important reason for increased aggression is the hatching of the young and subsequent care for them (Kostoglou et al., 2020). However, this was not the subject of our experiment.

We did not find a relationship between ambient temperature and nest defense behavior. Brown and Brown (2004) specified that Crowned Lapwings (*Vanellus coronatus*) in tropical Africa reduced their nest defense activity at temperatures above 25°C. High daily temperatures prevailed in our study area, where temperatures of more than 50°C can be reached (own observations). Our experiments were carried out in the range between 16°C and 54°C (mean = 32.1°C), and only 18% of the experiments were conducted at temperatures below 25°C. It is, therefore, likely that the temperature effect could not be detected, as (less common) day periods with temperatures below 25°C were underrepresented in our sample. We also have a small sample showing that defense activity will increase at the highest temperatures, around 50°C, when we would intuitively expect a more intensive defense of eggs at risk of overheating (Amat & Masero, 2007).

5 | CONCLUSION

This study provides new insight into the complexity of the nest defense patterns in ground-nesting birds inhabiting a hot desert environment. We have experimentally confirmed that Red-Wattled Lapwing parents distinguish between potential predators and adjust their defense strategy accordingly. In addition to currently breeding neighbors, nonbreeding individuals were present at the nests during the nest defense of the parents. Conspecific visitors play an important role in nest defense, in that their presence increases the strength of the parental reaction, or in that they assist in distracting a predator. Both parents defend the nest to a similar extent, perhaps due to the strong environmental demands in the subtropical desert. The distinctions made in the reactions to different predators, the choice of a proper defensive strategy, and the presence of variously motivated conspecifics indicate the complexity of nest defense behavior in birds. We call for comparative experimental research on a broader scale including various bird species, predator models, and environments to reveal the drivers of these defense behavior patterns.

AUTHOR CONTRIBUTIONS

Miroslav Šálek, Kateřina Brynychová, and Martin Sládeček conceived the study. Miroslav Šálek and Martin Sládeček analyzed the data. Miroslav Šálek, Kateřina Brynychová, and Martin Sládeček wrote the manuscript. All co-authors collected the data and commented the manuscript.

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DATA AVAILABILITY STATEMENT

The raw data and the R codes that enabled replications of all analyses performed in this paper, and that were also used for generating all the figures, are available from Open Science Framework: https://osf.io/bfvgj/

ETHICS STATEMENT

This study was conducted in accordance with the current laws of the United Arab Emirates.

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Chapter 3

Brynychová, K., Šálek, M. E., Vozabulová, E., & Sládeček, M. (2020). Daily rhythms of female self-maintenance correlate with predation risk and male nest attendance in a biparental wader. *Journal of Biological Rhythms, 35*(5), 489-500.

Daily Rhythms of Female Self-maintenance Correlate with Predation Risk and Male Nest Attendance in a Biparental Wader

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Abstract Parents make tradeoffs between care for offspring and themselves. Such a tradeoff should be reduced in biparental species, when both parents provide parental care. However, in some biparental species, the contribution of one sex varies greatly over time or between pairs. How this variation in parental care influences self-maintenance rhythms is often unclear. In this study, we used continuous video recording to investigate the daily rhythms of sleep and feather preening in incubating females of the Northern Lapwing (*Vanellus vanellus*), a wader with a highly variable male contribution to incubation. We found that the female's sleep frequency peaked after sunrise and before sunset but was low in the middle of the day and especially during the night. In contrast, preening frequency followed a 24-h rhythm and peaked in the middle of the day. Taken together, incubating females rarely slept or preened during the night, when the predation pressure was highest. Moreover, the sleeping and preening rhythms were modulated by the male contribution to incubation. Females that were paired with more contributing males showed a stronger sleep rhythm but also a weaker preening rhythm. If more incubating males also invest more in nest guarding and deterring daylight predators, their females may afford more sleep on the nest during the day and preen more when they are off the nest. Whether the lack of sleep in females paired with less caregiving males has fitness consequences awaits future investigation.

Keywords preening, sleep, biparental incubation, shorebirds, nest predation, Northern Lapwing *Vanellus vanellus*

Sleep and preening address basic animal life requirements (Van Iersel and Bol, 1957; Steinmeyer et al., 2010), and animals devote a lot of time to these self-maintaining activities (Connolly, 1968; Spruijt et al., 1992; Cotgreave and Clayton, 1994; Lesku et al., 2006). In most birds, a substantial part of the reproduction process involves time-consuming incubation. At the same time, bird parents need to forage, sleep, and take care of their bodies (Cotgreave and Clayton, 1994). As these activities may influence the

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risk of depredation, which is the most prevalent cause of nest failure (Ricklefs, 1969; Kubelka et al., 2018), incubating parents have to deal with a tradeoff between care for the offspring and the need for self-maintenance. The predation risk can be mitigated by subordinating the behavioral rhythms on the nest to the rhythm of predation pressure (Cervencl et al., 2011; Ekanayake et al., 2015), especially when both parents share the incubation duties (Komdeur and Kats, 1986; Weatherhead, 1990).

From a behavioral viewpoint, sleep is a temporary and rapidly reversible state of reduced susceptibility to surrounding stimuli with a restorative function (Siegel, 2003; Lima et al., 2005). Animals are more vulnerable to predation while they are sleeping (Lima et al., 2005; Lima and Rattenborg, 2007). In birds, unihemispheric slow-wave sleep may partially compensate for the reduced vigilance during sleep, because it allows birds to sleep with 1 eye open (Rattenborg et al., 1999; Rattenborg et al., 2000). At the same time, sleep makes individuals inconspicuous, and this may reduce detection by a predator (Lima et al., 2005; Lima and Rattenborg, 2007; Zimmer et al., 2011). Sleep on the nest can thus also be a defense tactic against a predator, particularly since the bird remains motionless and partially vigilant. Among birds, the length of sleep fluctuates widely from more than half of the day to a few hours per day, but also adaptive sleep loss during the reproduction period has been described (Roth et al., 2006; Lesku et al., 2012). Species differ in the extent to which they are flexible in the timing of their sleep (e.g., Hamilton et al., 2002; Chudzinska et al., 2013). Specifically, the timing of sleep during incubation may reflect not only the intensity of predation pressure but also the daily pattern of food availability (Meijer and Langer, 1995) and the ability or the willingness of the partner to guard the nest (Grønstøl, 2003).

Birds also need to spend a large proportion of their time using their bill to preen their feathers (Delius, 1988; Cotgreave and Clayton, 1994). This is necessary for feather maintenance, for distributing the preen wax, and for controlling ectoparasites (van Rhijn, 1977; Delius, 1988). Preening reduces the vigilance of an individual, and unlike sleep, it makes the individual much more visible to predators (Smith et al., 2012). The timing of preening is probably very flexible (Delius, 1988), unlike the timing of sleep (Randler, 2014), and this could enable individuals to schedule their preening during periods when it is less risky.

During biparental incubation, parents need to synchronize their activities to minimize the time for which the nest remains unattended (Bulla et al., 2016b; Sládeěek et al., 2019b). A large proportion of the off-nest time of each partner is necessarily spent foraging (Ashkenazie and Safriel, 1979; Grønstøl, 2003; Bulla et al., 2015); thus, the time for self-maintenance activities such as sleeping and preening may be limited. These activities might be carried out more on the nest during incubation. Consequently, when there is a substantial variation in the division of incubation duties between the parents, the contribution of the generally less care-giving partner can play an important role in the timing of self-maintenance of the incubating parent. In particular, a higher male contribution can enable the female to sleep and preen more while she is off the nest. She can therefore be more vigilant (sleep less) and less conspicuous (preen less) during incubation, at least during the peak activity of predators. However, studies on the rhythmicity of self-maintenance activities are scarce. To the best of our knowledge, no study has investigated the link between the self-maintenance rhythm of a care-giving parent and the daily rhythm of predation, or the link between the self-maintenance rhythm and the partner's investment in parental care.

In this study, we used continuous video recordings to investigate the behavioral rhythms of incubating Northern Lapwing (*Vanellus vanellus*) females. The Northern Lapwing is a biparentally incubating, ground-nesting wader with a variable contribution of males to incubation and almost exclusive female incubation at night (Sládeček et al., 2019c). Consequently, some females sit on the nest for only 50% of the time, while other females almost 90%. We hypothesized a daily rhythm of sleep and preening on the nest, because incubating parents are visible and they need both to deter visually-oriented predators (e.g., corvids; Elliot, 1985b; Kis et al., 2000) during the daylight and to be safe at night, relying on crypsis and vigilance, when medium-sized mammals such as Red Fox (*Vulpes vulpes*) and martens (*Martes* sp.) are active (Seymour et al., 2003). We also hypothesized that a lack of male care would affect the daily rhythmicity of female self-maintenance behavior, because these females would need to spend more time on self-maintenance while incubating.

Specifically, we (1) investigated the timing of nest predation events within our population. Then we (2) tested whether sleeping and preening followed any daily rhythm and, if so, whether such rhythm was similar to the daily rhythm of predation pressure. Finally, we (3) tested whether females that were paired with more caregiving males slept and preened less during incubation, thereby changing the possible self-maintenance rhythm.

METHODS

The study was conducted between March and June 2015 and 2016, in the České Budějovice basin, Czech Republic (49° 15′N, 14° 05′E). To assess the daily pattern of nest predation pressure, we used 33 cases in which Northern Lapwing nests were depredated within our study area and where the time of depredation was known. We further assumed that other ground-nesting waders in the study area experienced the same predation pressure (Macdonald and Bolton, 2008; Mason et al., 2018), and we therefore also included 17 cases of Little Ringed Plover (*Charadrius dubius*) nests that we followed as a part of a different project. Thus, we used a total of 50 predation events, of which 21 were recorded by video cameras, 23 by temperature data loggers, and 6 by the Frequency Identification System (where we assume that the approximate time of depredation is the time of the last incubation record).

We monitored the incubation on 55 nests of Northern Lapwing. Using small cameras placed approximately 1.5 m from the nest, we obtained continuous video recordings of 3 days (median, range: 1-5; Sládeček et al., 2019c). Since it takes an immense amount of time to extract the detailed behavior, we randomly chose a 1-day complete record for each nest (i.e., 24 h of uninterrupted recording).

We extracted behaviors from the recordings using Boris software version 6.3 (Friard and Gamba, 2016), with precision to within 1 s. First, we determined the beginnings and the ends of all incubation bouts, taken as the time when the bird stands on both legs in the nest. Within the pair, we identified the sex of the incubating bird, using a set of sex-specific plumage traits, for example, the crest length and the extent of melanin-based ornaments on the face and breast, which are well identifiable features (Meissner et al., 2013; Schonert et al., 2014).

Second, we extracted the beginning and the end of each sleeping bout. Of the 2 sleeping postures described elsewhere (Amlaner and Nigel, 1983; Dominguez, 2003; Gauthier-Clerc and Tamisier, 2012), the birds slept predominantly with the head turned backward and partly tucked between the shoulder coverts. In rare cases (i.e., ~2% of the sleeping bouts), the birds slept with their head forward (as during regular incubation) but drooping (see videos in the Supplementary Material). Note that while remaining in the sleeping position, the bird often opened 1 eye for a short time and scanned the surroundings. We interpret these periods as sleep, and we include them in the sleeping bouts, as this behavior seems to be connected with unihemispheric slow-wave sleep, which has frequently been reported in birds (Rattenborg et al., 1999; Rattenborg et al., 2000; Roth et al., 2006).

Third, we extracted preening, defined as rapid bill movements between the feathers and the preen gland (van Rhijn, 1977). Since preening is often performed in clusters of preening bouts lasting from 1 s to several seconds, interrupted by breaks of similar length, we extracted preening as an occurrence (“yes”/”no”) of this behavior during each 30-s interval of incubation by the female.

Statistical Analysis

All procedures were performed in R version 3.5.0 (R Core Team, 2017). General linear models were fitted using the “lm” function, and general linear mixed-effects models were fitted using the “lmer” function from the “lme4” R library (Bates et al., 2015). For all model-based parameter estimates, we report the effect sizes as the median and the Bayesian 95% credible interval (95%CrI), based on the posterior distribution of 5000 values simulated by the “sim” function from the “arm” R library (Gelman et al., 2016).

To test the daily rhythmicity of the predation, we calculated the general linear model with the number of known predation events for each hour of the day as response variable. We used 2 mixed-effect models to explain the variation in female sleeping behavior. In the first model, the dependent (response) variable was the ratio of female sleep to the overall time for which she attended the nest within a particular hour (“sleep”). That is, the hours when a female did not incubate were excluded from this analysis. We weighted the model by the square root of the female incubation time during a particular hour. Note that an alternative approach, with the absolute time of sleep within an hour (i.e., regardless of female nest attendance per hour), yields similar results (Suppl. Table S1). In the second model, we used the length of the sleeping bouts as a response variable. To describe the variations in preening behavior, we used the number of preening records, divided by the overall time for which the female attended the nest within a particular hour (“preening”) as a response variable. For this analysis, we used only hours with more than 10 min of female incubation (to exclude possible extreme proportions of preening events during short video recordings), and we weighted the model by the square root of the female incubation time during a particular hour.

We used a similar set of predictors in all models. To test for the daily rhythmicity in a response, we transformed the time to radians ($2 \times \text{time} \times \pi/\text{period of supposed rhythmicity}$) and fitted the sine and the cosine of the radians (Bulla et al., 2016a). As the period of rhythmicity, we used either a 24-h cycle or a 12-h cycle, based on a general pattern visualized from the raw data (Suppl. Figs. S1, S2; supplementary actograms in Sládeček et al., 2019a). Moreover, because birds (and also predators) probably react to actual changes in the light, we included in each model a binomial predictor indicating whether it was "day" or "night" during a particular hour. An hour was assigned as "night" when the sun was more than 6° below the horizon for more than one half of the hour, and vice versa. As a measure of the male contribution to incubation, we used the proportion of male nest attendance in a given day (i.e., 24 h). In all models, we also included the interaction between the male incubation effort and the time of day.

Further, to avoid misinterpretations of the results, we defined and tested the effect of potentially confounding variables, that is, the date within the season on which the nesting started, the time within the incubation period at which the video recordings were made, and 2 weather variables, temperature (daily means) and precipitation (daily sums). Measurements from České Budějovice (H. Zajíčková, Czech Hydrometeorological Institute, České Budějovice) were used for both weather variables. Since neither of these predictors has a substantial effect on sleep (Suppl. Table S2a, b) or preening (Suppl. Table S2c), we did not include these predictors in the models presented in the main text. The full models including the effects of these predictors are presented in Supplementary Table S2a-c.

All continuous predictors, except for the time of day, were included in all models z-transformed (mean centered and divided by the standard deviation; Schielzeth, 2010). In all models, we fitted nest identity as a random intercept; time predictors were included as random slopes (Schielzeth and Forstmeier, 2009).

RESULTS

Daily Variation in Predation

Nests were depredated almost exclusively at night; that is, 42 of 50 depredation events occurred when the sun was >6° below the horizon (Fig. 1a; Table 1a). In addition, the video-recorded predators were mammals only: 15 Red Foxes (*Vulpes vulpes*), 4 Stone Martens (*Martes foina*), 1 European Badger (*Meles meles*), and 1 Wild Boar (*Sus scrofa*).

Nest Attendance

In total, we monitored 55 nests and extracted the incubation record of a random complete day (24 h) for each nest. Within this time, the females spent 17.8 ± 2.7 h on incubating (mean ± SD, range: 6.5-21.8 h), while the males spent 2.0 ± 1.6 h on incubating (mean ± SD, range: 0-6.4 h), with clear preference for daylight incubation (Fig. 1b). Thus, the nests were not attended by either of the parents for 4.1 ± 2.3 h (mean ± SD, range: 0.8-14.7 h). For a detailed description of the Lapwing incubation pattern, see Sládeček et al. (2019c).

Sleep

Incubating females slept on their nests for 3.0 ± 1.8 h of 24-h days (mean ± SD, range: 13 min–7.0 h), which corresponds to 17.5% of their incubation time (mean, range: 1.2%-45%). The sleep was divided mostly into very short sleeping bouts, with a median length of only 1.7 min (range: 3 s–1 h; Fig. 1d, see also Suppl. Fig. S3 and supplementary actograms in Sládeček et al., 2019a). The between-female variation in the overall sleep length has been associated with the number of sleeping bouts, rather than with the length of the sleeping bouts (Suppl. Fig. S4). The daily sleeping rhythm was strongly bimodal, with maxima in the morning and in the late afternoon and minima in the middle of the day and especially at night (Table 1b; Fig. 1c; Suppl. Fig. S5). In addition, female sleep was associated with male contribution to incubation. Contrary to our hypothesis, females with more help from their mate slept more, and the bimodal ~12-h sleep rhythm was stronger than in females with little or no male help (Table 1b; Fig. 1c; Suppl. Figs. S1, S5).

The length of the sleeping bouts followed a daily rhythm, with the longest sleeping bouts during the night (median around midnight: 4 min) and the shortest sleeping bouts in the middle of the day (median around noon: 1 min; Table 1c; Fig. 1d). This pattern was not associated with the male contribution to incubation.

Preening

Preening of females on their nests occurred 122 ± 83 times per 24 h (median ± SD, range: 7-398), which corresponds to a 6.7% median probability that preening occurs within a 30-s interval of female incubation. However, the median probability of preening during a 30-s interval ranged from 0% to more than 27% between females.

The preening behavior followed a daily rhythm, with the maximum in the middle of the day (median after midday: 21.7%) and the minimum at night (median after midnight 1.7%; Table 1d; Fig. 1e). In contrast to sleep, the more the male helped the female with incubation, the less the incubating female preened (Table 1d; Fig. 1e; Suppl. Fig. S6). Also, the females receiving more help had a weaker daily rhythm of preening (Table 1d; Fig. 1e; Suppl. Fig. S2, S6).

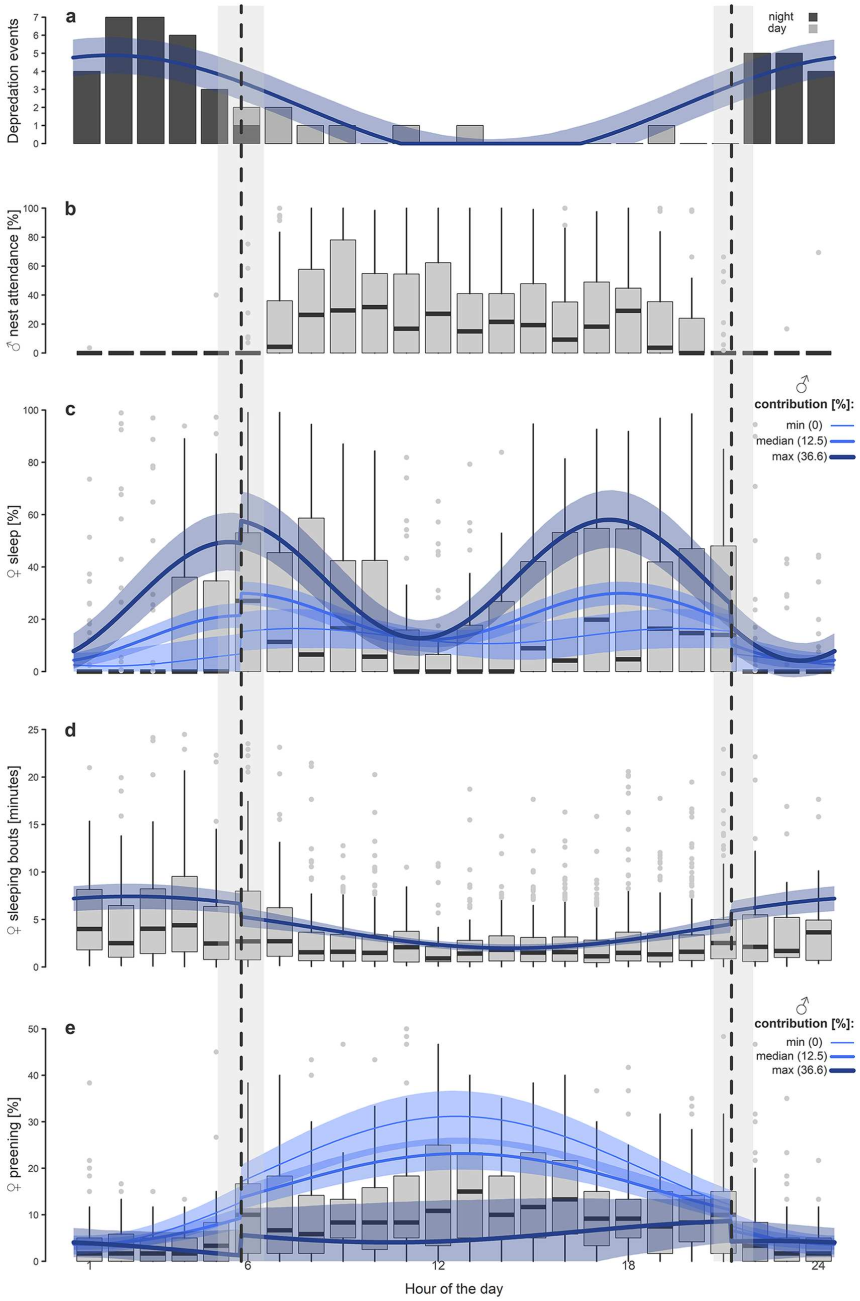

Figure 1. (a) Daily variation in nest predation. Bars depict the number of predation events in particular hours in the study area. (b) Daily pattern of male contribution to incubation. (c) Daily variation in female sleep. (d) Daily changes in the length of female sleeping bouts. (e) Daily variation in female preening behavior. Percentages in (b), (c), and (e) refer to the proportions within the given hour. Boxplots (b-e) depict the median (horizontal line inside the box), 25th to 75th percentiles (box), 25th and 75th percentiles minus or plus the 1.5× interquartile range, respectively, or the minimum and maximum value, whichever is smaller (whiskers), and outliers (circles). Curves (a, c, d, e) with shaded areas indicate the model prediction, with 95%CrIs based on the joint posterior distribution of 5000 simulated values from the model outputs (Table 1) and generated by the "sim" function in R (Gelman and Hill, 2007). Note that fits in (c-e) also include the effect of the night (i.e., whether sun was >6° below the horizon or not), which causes skips in the fit. Male contribution to incubation in (d) has been set to the mean value. Vertical dashed lines indicate the median and gray polygons indicate the range for the beginning and end of the dark part of the day (i.e., when the sun was >6° below the horizon).

Table 1 Predation pressure in relation to time of day.

a. Predation pressure in relation to time of day

Response	Effect Type	Effect	Estimate	Lower	Upper
				95% CrI	
Predation pressure (*n* predation events)	Fixed	**Intercept**	**2.083**	**1.499**	**2.642**
		Sin (24 h)	**0.864**	**0.047**	**1.693**
		Cos (24 h)	**2.692**	**1.868**	**3.504**

b. Daily pattern of female sleep

Response	Effect Type	Effect	Estimate	Lower	Upper
				95% CrI	
Female sleep	Fixed	**Intercept**	**0.215**	**0.188**	**0.242**
		M incubation	**0.059**	**0.035**	**0.083**
		Sin (12 h)	**0.036**	**0.006**	**0.065**
		Cos (12 h)	**–0.087**	**–0.114**	**–0.06**
		Night (yes)	**–0.086**	**–0.112**	**–0.06**
		M incubation: Sin (12 h)	**0.037**	**0.007**	**0.066**
		M incubation: Cos (12 h)	**–0.045**	**–0.071**	**–0.02**
	Random (variance)	Nest (intercept)	10%		
		Sin (12 h)	13%		
		Cos (12 h)	9%		
		Residual	69%		

(continued)

Table 1 (continued)

c. Daily pattern in the length of female sleeping bouts

Response	Effect Type	Effect	Estimate	95% CrI	
				Lower	Upper
Length of sleeping bouts (min)	Fixed	**Intercept**	**4.068**	**3.413**	**4.691**
		M incubation	0.503	−0.123	1.127
		Sin (24 h)	**0.961**	**0.605**	**1.294**
		Cos (24 h)	**1.819**	**1.080**	**2.512**
		Night (yes)	**1.353**	**0.598**	**2.097**
		M incubation: Sin (24 h)	0.214	−0.129	0.538
		M incubation: Cos (24 h)	0.075	−0.622	0.752
	Random (variance)	Nest (intercept)	17%		
		Sin (24 h)	3%		
		Cos (24 h)	16%		
		Residual	65%		

d. Daily pattern of female preening

Response	Effect Type	Effect	Estimate	95% CrI	
				Lower	Upper
Female preening	Fixed	**Intercept**	**0.151**	**0.131**	**0.172**
		M incubation	**−0.034**	**−0.052**	**−0.016**
		Sin (24 h)	−0.006	−0.019	0.007
		Cos (24 h)	**−0.070**	**−0.091**	**−0.048**
		Night (yes)	**−0.044**	**−0.066**	**−0.022**
		M incubation: Sin (24 h)	−0.003	−0.016	0.010
		M incubation: Cos (24 h)	**0.036**	**0.019**	**0.052**
	Random (variance)	Nest (Intercept)	24%		
		Sin (24 h)	9%		
		Cos (24 h)	17%		
		Residual	51%		

The posterior estimates (medians) of the effect sizes with the 95% credible intervals (CrIs) from a posterior distribution of 5000 simulated values generated by the "sim" function in R (Gelman et al., 2016). Variance components were estimated by the "lm" function (a) or by the "lmer" function (Bates et al., 2015) (b-d). Time was taken as "hour of day" transformed to radians (2 × hour × π/period of interest – 24 h) and was fitted as the sine and cosine of the radians. Male contribution was z-transformed (mean-centered and divided by SD). Estimates whose 95% CrIs did not contain 0 are highlighted in bold. Response variables were as follows: (a) the number of predation events during a particular hour known from our data set (see the Methods); (b) the relative proportion of sleep within the female incubation time and during the particular hour of the day; (c) the length of sleeping bout in minutes, and (d) the relative proportion of 30-s intervals within the female incubation time when the female preened. Models (b-d) were weighted by the square root of the female incubation time during the hour.

DISCUSSION

With the use of continuous video recordings of breeding Northern Lapwings, we revealed a strong daily rhythmicity in the self-maintenance behavior of incubating females. Female sleep showed a bimodal ~12-h rhythm, while female preening showed a unimodal 24-h rhythm. Self-maintenance was suppressed particularly during the night, when the predation risk for our population is the highest. We also revealed that the male contribution to incubation correlated with the intensity of female self-maintenance. Specifically, an increased male contribution to incubation was associated with a stronger sleep rhythm and a weaker preening rhythm of incubating females.

Dynamics of Behavioral Rhythms

The 3 self-maintenance traits—sleep, length of sleeping bouts, and preening—followed 3 different rhythms. Whereas the sleep peaked at dawn and before sunset, the sleeping bouts were longest during the night. In contrast, preening showed a unimodal pattern, with the maximum around noon. In other words, both sleeping and preening were suppressed during the night hours, when the predation pressure was also highest. In fact, predation risk has been suggested as an important driver of the timing of sleep and preening in various bird and mammal species (Randler, 2005; Amo et al., 2011; Javůrková et al., 2011).

Our findings suggest that incubating Northern Lapwing females strived to be vigilant at night. In contradiction with our results, previous studies on the Mallard (*Anas platyrhynchos*) showed that the sleep intensity of incubating females was highest during the night (Javůrková et al., 2011). Similarly, nonincubating captive ducks (Zimmer et al., 2011) and nonincubating wintering Great Tits (*Parus major*) in nest boxes (Stuber et al., 2014) slept more at night when the perceived predation risk was experimentally increased. Beauchamp (2007) suggested that lower nighttime vigilance in birds can result from unfavorable light conditions with limited visual perception and predator detection. Nonvigilant (e.g., sleeping) individuals might switch from ineffective visual cues to perceiving acoustic stimuli, which are better transmitted and therefore better used during the relatively noiseless night (Wiley and Richards, 1982). It is also possible that passerine birds in nest boxes are well protected against most predators and that ducks breeding on islands or in dense coastal vegetation can hear the predator rustling in the reeds (i.e., they can afford to sleep). However, open agricultural areas are different. Ground nests are easily silently accessible. Thus, silent night predators of eggs and incubating birds such as foxes or owls are detectable only over a short distance in the dark. Incubating birds in open agricultural fields may have no other antipredator strategy then to remain vigilant.

If lack of female sleep during the night may protect females against predation, what stands behind the sleeping peaks after sunrise and before sunset and the lack of sleep around noon? We provide 2 explanations that are not mutually exclusive. First, the females may need to sleep after and before the long sleepless nights. Second, the morning and afternoon sleep peaks may be another form of antipredator tactic, this time against daytime predators. Most predators that are active during the daylight (e.g., corvids and hawks) have peak activity similar to the peak sleeping activity of incubating female lapwings (Fig. 1a; Rutz, 2006; Roth and Lima, 2007) and usually use sight to detect their prey at a long distance. Notably, a male partner in lapwings is often on the watch. Thus, for an approaching visual daytime predator, a vigilant nonincubating partner will always be easier to detect than a sleeping (immobile) bird incubating the eggs. Moreover, the nonincubating vigilant parent emits a loud warning sound whenever he (or she) detects or actively deters approaching predators during the daylight hours (Elliot, 1985a; Kis et al., 2000), giving enough time for the sleeping bird on the nest to react. In addition, daytime predators can be detected at a great distance, so incubating birds can change their behavior in time, if necessary. Thus, sleeping on the nest during daylight may be an appropriate combination of antipredator tactics and self-maintenance. However, why females prefer preening to sleep during noon remains unclear. One explanation might be that predators are scarce around noon, and females can thus perform other activities associated with conspicuous movement on the nest, such as preening, egg turning, improving the nest lining, and feeding, which it is useful to perform at the time of lower predator activity. Noon is also the time when incubation attendance drops (Sládeček et al., 2019c).

Although night sleeping bouts were generally rarer than daytime sleeping bouts, the night sleeping bouts were paradoxically somewhat longer (median ~4 min) than the daylight sleeping bouts (median ~2 min). As Dukas and Clark (1995) suggest, the continuous vigilance of birds during the night may not be sustainable for the whole night, thus perhaps explaining why sleep-deprived birds occasionally fall into longer sleep bouts.

We found that the proportion of night predations (in the dark) was 84% (42 of 50 depredation events). Although the dynamics of the behavioral rhythms provide a good reflection of the pattern of real predation events, we can consider that a principal driver for changing the sleep behavior during incubation may be a switch in the light conditions, which can play the role of a proxy for the perception of predation risk. It is if the female cannot see the predator in the dark, she will resist the sleep. Note that the binomial predictor day/night was an important factor in all of our models. However, females started to sleep even before the end of the night, that is, before the approach of daylight (sunrise), while their sleep sharply ended after twilight (dusk; Table 1b; Fig. 1c). Interestingly, the Red Fox has a very similar pattern to the start and end of female sleep from March to May (i.e., a sharp drop in the dark before sunrise as well as peak activity shortly after dusk; Kämmerle et al., 2020). Thus, it is possible that the direct experience with dominant predators at the local level can adjust the general effect of light conditions on the sleep rhythm during incubation.

This high predation risk during the night multiplied by the inability to detect a predator over a long distance might be a crucial cause of using different antipredator behavior on the nest between night (vigilance) and daylight (sleep). Further research should therefore investigate whether reduced night vigilance or reduced sleep of incubating parents after sunrise and before sunset may increase nest and/or adult depredation.

Effect of Male Incubation Effort

Our study provides correlative evidence that the contribution of males to incubation is linked to the self-maintenance behavior of their female incubating partners. In contradiction to our hypothesis, females that were paired with more caregiving males slept more during incubation and also during the night. The male contribution to incubation is perhaps a proxy for general male investment; that is, males that incubate more are also more vigilant and active in defending the nest, patrolling around the nest, giving warning calls, and chasing away predators (Cramp and Simmons, 1983; Elliot, 1985a, 1985b; Kis et al., 2000). Indeed, Northern Lapwing females with a slightly greater off-nest sleeping time paired with males that incubated more (Grønstøl, 2003). If a male's defensive activity correlates with his willingness to incubate, females paired with more territory-defending males may be better protected and could afford to be less attentive. Such division of parental roles may be an example of social synchronization, which has only recently been described in wild animal populations (Bulla et al., 2016b; Leniowski and Węgrzyn, 2018).

Since our analysis covered a single randomly selected day from the incubation period of each nest, we cannot exclude the possibility that females with an extremely low amount of sleep slept more during the previous days or would sleep more in the subsequent days. However, incubation patterns, such as incubation attendance and male contribution, remain almost consistent in the course of the incubation period and are highly repeatable in the Northern Lapwing (Sládeček et al., 2019c). In addition, the sleeping effort changed little over the incubation stage and season (Suppl. Table S2a). Notably, biological rhythms such as sleep also remain repeatable in other species (Steinmeyer et al., 2010; Stuber et al., 2015; Stuber et al., 2016). Whether the sleep-deprived females compensate for the sleep deficit and thus sleep more during subsequent days deserves further investigation.

Sleep deprivation can have a negative influence on attention, motivation, memory (Rolls et al., 2011; Vyazovskiy et al., 2011), and reproductive output (Potdar et al., 2018). Note that females with little or no help from their partner can hardly compensate for the lack of sleep during their off-nest time, because they are off-nest for only 10% to 15% of the time, during which they need to forage. In addition, the Northern Lapwing seems to spend a negligible proportion of the off-nest time sleeping (Grønstøl, 2003). Note that lack of sleep over extended periods of time (even weeks) during reproduction has also been reported in the territory-defending Pectoral Sandpiper (*Calidris melanotos*; Lesku et al., 2012) and in off-nest foraging frigate birds (Rattenborg et al., 2016). The positive relationship between male incubation effort and female sleep suggests yet another advantage of being paired with a more caregiving partner.

In accordance with our hypothesis, females paired with more caregiving males spent less time preening on the nest. This suggests that these females can preen when they are off the nest. The reduced preening on the nest likely reduces movement on the nests and may increase vigilance, which can reduce nest detectability by predators. However, whether the time spent preening on the nest increases nest predation risk awaits future testing.

CONCLUSION

We have revealed different daily rhythms in the sleep and preening of incubating Northern Lapwing females. Their sleep followed ~12-h periodicity associated with sunrise and sunset, which corresponds with predator activity patterns. In contrast, preening followed a 24-h rhythm, with a peak in the middle of the day, when predation pressure was lowest. Interestingly, the intensity of the rhythms was modulated by the male contribution to incubation. Females paired with more contributing males had a stronger sleep rhythm and, conversely, a weaker preening rhythm. How the modulation of daily self-maintenance rhythms in species with biparental care affects reproductive success and individual fitness awaits further investigation.

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AUTHOR CONTRIBUTIONS

M.S., K.B., and M.E.Š. conceived the study, M.S. and E.V. collected the incubation data and extracted the incubation behavior from the recordings, K.B. extracted other behavioral data from the recordings, M.S. analyzed the data, M.S., K.B., and M.E.Š. wrote the manuscript.

CONFLICT OF INTEREST STATEMENT

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

ETHICAL APPROVAL

The study was conducted in accordance with the current laws of the Czech Republic.

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AVAILABILITY OF DATA AND MATERIALS

The raw data and the R codes that enabled replications of all analyses performed in this article and that were also used for generating all the figures are available from Open Science Framework (https://osf.io/r8tzg/).

NOTE

Supplemental material for this article is available online.

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Chapter 4

Perennial monogamy is the preferred strategy for Red-wattled Lapwing breeding in a long seasonal hot environment

Unpublished manuscript

Perennial monogamy is the preferred strategy for Red-wattled Lapwing breeding in a long seasonal hot environment

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Abstract

Most bird species are monogamous and breed repeatedly throughout their lives. In many species, individuals face the dilemma of whether to stay with their current mate or find a new one, with some external conditions as possible drivers of this decision. Long-term partnerships are commonly associated with the short-season and unstable environment of the Arctic, whereas subtropics and tropics with longer breeding season and stable climates could offer more opportunities for multiple breeding with different partners. The Red-wattled Lapwing (*Vanellus indicus*), a biparental and long-lived shorebird that breeds in the hot Arabian desert with a long breeding season and high availability of potential mates, provides a unique opportunity to study mate fidelity and divorce rates of birds under conditions of a long breeding season but in a demanding hot environment. We found that the lapwings were extremely faithful, both within and between seasons. In addition, instead of finding a new mate, many previously breeding pairs skipped nesting for part of their lives without looking for a replacement mate. Birds benefited from perennial monogamy through higher number of breeding attempts per season. We suggest that it is not the length of the breeding season but the challenging hot environment, which may represent a different extreme but with the same impact as the cold Arctic environment, that promotes strict mate fidelity in long-lived birds and plays an important role in mate choice.

Introduction

Reproduction in most birds is associated with biparental care for the offspring and consists of repeated breeding attempts either within one season or between seasons. Over the course of a lifetime, the decision to stay with the same partner or to switch to a new mate for the next breeding attempt may present a serious dilemma. Although some (usually long-lived) species are known to have a high or even lifelong mate fidelity (Black, 1996), other (usually short-lived) species exhibit short-term mate fidelity and change mates before each breeding attempt (Choudhury, 1995). The predominant strategy can be thus species-specific, depending on the species' lifetime expectancy, but also length of breeding season may play a role. In addition, the decision can vary according to the current circumstances in the population, such as the availability of potential mates or population density, where divorce may be more common with increasing opportunities to choose a better mate (Dubois et al., 1998).

Higher latitudes characterized by a harsh climate combined with a short breeding season allow only one successful breeding attempt per season (including possible replacement clutches). It is therefore beneficial to breed with a known partner in a known place, which encourages long-term mate fidelity. The prolonged pair bond over breeding seasons (called 'perennial monogamy') is advantageous in these conditions for at least three reasons. First, remating with the partner from the previous breeding season saves the time required for courtship and pair formation. Faster entry into the breeding process by mutually familiar partners accelerates the onset of egg laying (Gochfeld, 1980). Nesting early in the season is generally reported to be more successful than nesting later in the season (e.g., Perrins, 1970; Fowler, 1995). Second, the short breeding season limits the time available to find a new mate and thus the time available to replace a failed clutch (McKinnon et al., 2012; Fox, 2021). For this reason, it is advantageous to continue the replacement breeding with the same partner. Third, the previous shared experience and a good mutual knowledge of faithful partners may improve the coordination of parental duties in offspring care (Choudhury, 1995; Spoon et al., 2006; Griggio & Hoi, 2011) and increase the chance of successful reproduction. Therefore, long-term and faithful partnership is the best option for long-lived birds living at high latitudes with a short breeding season (Green et al., 1977; Saalfeld & Lanctot, 2015).

Populations breeding at low latitudes, such as the subtropics and tropics with stable, generally milder environments, and long breeding seasons, may not have such strong requirements for high mate fidelity for several reasons. Firstly, the long-season environment does not limit the time needed to find a new mate at the beginning of each season, and secondly, it provides sufficient time for replacement or multiple breeding within a season. However, there is insufficient evidence regarding the advantages and disadvantages of changing mates within a season for bird species in long-seasonal environments. Nevertheless, the benefits of divorce and selecting a new partner for the following breeding season may outweigh potential drawbacks (Culina & Brouwer, 2022). Pairs with poor reproductive performance often divorce in order to increase behavioural compatibility with new partners (Spoon et al. 2006), which may improve next breeding success (Coulson, 1966; Ens et al., 1993; Choudhury, 1995; Black, 1996; Halimubieke et al., 2020). For example, Great Tit (*Parus major*) females even increased their clutch size with new partners after divorce (Dhondt & Adriaensen, 1994). Pairing with a new and better mate also may increase genetic compatibility of the partners (Tregenza

& Wedell, 2000), or increase genetic diversity of the offspring (Jennions & Petrie, 2000). Culina et al. (2015) showed that in birds that breed once per season, an interseasonal mate exchange may be adaptive and therefore might outweigh mate fidelity. However, there is a lack of studies on mate fidelity and divorce rates within and between seasons in long-lived birds inhabiting long-seasonal environments where they have opportunities to breed multiple times with multiple partners even within a single season.

In the species inhabiting long-seasonal environment allowing multiple breeding within one season, factors such as the availability of new partners or fates of previous breeding attempts may then play an important role in decision whether stay faithful or divorce. For example, females of Kentish Plover (*Charadrius alexandrinus*) tend to leave their mates immediately after the eggs hatch whenever they have the opportunity to attract a new unpaired male, thus starting another clutch more quickly (Lessells, 1984; Székely & Lessells, 1993; Kosztolányi et al., 2009; Halimubieke et al. 2020). Paradoxically and in contradiction with other studies (e.g., Coulson, 1972; Johnston & Ryder, 1987; Ens et al., 1993), successful hatching in these plovers led to divorce, whereas nest failure resulted in retention of the partners for subsequent breeding (Halimubieke et al. 2020). Therefore, the Kentish Plover females opportunistically achieve the chances of having more offspring within a season by partial polygamy (Fraga & Amat 1996, Székely 1996). Thus, partner's fidelity and divorce rates are likely to be more variable in a long-season environment, which calls for additional research. In particular, it remains unclear how partner's fidelity and divorce rates within a season and between seasons apply to strictly monogamous precocial species breeding in high population density in the demanding (hot) environment with long breeding season.

In this study, we examined both within-season and between-season mate fidelity and divorce rates in a resident population of the Red-wattled Lapwing (*Vanellus indicus*) breeding in the hot environment of Arabian Desert. This socially monogamous lapwing (Muralidhar & Barve, 2013) is one of the larger long-lived shorebirds with possible double brooding system (del Hoyo et al., 1996), referring to the same pair rearing two broods in succession, which seems to be relatively uncommon among waders but occurring mainly in tropical plovers (Blomqvist et al., 2001). The target population faces a long seasonal environment that allows breeding from late January to August. Assuming 75 days of parental care from egg laying to chick fledging in successful nests (del Hoyo et al. 1996), each pair can breed up repeatedly in a season, including replacement clutches after nest failure. In addition, an abundant pool of potential new partners and generally dense population (ca. 245 adults on 6.6 km^2; Elhassan et al., 2021; Brynychová et al., 2022) provides opportunities for multiple breeding with different partners in a season and mate exchanges between seasons. Although the tropics and subtropics offer predominantly mild environments, this rule may not apply in deserts where this population experiences extremely high temperatures during part of breeding season. Therefore, we investigated mate fidelity and divorce rates, and asked how mate fidelity or partner exchange influence fitness indicators in this breeding system. We expected opportunistically increased divorce rates in the population in line with the supply of potential mates and high population density to improve mate compatibility and breeding performance (i.e., more frequent divorce occurring after nest failure, laying larger eggs, and/or having higher nest success after divorce). On the other hand, in the group of faithful pairs from previous season, we expected better coordination and familiarity of the partners manifested by a) earlier nesting initiation and b) greater number of nesting attempts per season, including cases of double brooding. Specifically, we tested how mate fidelity and mate switching are predicted by previous nesting success and how they influence indicators of breeding performance (egg size and nest success) and partner familiarity (through overall clutch production in a season).

Methods

We studied the Red-wattled Lapwings in core part of Al Marmoom Conservation Reserve (6.3 km^2) near Dubai in breeding seasons 2018-2023. The area includes artificial system of lakes with small islands, surrounding plantations, desert dunes and a dense network of roads. The lapwing population consists of approximately 245 adults, a substantial part of which breed regularly in the area (Elhassan et al. 2021). We searched for the nests across the entire study area from a car driving slowly on the road or through well passable sections with scattered greenery. The position of each nest was stored in GPS for subsequent visits. The onset of egg laying we determined using flotation test (Liebezeit et al., 2007) and the eggs in complete clutches we measured using vernier calliper (accuracy 0.05 mm). The volume of the eggs was calculated according to the formula V (in cm^3) = 0.425*length × width^2 + 1.678 (Galbraith, 1988).

Adults were captured on nests using spring traps and marked with a unique combination of a metal ring and four coloured rings to identify individuals from a distance. Each adult was also equipped with a flag containing an RFID chip. We affiliated the marked parents to the nests either using binoculars from a car or using RFID (e.g., in denser vegetation on islands). If we recorded a mate exchange with an unmarked adult, we captured and marked the unknown partner as soon as possible. For all nests, we aimed to determine fate (successful hatching or failure as predation, abandonment or destruction by other means, for more details see Sládeček et al. 2021). We recorded all nesting attempts of all marked birds throughout the breeding season from late January to mid-August each year. We also looked for remains of dead individuals after their predation, and the surrounding lands we repeatedly visited to look for possible emigrants. In addition to thorough identification of individuals by rings during field work, every March (at the beginning of the breeding season) and June (in the second part of the breeding season), we surveyed the entire study area to record, if possible, all birds (marked and unmarked breeding and non-breeding) present in the study area.

We considered a pair faithful, if same partners bred repeatedly together either within a season or between seasons (i.e., the last breeding in previous year and the first breeding in the current year). The divorce was defined as nesting with a new mate while the previous partner was simultaneously recorded alive (breeding or not). As widowed, we considered only those individuals whose partners we found dead. Other cases of pair break-up, where one of the parents continued to breed with a new partner but the second partner disappeared, were defined as having an unknown cause of pair break-up (one partner disappeared). This category may include not only death but also emigration or possible overlooking of the individual in the study area. Unmarked pairs we excluded from analysis.

As double brooding we considered situations when unfledged chicks from the previous nest were still alive nearby the nest at the start of a new clutch. As the age of fledging, we arbitrarily set the 45th day of life (own observations).

To assess whether both partners may remain parallel non-nesting (i.e., not nesting with another partner despite the presence of the previous partner), we calculated the periods of pairs that remained non-nesting but still present in the study area during the breeding season. We limited the period of co-presence of both partners to a minimum of 240 days (8 months) to include pairs that would have finished breeding in the previous season (July) but avoided to breeding next year by April (i.e., 240 days in total).

We performed all statistical analyses in R 3.6.2 (R Core Team, 2019). The linear mixed-effects models we fitted using the “lmer” function from the “lmerTest” R library (Kuznetsova et al., 2017). First, we analysed the effect of pair status (stable or newly created pairs in a new breeding season) on the date of initiation of the first clutch in a new season (with values on logarithmic scale). Second, we analysed the effect of pair status, the date of egg laying start (centred using the “scale” function) and their interaction on mean egg size in a clutch as response variable. In both models, we included female identity and year as crossed random effects. Finally, we tested the effect of pair status on number of clutches laid within one season. Because the same females could have different status between years, we calculated the average number of clutches for each female and her status over the whole study period (2018-2023) and tested the difference in the mean clutch numbers per female in faithful pairs and newly formed pairs using Welch Two Sample t-test.

Results

Fidelity and divorce rates

We recorded 328 subsequent breeding attempts of individually marked pairs, consisting of 194 (59.1%) within-year breeding events and 134 (40.9%) between-year events (Table 1). The partners remained faithful in most events within year (n = 190; 97.9% cases) as well as between years (n = 97; 72.4% cases). On the contrary, partner's exchange occurred less frequently (n = 4 and 37 cases, i.e., at 2.1% and 27.6% of cases within and between years, respectively).

Table 1. Pair fidelity vs widowed or divorced pairs: summary results.

	Cases	Pairs
Stable within year	190	105
Divorce within year	2	2
Widowed within year	2	2
Sum of within-year attempts	194	109
Stable between years	97	60
Partner disappeared between years	30	30
Divorce between years	6	3
Return to the partner after divorce	1	1
Sum of between-year attempts	134	94

Causes of partner's exchange

Rare partner exchanges occurred due to both divorce and widowhood. We recorded two divorces and two widowhoods (2 males died) within a year, and six divorces between the years. In one case, the partners returned to each other in the next season after breeding with another partner. In 30 breakups of pairs between years, one partner was further not observed (disappeared), so the reason for the mate exchange remains uncertain. Fifteen males and 15 females disappeared, indicating that there was no tendency for one sex to disappear more often than the other. Partner's replacement occurred after 13 out of 96 failed nests and after 23 out of 218 successfully hatched nests (i.e., 13.5% vs

10.6%; χ^2=0.59, df=1, P=0.44) indicating that nest failure was not a critical reason for divorces of pairs and searching for new mates.

Consequences of partner's exchange and faithfulness

The pairs which remained faithful from previous year started to breed in a new season non-significantly earlier (median date=2nd March, n=93) than newly formed pairs (median date=7th March, n=34; Table 2). Egg size in clutches laid in the early-season did not differ between faithful pairs (mean =16.37±1.08 cm^3, n=89) and newly created pairs (mean =16.39±1.12 cm^3, n=27; Table 3) and faithful pairs did not breed more successfully (200 from 271 nests hatched, i.e. 73.8% nests) than newly created pairs (25 from 39 nests hatched, i.e. 64.1%; χ^2=1.61, df=1, P=0.20) indicating that pair status did not influence the two breeding performance indicators, egg size and nest success.

Table 2. Effects of pair status (stable or newly created pairs) in a new breeding season on initiation of the first clutch in a new season. The mixed-effect model includes female identity and year as random effects.

	Estimate	Std.Error	Df	t-value	P
Intercept	4.17	0.033	78.0	126.18	<0.001
Faithful pairs	-0.16	0.204	86.9	-0.81	0.422

Table 3. Effects of egg laying start (using centred values) and pair status (stable or newly formed pairs) at the beginning of breeding season on mean egg size in clutch. The mixed-effect model includes female identity and year as random effects.

	Estimate	Std.Error	Df	t-value	P
Intercept	16.35	0.159	8.2	102.58	<0.001
Start of egg laying	-0.24	0.094	74.6	-2.58	0.012
Faithful pairs	-0.12	0.206	90.1	-0.59	0.559
Start of egg laying: Faithful pairs	-0.10	0.176	53.3	-0.56	0.576

Finally, we found the difference between the number of nests initiated within one season by females faithful from previous season and females of newly created pairs. We found that faithful females initiated more clutches throughout a season (median =2, maximum=4, n=93) than females from new pairs (median =1, maximum=3, n=26; Welch Two Sample t-test for means per female and her status, t=2.9, df=50.8, P=0.006, Figure 1). We confirmed 15 cases of double-brooding events in different pairs. The initiation of new clutches followed at the age of 10-41 days of chicks (mean 27.7 days, median 28 days). In all cases with known status at the start of breeding season, they were faithful pairs from the previous season (n= 8). In seven cases, this status was unknown.

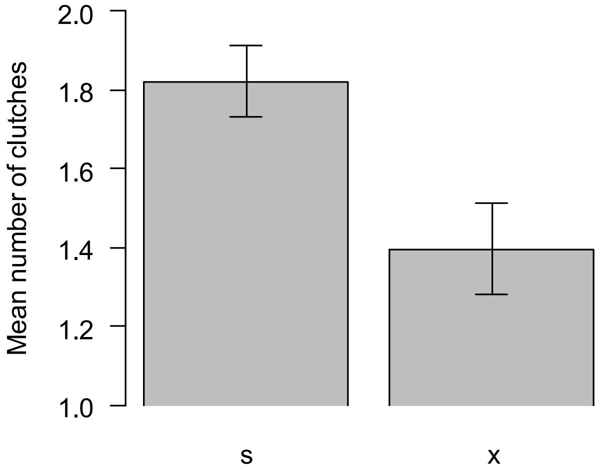

Figure 1. Effects of pair status (s: stable, x: newly formed pairs) at the beginning of breeding season on the number of clutches laid within the season. The confidence intervals indicate standard errors.

Non-breeding pairs

In the set of non-nesting partners remaining alive in the study area during breeding season for more than 8 months (240 days), the minimum time in which both partners were present without recording of a breeding attempt was 280 days while the maximum was 1119 days (median=348 days, n=22 nonbreeding pairs; Figure 2). In eight cases, both partners remained at the site non-breeding for a sum period of the entire breeding season, four of them were present even for at least two breeding seasons.

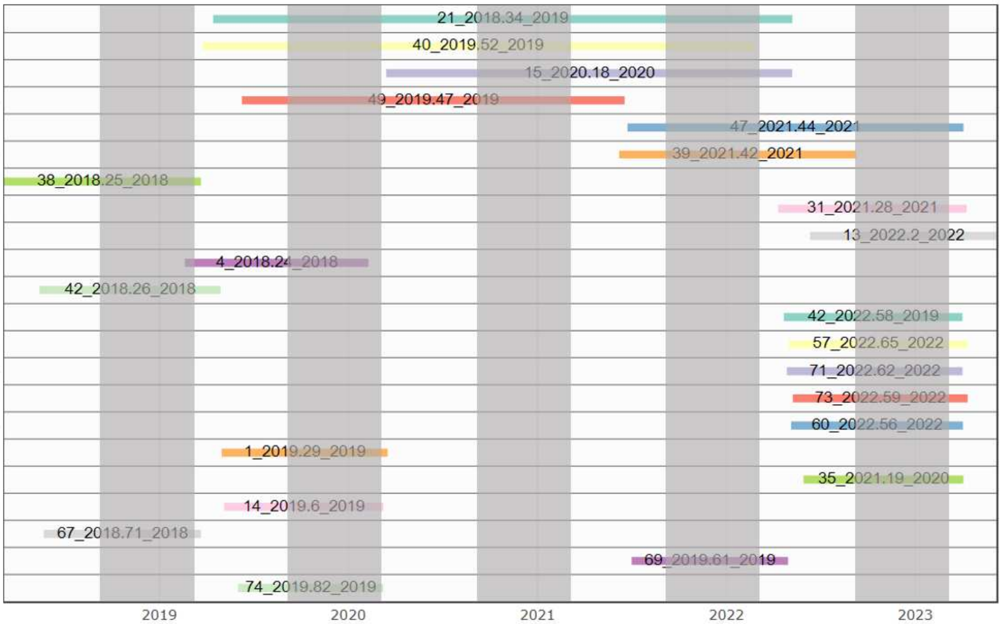

Figure 2. Occurrence of non-breeding partners (indicated by ID males and females, respectively) in the study area since the date of their last joint nesting (colored line). White parts represent breeding season (February-July), grey columns non-breeding periods (August-January). No other breeding attempts were recorded for both partners in spite of their presence in the area until at least one individual disappered (end of colored line).

Discussion

This study documents that the breeding population of Red-wattled lapwings inhabiting long-season environment in the hot Arabian desert strongly prefers mate fidelity to divorce regardless of high population density and availability of potential new mates, both within a season and between seasons. The most common mate exchange that we recorded was accompanied with a disappearance of one parent, while only rarely were both partners later observed breeding with new mates. At the same time, the decision to remain faithful or change the partner was not influenced by the fate of the previous clutch. Partners fidelity or mating with a new mate had no effect on egg size, hatching success or timing of the first clutch in a new season, but the mate fidelity increased the number of breeding attempts within a season. Also, instead of trying to maximize fitness by finding a new mate when one member of the pair lost the desire to breed, cases were recorded where both partners were present in the area throughout the breeding season without further breeding attempts.

We found an extremely high fidelity (almost 98%) of repeatedly breeding partners within the long breeding season in the area, despite high population density and the availability of other non-breeding conspecifics, i.e., potential new mates. Thus, it is clear that neither the long breeding season, sufficient supply of potential mates, nor other additional benefits of mate exchange (for a review see Culina & Brouwer 2022) were the drivers of divorce rates, and that even with these potential but unused benefits, the benefits of a high within-season mate fidelity for repeated nesting prevail. As a long-lived species, Red-wattled lapwings may generally seek to maximize pair fidelity in order to gain the benefits of familiarity within a pair bond (Pyle et al., 2001; Naves et al., 2007; Sánchez-Macouzet et al., 2014; Mercier et al., 2021). Mutual knowledge of partners, leading to improved breeding cooperation, is likely to be important in this respect, particularly because the obligatory biparental care for offspring is required in such a challenging environment. In this case, the fitness of both partners is not only affected by their reproductive abilities, but also by how the partners coordinate their efforts (Wagner et al., 2019). The need for close cooperation between familiar partners can be particularly acute during the hottest parts of the day, when parents must regularly rotate at short intervals at the nest and, in the case of double brooding, still are caring for the chicks. In newly formed pairs, however, the undeveloped harmony between the partners can lead to an imbalance in parental care, with potentially fatal consequences for both the eggs and the incubating parent (Tieleman et al., 2008; AlRashidi, 2016; own unpublished data). Indeed, prolonged pair bond may align the incubation behaviour of both partners as shown elsewhere (e.g., Delesalle, 1986; Prior, 2020). In addition, partner familiarity resulting from inter-seasonal mate fidelity may matter not only within a year but also between years, as discussed below.

The shared experience may be closely related to the previously shared nest site, which is familiar to both partners (Cézilly et al., 2000). This not only allowed the parents to orient themselves well to local conditions, but also to start the next clutch earlier at a known site, either after successful or unsuccessful previous nesting attempt. The lapwing pairs tended to maintain their breeding nest sites (own unpublished data), and, therefore, after nest failure, a rapid clutch replacement of faithful pairs may easily occur near the previous nest. In addition, in this precocial species, where chicks can forage independently shortly after hatching and other parental care for them may not be as intensive as in altricials (e.g., passerines), parents may start a new clutch at the same site before the chicks fledge. In these cases, the young can take advantage of parental warming (brooding) at the nest (Kolešková et al., 2023) parallel with egg incubation. In fact, this system, called double brooding, has been reported as part of the reproductive strategy in a number of bird species, including lapwings (Parish et al., 1997; Wallander & Andersson, 2003), and was also observed in the Red-wattled Lapwing (own unpublished data). Double brooding may shorten the total length of breeding process of faithful partners due to overlapping of their subsequent breeding attempts and thus increase the total number of the attempts within a season. On the other hand, this strategy cannot be applied after divorce, when only one (true) parent remains at the nest site with the chicks.

Partners fidelity between years was also high (72%), although lower than the fidelity within years. The higher proportion of new pairs at the beginning of the new season, after the dissolution of pairs from the previous season, can best be explained by the death of one of the partners during the six months long non-breeding period. Although there were very few confirmed events of death, they can be inferred indirectly from the frequent disappearance of birds from the study area, for which death is the most likely explanation. Deceased individuals could be depredated or lethally parazitized and then quickly consumed or carried away by terrestrial predators or scavengers such as foxes or ravens, which are common in the area (own observations). On the other hand, abandonment of the study area and search for a new mate outside it is less likely because the study lake system represents by far the most attractive breeding refuge in the wider area, without expected drive for dispersal of already established residents into the surrounding suboptimal desert habitats. This is also consistent with the equal representation of both sexes among the disappeared individuals because in the case of active emigration from the site, one would expect a bias in favour of one sex (Végvári et al., 2018). Another explanation for the rare cases of divorce, which unfortunately we cannot confirm, may be related to the low age and experience of the breeders (Gill & Stutchbury, 2006; Culina et al., 2015; Gousy-Leblanc et al., 2023). Indeed, it is often stated that the likelihood of mate fidelity increases with age and experience of parental care. Thus, sporadic cases of divorce may be caused by young, inexperienced breeders attempting to reproduce.

In summary, strong intra- and inter-seasonal fidelity makes the Red-wattled Lapwing a perennial monogamous species with the advantage of strong long-term mate fidelity regardless of breeding in a high-density population and availability of potential new mates. Benefits include an increased number of breeding attempts, including their overlap via a double brooding system. We explain this phenomenon by an increased familiarity between partners that leads to elaborate cooperation in parental care and by a high nest site fidelity of both partners. On the other hand, staying in a pair or forming a new pair did not affect indicators of breeding performance such as egg size or nesting success. These attributes are thus probably more a matter of quality of the individual and nest site, independent of mating status. Contrary to the Kentish Plover inhabiting similar environment, Red-wattled lapwings do not appear to breed at all costs. Rather, many pairs stop nesting and remain at the site even during the breeding season without seeking a new reproductive partner. This study suggests that a strong partnership associated with perennial monogamy and nest site fidelity is profitable strategy for maximizing fitness in birds, not only in high latitudes such as the Arctic with short breeding season, but also in the demanding conditions of the hot desert, where the season allows multiple breeding per season. Further studies on other species and a subsequent comparative study are desirable.

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